

Nitin Trivedi  
C. R. K. Reddy  
Alan T. Critchley *Editors*

# Recent Advances in Seaweed Biotechnology

Biomass, Emerging Applications and  
Bioeconomy

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*Editors*

Nitin Trivedi  
Marine Biotechnology  
Gujarat Biotechnology University  
Gandhinagar, Gujarat, India

C. R. K. Reddy  
Centre for Energy Biosciences  
Institute of Chemical Technology  
Mumbai, India

Alan T. Critchley  
Verschuren Centre  
Sydney, Nova Scotia, Canada

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# Chapter 13

## The Vibrant Spectra of the Oceans: Unravelling the Diversity, Functions, and Applications of Seaweed Pigments



Marta V. Freitas, Clélia Afonso, Leonel Pereira, and Teresa Mouga

**Abstract** Seaweeds are photosynthetic organisms that harvest sunlight and convert it into essential energy through a highly effective biochemical process powered by light, which in turn is captured and directed to the reactive centers by pigments. Seaweed pigments are fundamental to the seaweed photosynthetic process and are also responsible for their current taxonomic classification into three distinct divisions. The Chlorophyta comprises the green seaweeds, which hold high levels of both chlorophyll *a* and *b*, along with lesser amounts of  $\beta$ -carotene and xanthophylls. The Ochrophyta integrates the brown seaweeds (class Phaeophyceae), which are particularly rich in the xanthophyll fucoxanthin, while also showing lower levels of other xanthophylls, chlorophyll *a* and *c*, and  $\beta$ -carotene. The Rhodophyta houses the red seaweeds, which are characterized by holding high levels of phycoerythrin, as well as lower quantities of phycocyanin, chlorophyll *a*,  $\beta$ -carotene, and xanthophylls. However, regardless of their designation, seaweed species exhibit a significant range of colors and hues that go beyond “green,” “brown,” and “red,” rendering them visually unique, due to the relative composition and abundance of each pigment within their living cells. Nowadays, science has unveiled not only the diversity of these pigments, but also their biological function. Targeted extraction methods

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M. V. Freitas (✉)

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network, ESTM, Polytechnic of Leiria, Edifício Cetemares, Peniche, Portugal

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network, ESTM, Polytechnic of Leiria, Edifício Cetemares, Av. Porto de Pesca, Coimbra, Portugal  
e-mail: [marta.freitas@ipleiria.pt](mailto:marta.freitas@ipleiria.pt)

C. Afonso · T. Mouga

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network, ESTM, Polytechnic of Leiria, Edifício Cetemares, Peniche, Portugal

L. Pereira

CFE - Centre for Functional Ecology: Science for People & Planet, Marine Resources, Conservation and Technology - Marine Algae Lab, University of Coimbra, Department of Life Sciences, Calçada Martim de Freitas, Coimbra, Portugal

and potential end-use applications for these pigments have been researched and developed, with the resulting product often designed to protect and promote human health. Today, humankind acknowledges the benefits of natural products obtained from the oceans, including those obtained from seaweed pigments. This chapter aims to supply insight on the diversity, functions, and applications of the pigments found in all the three divisions, thus contributing to a greater understanding of the benefits these functional molecules can provide to humanity.

**Keywords** Photosynthesis · Chlorophylls · Carotenoids · Phycobiliproteins

## 13.1 Introduction

### 13.1.1 *The Role of Pigments in Photosynthesis*

Photosynthesis, from the Greek *photo* (light) and *synthesis* (putting together) (Online Etymology Dictionary 2023), is the process where autotrophic organisms, such as plants, algae, and cyanobacteria, harvest solar energy and convert it into chemical energy to synthesize carbohydrates, essential for growth and development. With this process, the photoautotrophs incorporate carbon dioxide and water and release oxygen to the environment. Therefore, photosynthesis is the vital process that upkeeps the atmospheric oxygen and balances climatic processes, being thus considered the patron process of all life on Earth.

Seaweeds, also known as macroalgae, are photosynthetic aquatic organisms, which, unlike terrestrial plants or seagrass, lack true roots, stems, and leaves, and a vascular system (Pereira 2021). Being primary producers, they are fundamental in upkeeping marine trophic chains, in providing shelter and nursery grounds for marine life (Kasanah et al. 2022). Together with microalgae, macroalgae supply the greatest part of the photosynthetic ability of Earth, being therefore the dominant producers of the oxygen that we all depend on to live (Chapman 2013; Pereira 2021). In seaweeds, the metabolites that are tasked with capturing the light energy and convert it into chemical energy are known as pigments. These pigments are found in the living cells of photosynthetic organisms and are classified as photosynthetic pigments (e.g., chlorophylls) or accessory pigments (e.g., carotenoids and phycobiliproteins).

Seaweeds are found in seawater or brackish water, restrict to depths reachable by sunlight so they can perform photosynthesis, but can colonize a variety of ecological niches (Pereira 2021). Sunlight falls directly on seaweeds at specific times of the day, or it can first interact with sediment, macrophytic components, and the water itself as depth increases before reaching the seaweed tissues. The light spectral composition and irradiance that reaches the seaweed is thus highly diverse and ultimately determines its relative pigment composition, to ensure the photosynthetic process remains effective. Along with a wide range of other secondary metabolites (phenols, sterols, vitamins, among others), pigments are produced by seaweeds as a

quick adaptation response to any abiotic changes in the environment (Talarico and Maranzana 2000). This is a fundamental ability that allows seaweeds to adapt to niches where abiotic changes accompany the tidal flux, such as tide pools (Pereira 2021).

Besides being directly involved in the photosynthetic process, pigments are also particularly effective photoprotective molecules able to shield the seaweed against ultraviolet radiation, which can reach biologically significant depths in aquatic ecosystems and can significantly damage the photosynthetic apparatus and hinder photosynthetic efficiency (Sen and Mallick 2021).

These seaweed pigments hold an amazing chromatic diversity, to which the organism owns the unique colors it displays. Seaweed pigments have also been settling the whole seaweed taxonomy since, at least, the last century (Pereira 2021). Green seaweeds, with pigmentation identical to that of vascular plants, are characterized by high amounts of chlorophyll *a* and *b* and small amounts of  $\beta$ -carotene and xanthophylls (lutein, neoxanthin, violaxanthin, and zeaxanthin) and thus belong to phylum Chlorophyta. Brown seaweeds owe their color to high concentrations of fucoxanthin, but also have low concentrations of chlorophyll *a* and *c*, violaxanthin, and  $\beta$ -carotene and therefore belong to phylum Ochrophyta, class Phaeophyceae. Finally, red seaweeds, which include species that are perfectly adapted to the low light levels, found at high ocean depths, hold high content in phycobilins (in particular R-phycoerythrin and R-phyocyanin), but low content in chlorophyll *a*,  $\beta$ -carotene, and xanthophylls (lutein and zeaxanthin), and thus belong to phylum Rhodophyta (Pereira and Neto 2015; Bonanno and Orlando-Bonaca 2018; Pereira 2021).

## ***13.1.2 Diversity and Function of Pigments in Seaweeds***

### **13.1.2.1 Chlorophylls**

Chlorophylls, whose name comes from the Greek “*khloros*” (green) and “*phullon*” (leaf), are non-polar green pigments that are key players in the photosynthetic process, being specifically involved as light harvesters and in the energy transference and storage processes, functioning as natural solar cells (Mandal and Dutta 2020; Kato et al. 2020).

There are several kinds of chlorophyll, namely, chlorophyll *a*, chlorophyll *b*, chlorophyll *c*<sub>1</sub> and *c*<sub>2</sub>, chlorophyll *d*, and chlorophyll *f*. All chlorophyll types are optimized to efficiently target and use the diverse spectral components of solar energy. Chlorophylls capture light from both ends of the electromagnetic spectrum, namely the blue and the red region, while scattering wavelengths from the green region. While all chlorophylls are able to absorb solar energy, not all are able to follow up, by converting it into chemical energy (Mandal and Dutta 2020). In seaweeds, there are only three types of chlorophylls: chlorophyll *a*, chlorophyll *b*, and chlorophyll *c*.

Chlorophyll *a* is present in all seaweed groups (Pereira 2021), as well as in all oxygenic photosynthetic organisms, being specifically found in the photosystem cores and in the light-harvesting antennas within chloroplasts (Kato et al. 2020). In fact, the reaction center of the photosystem I of all oxygenic photosynthetic organisms only contain this type of chlorophyll, which has its peak absorption at wavelengths 430 and 664 nm (Larkum et al. 2021). Regarding its chemical structure, chlorophyll *a* holds a porphyrin ring with a hetero polycyclic structure that surrounds a central  $Mg^{2+}$  ion. Around this central ion, nitrogen atoms are coordinately positioned, and an ester linkage attaches the polycyclic structure to a long phytol tail, being this a feature shared by all chlorophyll species (Mandal and Dutta 2020).

Chlorophylls *b* and *c* can only be found in green and brown seaweeds, respectively, with chlorophyll *b* being also found in plants. Both pigments are found only in the light-harvesting antennas (Kato et al. 2020). While chlorophyll *b* has its peak absorption at wavelengths 460 and 647 nm, chlorophyll *c* has its peak absorption at wavelengths 442 and 630 nm ( $c_1$ ), and 444 and 630 nm ( $c_2$ ) (Larkum et al. 2021). Chlorophyll *b* shares the same molecular structure of chlorophyll *a*, but while the former contains a methyl group ( $-CH_3$ ) in the second ring, chlorophyll *b* contains an aldehydic group ( $-CHO$ ) instead (Mandal and Dutta 2020). Chlorophylls *d* and *f* are only found in Cyanobacteria. Chlorophyll derivatives such as purpurin-18 *a*, pheophytin *d*, and phytyl-purpurin-18 *a* have been studied within the scope of chlorophyll profile assessment in a number of commercially valuable seaweed species from all taxonomic groups (Chen et al. 2017a).

### 13.1.2.2 Carotenoids

In nature, carotenoids are the most widely distributed pigments, being found in a wide diversity of photosynthetic organisms, namely algae, plants, photosynthetic bacteria, and several archaea and fungi (Koizumi et al. 2018; Maoka 2020). The animal kingdom, on the other hand, lacks the capacity to produce these pigments, likely because of the evolutionary loss of the necessary genes encoding enzymes for carotenoid biosynthesis (Bohn et al. 2021). Carotenoids show warm colors such as yellow, orange, red, and purple. Structurally, carotenoids are tetraterpene pigments, where most consist of eight isoprene units with a 40-carbon skeleton and a general structure of a polyene chain with nine conjugated double bonds and an end group at both ends of the polyene chain (Maoka 2020).

Carotenoids form a crucial component of the light-harvesting antenna complex within the thylakoid membrane of chloroplasts (Koizumi et al. 2018). Carotenoids are essential compounds involved in photosynthesis and photoprotection. In photosynthesis, their primary role is to enhance light absorption in the blue spectrum, effectively extending the range of light absorption (Bohn et al. 2021), as they harvest and transfer light energy to chlorophylls through singlet-singlet transfer. In photoprotection, carotenoids stand as the first line of defense against oxidative damage, by scavenging free radicals through energy transfer and chemical reaction (Zhao et al. 2022). Whenever chlorophylls have any excess energy, carotenoid

photoprotective mechanisms fall in place by absorbing this energy surplus through triplet-triplet transfer and subsequent release by polyene vibration. Carotenoids also have the ability to quench free radicals such as singlet oxygens that are produced by oxygen, light, and the photosynthetic process itself (Schubert et al. 2006; Viera et al. 2018; Maoka 2020; Swapnil et al. 2021).

Carotenoids are divided into two main groups, carotenes and xanthophylls. Carotenes are unsaturated hydrocarbons (Osório et al. 2020), existing about 50 kinds in nature (Britton et al. 2004), being  $\alpha$ -carotene,  $\beta$ -carotene, and lycopene well-known examples (Poojary et al. 2016). Carotenes, essential photosynthetic pigments, play a crucial role in primary light absorption (Aldred et al. 2009) as well as in the photoprotective system of seaweeds (Asada 2006; Takahashi and Murata 2008). Although various carotenes can be detected in seaweeds, depending on the algal species, the presence of  $\beta$ -carotene stands out as one of the major carotenes commonly found (Murray and Capelli 2020). Xanthophylls are similar to carotenes but have, at least, one functional group with oxygen and have a highly diverse structure. These pigments may be present as protein complexes, fatty acid esters, glycosides, and sulfates and are found in a far greater number in nature, with 800 kinds described, until 2018 (Britton et al. 2004; Maoka 2009). Popular examples include lutein, fucoxanthin, astaxanthin, zeaxanthin, and  $\beta$ -cryptoxanthin (Poojary et al. 2016; Pereira et al. 2021). Xanthophylls are essential in photo-inhibition protection, by reducing and dissipating the energy reaching the photosynthetic reaction centers, through non-photochemical quenching (Maoka 2020).

Carotenoids are distinctly distributed across algae taxonomical groups, and their profile can be used for taxonomic classification (Poojary et al. 2016). Green algae have  $\beta$ -carotene, lutein, violaxanthin, neoxanthin, and zeaxanthin (Quitério et al. 2021), and their synthesis share common pathways with those observed in terrestrial plant species (Eismann et al. 2020). Brown seaweeds are especially rich in xanthophylls, with the major compounds being neoxanthins A and B, fucoxanthin, and violaxanthin, but they also have carotenes, especially  $\alpha$ -carotene and  $\beta$ -carotene (Yuan et al. 2018; Park and Lee 2021; Quitério et al. 2021). Fucoxanthin is the main pigment responsible to convey brown algae their color and is one of the most abundant carotenoids in nature (about 10% of natural carotenoid production) (Osório et al. 2020). Red seaweeds usually exhibit a pattern composed of  $\alpha$ -carotene and  $\beta$ -carotene and from one to three xanthophylls: lutein, antheraxanthin, and zeaxanthin (Esteban et al. 2009; Quitério et al. 2021), and differences in carotenoid composition are found between classes within this phylum (Takaichi et al. 2016).

### 13.1.2.3 Phycobiliproteins

Phycobiliproteins are soluble protein pigments, brilliant colored and fluorescent, that are found in the photosynthetic light-harvesting antenna complexes in Rhodophyta macro- and microalgae, and also in Cyanobacteria, Cryptomonads, and Glaucophytes (Chini Zittelli et al. 2023). These natural-soluble pigments are proteins, that exhibit fluorescence emission (Qiang et al. 2021). In most red algae,

distinct types of phycobiliproteins are assembled into supramolecular complexes anchored to the thylakoid membrane of the algae cell, through peptide links. These complexes, known as phycobilisomes, are highly efficient in capturing solar energy and transferring it into photosystems and are also acknowledged for being effective photo-protectors against high radiances, and opportune nutrient reservoirs whenever nitrogen and phosphorus are scarce (Sonani et al. 2016). Phycobilisomes assume distinct forms, being usually bundled, double-barrel-shaped, semicircular, or semiellipsoidal (Qiang et al. 2021).

Phycobiliproteins are grouped into four categories according to their absorption properties, and the distinct color transmitted by the chromophores: phycoerythrin ( $\lambda$  max = 540–570 nm, red-pink), phycocyanin ( $\lambda$  max = 610–625 nm, blue), allophycocyanin ( $\lambda$  max = 650–660 nm, blue-green), and phycoerythrocyanin ( $\lambda$  max = 560–600 nm, magenta) (Sonani et al. 2016; Kannaujiya et al. 2017, 2021; Puzorjov and McCormick 2020). These pigments are further categorized according to their source, namely, C for cyanobacteria, R for Rhodophyta algae, and B for algae from the order Bangiales. With the exception of phycoerythrocyanin, which is exclusive to cyanobacteria (Dagnino-Leone et al. 2022), all abovementioned phycobiliproteins can be found in red algae.

Phycobiliproteins have, as main components, protein subunits  $\alpha$  and  $\beta$  that form monomeric  $\alpha\beta$  units. These units self-assemble and organize themselves on the thylakoid membrane to form phycobilisomes, which are large protein complexes (Chini Zittelli et al. 2023). The phycobiliproteins that compose a phycobilisome are variable within and between biological species (Chini Zittelli et al. 2023), and while red seaweeds have substantial quantities of phycoerythrin, and fair amounts of phycocyanin and allophycocyanin, they do not have phycoerythrocyanin, which is a pigment characteristic of Cyanobacteria (Basheva et al. 2018).

In Rhodophyta, phycobiliproteins comprise up 50% of all water-soluble proteins (Dumay et al. 2014). These molecules are rearranged in an antenna or rod-like structure, with a central allophycocyanin core from where the subunits phycoerythrin, phycocyanin, and allophycocyanin loop outward in an orderly fashion: phycoerythrin (the pigment with the highest energy state) stands placed in the outermost part of the phycobilisome to capture the light energy and transmit it to an adjacent phycocyanin which, in turn, transfer this energy to the allophycocyanin (the pigment with the lowest energy state), placed next to the chlorophyll *a* photosystem reaction center (Qiang et al. 2021; Chini Zittelli et al. 2023). This unidirectional and highly effective energy capture and transport system allows red seaweeds to be remarkably effective in harvesting a wider range of light wavelength and optimizing the whole photosynthetic process, when compared to other seaweed groups (Hsieh-Lo et al. 2019). In the present era, it is recognized that the function of phycobiliproteins goes beyond just light absorption. Phycobilisomes also seemingly play a crucial role as photo-protectors against intense light levels and also serves as a nutrient source during periods of inadequate nitrogen and phosphorus supply (Jesús et al. 2016). In seaweeds, phycoerythrin and phycocyanin are found within the Rhodophyta phyllo (Hsieh-Lo et al. 2019).

Phycoerythrin, the crimson pigment, derives part of its name from the Greek word “erythros” meaning “red,” and it holds the greatest variety of chromophores among phycobiliproteins (Dagnino-Leone et al. 2022). Phycoerythrin serves as a photosynthetic pigment found in red macroalgae (Rossano et al. 2003), red microalgae (Román et al. 2002), and cryptomonads (Van Der Weij-De Wit et al. 2006). As stated before for all phycobiliproteins, the classification of phycoerythrin is determined by its original source, leading to R-Phycoerythrin (phycoerythrin obtained from Rhodophyta, with a peak absorption wavelength of 545–565 nm), C-Phycoerythrin (phycoerythrin obtained from Cyanobacteria, with a peak absorption wavelength of 540–570 nm), and B-Phycoerythrin (phycoerythrin obtained from Bangiales, a specific family of filamentous red macroalgae, with a peak absorption wavelength of 546–565 nm) (Fleurence 2003; Kannaujiya et al. 2021). Additionally, these compounds exhibit slight variations in their absorption characteristics, besides their origin (Mysliwa-Kurdziel and Solymosi 2016). Under conditions of low light but high nutrient load, phycoerythrin stands as the primary soluble protein produced by the cell of red algae (Glazer 1994).

Phycocyanin, the blue pigment, gets part of its name from the word “cyan” in English, which has its origins in the Greek word “kyanos.” Phycoerythrin is categorized based on its source; therefore, R-Phycocyanin is found in Rhodophyta, C-Phycocyanin in Cyanobacteria and Cryptophyta, and B-Phycocyanin in Bangiophyceae (Dumay and Morançais 2016). Besides being from distinct sources, these pigments also exhibit slight variations in their absorption characteristics (Fernández-Rojas et al. 2014; Mysliwa-Kurdziel and Solymosi 2016).

Allophycocyanin, the blue-green pigment, derives its name from the Greek words “allos” (other) and “kyanos” (blue). Within phycobilisomes, allophycocyanin is located at the core, where assembled trimers ( $\alpha\beta$ )<sub>3</sub> and phycocyanobilin bind to an  $\alpha$  or  $\beta$  phycobilisome subunit (Chen and Jiang 2018).

### ***13.1.3 Prospects and Applications of Seaweed Pigments***

Marine biotechnology, or blue biotechnology, pertains to the application of marine resources and tools for a diversity of applications, namely medical, cosmeceutical, environmental, and industrial. Blue biotechnology is a field with amazing potential and promise, as 70% of the planet is covered by ocean, which in turn harbors 90% of all Earth’s organisms (Thompson et al. 2017), and yet a huge slice of this biodiversity remains unexplored. Therefore, there is great potential in unraveling novel natural marine products from the materials, extracts, and molecules the oceans provide (Kasanah et al. 2022), with algae, both micro and macro, being no exception to this. However, regarding the biotechnological application of algae in industry, research endeavors have been mainly focused on microalgae (Dufossé et al. 2005; Begum et al. 2016; Morocho-Jácome et al. 2020; Silva et al. 2020; Chini Zittelli et al. 2023; Sun et al. 2023; Borovkov et al. 2023), although efforts have recently targeted a number of seaweed species from all the three groups, outlined further below.

Seaweeds hold a variety of bioactive compounds with diverse structures, including natural pigments (Osório et al. 2020). Due to their natural properties, there is an increasing demand for these seaweed-derived compounds, as consumers today prefer natural and eco-friendly products and strive for healthier lifestyles. Consequently, markets have started investing in and shifting toward natural-origin products, to replace highly processed and synthetic alternatives. In terms of pigments, synthetic colorants have traditionally been used, due to their accessibility, low cost, high yield, and stable coloring properties (Muñoz-Miranda and Iñiguez-Moreno 2023). However, the development of synthetic colorants involves the inclusion of harmful substances, like heavy metals or dyes in high concentrations, which not only pose risks to the environment but also to human health, potentially leading to cancer occurrences (Nawaz et al. 2020).

On the other hand, natural pigments obtained from seaweeds are known to have biological activities with substantial relevance on a pharmaceutical and biomedical context, such as antioxidant and free-radical scavenging activities. These promote human health (Muñoz-Miranda and Iñiguez-Moreno 2023) and include antioxidant, antimicrobial (Gomes et al. 2022), antitumoral, antimutagenic, antidiabetic, anti-obesity, photoprotective, and neuroprotective activities (Lanfer-Marquez et al. 2005; Stahl and Sies 2012; Chini Zittelli et al. 2023). Due to their notable spectroscopic properties, a number of these natural pigments have also been regarded as a valuable tool in biomedical research, therapeutic science, and clinical diagnosis (Dashwood 1997; Pagels et al. 2019; Li et al. 2019a).

Moreover, these pigments can be applied as substitute of synthetic dyes and colorants, which appeals to the food, cosmetic, and textile industry, among other applications. Examples include the inclusion of these pigments in food products such as bakery, dairy, functional foods, and deserts and in cosmetic products aimed to care and protect the skin against UV radiation and to prevent and treat hair loss (Chini Zittelli et al. 2023).

Techniques to extract pigments from natural sources are nowadays known to be fast and efficient, regarding yield, time, and costs (Muñoz-Miranda and Iñiguez-Moreno 2023). However, these advantages do not seem to be seen yet in protocols designed to obtain pigments from macroalgal biomass. Terrestrial plants, fungi, yeasts, bacteria, and microalgae are yet the prime providers of pigments (Dufossé 2016; Muñoz-Miranda and Iñiguez-Moreno 2023), especially carotenoids and phycocyanins, on an industrial scale (Dufossé 2016). These pigments have been applied mostly on the cosmetic and human nutrition sectors (World Intellectual Property Organization (WIPO) 2016), and patents are regularly developed that focus especially on chlorophylls and carotenoids (World International Property Organization 2021). Specifically, regarding seaweeds, the most valuable cultivated species from where pigments may be extracted are the green seaweeds *Ulva clathrata*, *Monostroma nitidum*, and *Caulerpa* sp., the brown seaweeds *Saccharina japonica*, *Undaria pinnatifida*, and *Sargassum fusiforme*, and the red seaweeds *Porphyra* sp., *Eucheuma* sp., *Kappaphycus alvarezii*, and *Gracilaria* sp. (Muñoz-Miranda and Iñiguez-Moreno 2023).

### 13.1.3.1 Prospects and Applications of Chlorophylls

The ability of chlorophyll to act as a solar power cell, by harvesting light energy and store it as chemical energy, has inspired scientists to study and harness the process to obtain chemical fuel from solar energy through chlorophyll centric technologies, namely for hydrogen production (Mandal and Dutta 2020). The chlorophyll used to explore this venue was chlorophyll *a*, although it is not obtained from seaweeds, but rather from microalgae of the genus *Spirulina* (Saiki and Amao 2002; Tomonou and Amao 2002; Himeshima and Amao 2005; Takeuchi and Amao 2005).

The activity of chlorophylls involves not only solar energy, but also electromagnetic radiation within the visible range (Mandal and Dutta 2020) and fluorescence properties (Padhi et al. 2021). This means this pigment has unique properties and is an excellent and versatile biomaterial that must be considered to the benefit of humankind.

The biological activities and health benefit effects of natural chlorophylls present in seaweeds have been recently studied. However, studies focusing on the qualitative and quantitative characterization of their chlorophyll profile are yet scarce (Chen et al. 2017a). Chlorophyll is known for its antioxidant and antibacterial activities (Lanfer-Marquez et al. 2005; Pérez-Gálvez et al. 2020). Additionally, chlorophylls have been clinically applied for years in photodynamic therapy of tumors and their chemo-preventive properties are well acknowledged. Chlorophylls also show antimutagenic activity in genotoxicity assays and are able to protect against cancer biomarkers (Dashwood 1997).

Chlorophyll has been tested as a biomarker to screen plant health and physiological condition and detect diseases, mostly on crops relevant to agriculture (Chaerle et al. 2004; Tung et al. 2013; Guo and Tan 2015), but also to measure coral reef health (Febbo et al. 2012) and survey macroalgal blooms (Lin et al. 2011). Chlorophyll markers were also used to test the effects of environmental stress upon plants (Peguero-Pina et al. 2008; Wang et al. 2018; Li et al. 2019b; van der Westhuizen et al. 2020; Stefanov et al. 2023), to monitor nutrient levels in crops (Schächtl et al. 2005; Long et al. 2013; Liu et al. 2022; Chen et al. 2023) and herbicide levels both in soil (Huang et al. 2012) and water samples (Bi Fai et al. 2007).

Due to their significant fluorescent ability, chlorophylls have been considered in the development of optical and electrochemical biosensors. Devised applications include chlorophyll-based biosensors to assess microalgal cell viability in ballast water (Wang et al. 2013; Li et al. 2022), to detect harmful agents (Merz et al. 1996; Frense et al. 1998; Védrine et al. 2003; Husu et al. 2013), to measure dissolved oxygen in water (Brasil Silva et al. 2017), to detect biological warfare agents in gases (Sanders et al. 2001), and to detect chlorophyll levels in fecal matter from livestock (Pemberton et al. 2007). Assessing herbicide levels in the environment is a very popular application for chlorophyll-based optical sensors (Mandal and Dutta 2020).

Additionally, chlorophylls have been clinically applied for years in photodynamic therapy of tumors, and their chemo-preventive properties are acknowledged. Chlorophylls also show antimutagenic activity in genotoxicity assays and show promise as anticancer agents (Dashwood 1997).

Chlorophylls are additionally being considered as a pigment in the textile, cosmetic, and animal feed industries (Solymosi and Mysliwa-Kurdziel 2016; Janarthanan and Senthil Kumar 2017; Jesumani et al. 2019; Morais et al. 2021). A synthetic formulation of chlorophyll, registered as the food additive E140, is extensively used in the food industry to color foods and beverages.

Typically, chlorophyll has predominantly been sourced from microalgae and occasionally from higher plants, in the various applications explored thus far. However, despite not extracting chlorophyll from macroalgae, the abovementioned examples are still referenced to illustrate the diverse array of potential applications for chlorophylls. In seaweeds, chlorophylls and chlorophyll derivatives have been extracted essentially for research purposes, namely from the green seaweeds *Boodleopsis verticillata*, *Cladophora graminea* (Urrea-Victoria et al. 2023), *Halimeda macroloba* (Nazarudin et al. 2020), *Rhizoclonium riparium* (Urrea-Victoria et al. 2023), *Ulva* spp. (formerly *Enteromorpha* spp.) (Chen et al. 2017a), and *Ulva* spp. (Lin et al. 2011; Zhu et al. 2017; Chen et al. 2017a; Nazarudin et al. 2020), the brown seaweeds *Cladosiphon okamuranus* (Fujii et al. 2012), *Sargassum ilicifolium* (Nazarudin et al. 2020), *Laminaria ochroleuca*, and *Undaria pinnatifida* (Chen et al. 2017a), and the red seaweeds *Bostrychia* spp., *Catenella impudica* (Urrea-Victoria et al. 2023), *Chondrus crispus* (Robertson et al. 2015), *Gracilaria salicornia* (Lumbessy et al. 2021), *Gracilaria tenuistipitata* (Torres et al. 2014), *Grateloupia elliptica* (Lee et al. 2021a), *Kappaphycus alvarezii* (Brotosudarmo et al. 2018), *Palmaria palmata* (Robertson et al. 2015), and *Porphyra* spp. (Robertson et al. 2015; Chen et al. 2017a), to cite a few examples. Chlorophyll *a* from red seaweeds, identified chemically as CAS 479-61-8, has received the endorsement of the European Food Safety Authority (EFSA) for inclusion in food processing. Concurrently, it remains under ongoing scrutiny as a potential pigment for various sectors including textiles, animal feed, and cosmetics (Ferreira et al. 2021; Muñoz-Miranda and Iñiguez-Moreno 2023).

There are two primary methods commonly used to extract chlorophylls from seaweeds. The first method involves the use of organic solvents, such as alcoholic or acetone-based solutions, while the second method utilizes cell disruption techniques, such as mechanical or ultrasonication methods. There is, as well, a growing interest in adopting innovative and environmentally friendly approaches to extract chlorophyll from seaweeds. Some of these promising “green” techniques include microwave-assisted extraction and green solvent extraction methods (Samarasinghe et al. 2012; Zhu et al. 2017; Chen and Roca 2019; Martins et al. 2023).

### 13.1.3.2 Prospects and Applications of Carotenoids

Carotenoids have been the focus of investigation since the early nineteenth century (Takaichi 2011). Today, we know these pigments are crucial for our body, but must be acquired from dietary sources as, since as mentioned, the animal kingdom cannot synthesize them (Gammone et al. 2015). Fruits, vegetables, and their processed variants are the most popular sources to obtain this compound (Darvin et al. 2011;

Gammone et al. 2015). Carotenoids also enrich the nutritional content of various other natural food sources, such as eggs, fish, algae, fungi, and yeasts (Meléndez-Martínez et al. 2020; Rapoport et al. 2021). In the human diet, approximately 50 different carotenoids can be identified (Gammone et al. 2015).

Carotenoids have undergone extensive research and are recognized for their significant biological activities, particularly their potent antioxidant properties in scavenging free radicals as their main acting mechanism (Krinsky and Johnson 2005; Pangestuti and Kim 2011a). Consequently, carotenoids have been extensively used as nutraceuticals and cosmeceuticals. Carotenoids hold significant recognition in the cosmetic industry, contributing to improved skin health by bolstering dermal defense against UV radiation (Swapnil et al. 2021), and recent research suggests that carotenoids also influence skin moisture, texture, and elasticity as well (Zerres and Stahl 2020). As antioxidant agents, they work synergistically with other reducing agents like polyphenols and vitamins (C and E) (Chan et al. 2015). Carotenoids also play a crucial role in enhancing immune defenses and reducing the risk of chronic diseases and age-related ailments, including inflammatory diseases, cardiovascular disorders, bone/skin/eye conditions, diabetes, and cancer (Fiedor and Burda 2014; Gammone et al. 2015; Kulczyński et al. 2017; Eggersdorfer and Wyss 2018; Viera et al. 2018; Ojulari et al. 2020; Dias et al. 2021; Swapnil et al. 2021; Pereira et al. 2021). Moreover, they promote mental and metabolic well-being during pregnancy and early life (Dias et al. 2021). However, the most noteworthy biological role carotenoids have is their innate role as a provitamin A, rendering them effective in preventing vitamin A deficiencies (Maeda et al. 2018; Meléndez-Martínez et al. 2020; Quitério et al. 2021). Additionally, carotenoids serve as sources of color, odor, and taste in various contexts (Yabuzaki 2017).

Also, carotenoids have been used as feed supplements in aquaculture (Vílchez et al. 2011; Lim et al. 2018; Nakano and Wiegertjes 2020; Elbahnaswy and Elshopakey 2023), and vastly considered as a natural alternative pigment as food colorant (Poojary et al. 2016). However, the current major commercial carotenoids are chemically synthesized (Rodríguez-Amaya 2015), instead of being obtained from natural sources, which have raised concerns regarding public health, safety, and environment burden, among consumers. Consequently, current market trend is to grow toward the commercialization of natural carotenoid-based products (Poojary et al. 2016).

Terrestrial plants are one of the primary sources of natural-based carotenoids; however, the possibility of obtained carotenoids from algae instead has garnered attention from industry due to the advantages they offer regarding cost, scale, time, and yield (Poojary et al. 2016). Extensive research has already been published, which focus either on macroalgae carotenoids in general (Schubert et al. 2006), or focus in specific *taxa* or species, such as the green seaweeds *Caulerpa prolifera* (Hegazi et al. 1998), *Caulerpa lentillifera* (Balasubramaniam et al. 2020), the brown seaweeds *Padina australis* (Brotosudarmo et al. 2018), *Padina pavonica* (Hegazi et al. 1998), *Saccharina latissima* (Gevaert et al. 2002), and *Sargassum polycystum* (Balasubramaniam et al. 2020), and the red seaweeds *Euchema denticulatum* (Balasubramaniam et al. 2020), *Gracilaria tenuistipitata* (Torres et al. 2014), *Jania*

*rubens* (Hegazi et al. 1998), *Kappaphycus alvarezii* (Brotosudarmo et al. 2018), and *Neopyropia yezoensis* (Koizumi et al. 2018; Xie et al. 2020). It has also been suggested to cultivate *Ulva* sp., a green macroalga with a wide array of commercial purposes, to obtain raw material for carotenoid enrichment and production, to strategically improve its nutritional value (Eismann et al. 2020).

Various methods have been employed for carotenoid extraction, with liquid-liquid extraction being the most common approach, followed recently by alternative extraction procedures such as ultrasound-assisted extraction, microwave-assisted extraction, enzymatically assisted extraction, pressurized liquid extraction, extraction methods based on electrotechnology and supercritical/subcritical fluid extraction (Singh et al. 2015; Poojary et al. 2016; Xu et al. 2017; Saini and Keum 2018). By having a high degree of hydrophobicity, carotenoids are effectively extracted with non-polar solvents such as *n*-hexane, diethyl ether, dimethyl ether, dichloromethane, or mixtures of organic solvents such as acetone and octane, or green/food-grade solvents such as ethanol, limonene, and solutions of water and organic solvents (Poojary et al. 2016). The analysis of carotenoids in seaweeds is conducted using high-performance liquid chromatography (HPLC), in which identification is achieved by comparing their retention times and absorption spectra with authentic standards (Hegazi et al. 1998; Koizumi et al. 2018). Carotenoids that are extensively researched and are worth mentioning further below are the well-known  $\beta$ -carotene for its ubiquitous presence in seaweeds, and the xanthophylls fucoxanthin, for its high presence in brown seaweeds, and astaxanthin, for its reportedly strong activity, particularly when sourced from algae. Lutein and zeaxanthin will also be briefly mentioned.

$\beta$ -Carotene is possibly the most well-known carotene, holding several well-documented benefits for human health, such as antioxidant, anti-inflammatory, anticancer, and antiaging (Mayne 1996; Sies and Stahl 2004; Stahl and Sies 2012; Carpena et al. 2021). This carotene has, therefore, an outstanding potential and applicability in the food, cosmetic, and pharmaceutical industries (Phan et al. 2018; Carpena et al. 2021). In seaweeds, research has shown that it is possible to manipulate  $\beta$ -carotene yields in the red seaweed *Neopyropia yezoensis* (Xie et al. 2020). However, to date, the most efficient source to obtain  $\beta$ -carotene is the green microalgae *Dunaliella salina* (Barbosa et al. 2023), provided its production is properly induced by manipulation of culture conditions (Lamers et al. 2008). Nevertheless, the majority of its industrial production results from chemical synthesis (Ye et al. 2008).

Fucoxanthin, a brown pigment, is one of the most abundant marine carotenoids, is effortlessly found in brown seaweeds (Pereira et al. 2021) and has a wide range of benefits for human health. Fucoxanthin is renowned for its ability to modulate processes in the central nervous system. Additionally, it exhibits antioxidant, antibacterial (Karpinski and Adamczak 2019; Liu et al. 2019), antiphototoaging (Noviendri et al. 2022), antiallergic, anticancer (Pádua et al. 2015; Méresse et al. 2020; Ming et al. 2021), anti-inflammatory (Yang et al. 2013), antidiabetic (Park et al. 2011), antiobese (Ojulari et al. 2020), antiangiogenic (Pereira 2016), and antiobesity activities, while also showing potential for treating neurodegenerative diseases (Schepers

et al. 2020; Yang et al. 2021), which makes this pigment particularly sought out by the pharmaceutical, cosmetic, and food industries (Peng et al. 2011; Aziz et al. 2020; Ojulari et al. 2020). The main algal provider of fucoxanthin is the brown seaweed *Undaria pinnatifida*, that which produce this pigment in high quantities (Liu et al. 2019; Garcia-Perez et al. 2022; Lourenço-Lopes et al. 2023), but other brown species have also been looked at, such as *Fucus* spp. (Garcia-Perez et al. 2022; Resende et al. 2023), *Laminaria* spp. (Ming et al. 2021; Garcia-Perez et al. 2022), *Ascophyllum nodosum*, *Bifurcaria bifurcata*, *Himantalia elongata*, *Pelvetia canaliculata* (Garcia-Perez et al. 2022), *Sargassum* spp. (Yang et al. 2013; Nomura et al. 2013; Conde et al. 2015; Garcia-Perez et al. 2022), and *Sphaerotrichia divaricata* (Maeda et al. 2018). Additionally, brown algae from the genus *Alaria*, *Ascophyllum*, *Carpophyllum*, *Cladosiphon*, *Cystophora*, *Cystoseira*, *Dictyota*, *Ecklonia*, *Ectocarpus*, *Eisenia*, *Himantalia*, *Ishige*, *Kjellmaniella*, *Myagropsis*, *Padina*, *Pelvetia*, *Petalonia*, *Saccharina*, *Sargassum*, *Scytosiphon*, *Sporochnus*, and *Turbinaria* have been targeted as well (Muradian et al. 2015), and their commercial exploration could be an hypothesis to put forward, provided such can be done sustainably by, for example, cultivating the required biomass if possible.

Astaxanthin, a red pigment, is worth mention as it has an antioxidant activity 10 times stronger than a number of other carotenoids such as  $\beta$ -carotene, lutein, and zeaxanthin (O'Connor and O'Brien 1998). This pigment is known for being able to suppress free radical production and inhibit the cellular toxicity induced by reactive oxygen species, which thus labels it as being a super vitamin E (Miki 1991). Astaxanthin has also great potential as a novel geroneuroprotector (compound that slow the rate of biological aging) due to its chemical-physical properties (Schubert et al. 2018; Sorrenti et al. 2020). Additionally, it shares many of the health benefits previously mentioned for other carotenoid classes, namely as a promoter of cardiovascular health, immune response, cancer prevention, and skin health (Davinelli et al. 2018; Fakhri et al. 2018) This renders this pigment particularly interesting, as astaxanthin, when extracted from algae, reportedly has the strongest biological activity when compared to that obtained from other biological sources (Ye et al. 2019). Such has been the key factor triggering the global demand for this pigment on an aquaculture context, as astaxanthin targets a wide range of aquatic animal health conditions, improves their survival, growth, fitness, and reproductivity, and dramatically improves their coloration, thus boosting their market value (Lim et al. 2018; Elbahnaswy and Elshopakey 2023). In seaweeds, research has shown that the content of astaxanthin changes according to season in the red seaweed *Catenella caespitosa* (Banerjee et al. 2009). Brown seaweeds, such as *Undaria pinnatifida*, *Saccharina japonica* (formerly *Laminaria japonica*), and *Sargassum fusiforme* (formerly *Hizikia fusiformis*), are rich in astaxanthin and fucoxanthin; these seaweeds feature in the traditional Okinawan diet, known for its healthy aging properties (Willcox et al. 2014). However, the main source of astaxanthin among algae, besides the commercially produced chemical counterpart, has been the green microalgae *Haematococcus lacustris* (formerly *Haematococcus pluviialis*) and *Chromochloris zofingiensis* (formerly *Chlorella zofingiensis*) (Han et al. 2013).

Lutein and zeaxanthin are carotenoids whose biotechnological potential has been studied. Being stored in the eye macula (Murillo et al. 2019; Gomes et al. 2022), both carotenoids have proven their usefulness as antitumoral compounds (Firdous et al. 2015), as photoprotective agents (González et al. 2003), and as eye health promoters (Stahl and Sies 2005; Ma and Lin 2010; Murillo et al. 2019; Saha et al. 2020; Becerra et al. 2020), and therefore are explored in food, cosmetics, and pharmaceutical industries (Shi et al. 2002; Fernández-Sevilla et al. 2010; Saha et al. 2020; Becerra et al. 2020). Either one of these carotenoids has been studied from macroalgae such as the red seaweeds *Corallina officinalis* (Sajilata et al. 2008; Koo et al. 2012), *Gracilaria corticata*, *Grateloupia filicina* (Bhat et al. 2021), and *Neophyropia yezoensis* (Xie et al. 2020). However, and again similarly to other carotenoids, the production of these pigments, namely zeaxanthin, using microalgae instead remains an attractive venue (Becerra et al. 2020; Bourdon et al. 2021).

### 13.1.3.3 Prospects and Applications of Phycobiliproteins

Phycobiliproteins exhibit remarkable spectroscopic properties, including high absorption coefficient, excitation and emission spectra, quantum yield, low interference, quenching stability, and water solubility (Niu et al. 2013; Kannaujiya et al. 2017, 2021). These exceptional properties have led to their widespread application and documentation in various fields, such as biomedical research, clinical diagnostics, therapeutic science, and the cosmeceutical and pharmaceutical industries (Pagels et al. 2019; Li et al. 2019a; Dagnino-Leone et al. 2020; Chini Zittelli et al. 2023). Notably, these pigments have found extensive use as photosynthesizers in cancer therapy (Bei et al. 2002) and fluorescent sensors in flow cytometry and immunofluorescence microscopy (Leney et al. 2018).

The primary reason for the significant commercial interest in phycobiliproteins lies in the health benefits they offer, acting as antioxidants and free-radical scavengers (Yabuta et al. 2010; Pangestuti and Kim 2011b; Nagaraj et al. 2012; Hemlata et al. 2018), with therapeutic and nutraceutical effects (Fernández-Rojas et al. 2014; Manirafasha et al. 2020; Dagnino-Leone et al. 2022). Moreover, they have demonstrated effectiveness in neuroprotection, antibacterial (Hemlata et al. 2018), antiviral (Shih et al. 2003), anti-inflammatory (Lee et al. 2017), antiallergic (Lee et al. 2021c), antitumoral (Pattarayan et al. 2017; Hao et al. 2018; Hemlata et al. 2018), antiaging (Lee et al. 2021c) and have shown promise as agents for combating Alzheimer's disease. Additionally, they have been found to provide hepatoprotective and immunomodulatory benefits (Nagaraj et al. 2012; Cian et al. 2012) and are considered as potential hypocholesterolemia agents (Sonani et al. 2016; Kannaujiya et al. 2021).

Phycobiliproteins are considered the primary food colorants and preservatives obtained from algae and highly regarded as an excellent green alternative to their chemical counterparts (Chen et al. 2017b; Nowruzzi et al. 2022; Dagnino-Leone et al. 2022). Phycoerythrin has extensive applications as a natural dye in the food and cosmetic sectors (Mysliwa-Kurdziel and Solymosi 2016; Kannaujiya et al.

2021; Ma et al. 2022; Chen et al. 2022). For example, phycoerythrin extracted from the microalgae *Porphyridium* sp. has garnered significant attention and research due to its ability to emit a vibrant yellow fluorescence. This unique characteristic has led to its thorough exploration and experimentation in the creation of food products with singular visual effects. These include visually captivating cake decorations, soft drinks, and alcoholic beverages that exhibit fluorescence under ultraviolet light or when subjected to specific pH levels (Dufossé et al. 2005).

The potential application and market value of phycobiliproteins is determined by their purity level, specifically the ratio of  $A_{\max} \text{ PBP}/A_{280}$ , and consequently, the potential application from all the possibilities listed above. When this ratio is greater than or equal to 0.7, it is considered food grade, for ratios between 0.7 and 3.9, it is categorized as reagent grade, and lastly a ratio of  $A_{\max} \text{ PBP}/A_{280}$  equal to or greater than 4.0 indicates analytical grade. Both reagent and analytical grade phycobiliproteins are priced higher than food-grade phycobiliproteins (Hsieh-Lo et al. 2019; Qiang et al. 2021).

Within macroalgae, phycoerythrin has been studied not only from the highly acknowledged red seaweeds *Gelidium* sp. (Mittal and Raghavarao 2018; Mittal et al. 2019), *Gracilaria* spp. (Nguyen et al. 2020; Pereira et al. 2020; Zhao et al. 2020), *Grateloupia turuturu* (Munier et al. 2014, 2015; Le Guillard et al. 2015), *Palmaria palmata* (Dumay et al. 2013; Lee et al. 2017), and *Porphyra/Pyropia* sp. (Wang et al. 2020; Sano et al. 2020; Huang et al. 2021), but also from several other non-commercial or otherwise less-known species (Ismail and Osman 2016; Malairaj et al. 2016; Sfriso et al. 2018; Saluri et al. 2019; Freitas et al. 2022). However, considering the amazing diversity of red seaweeds worldwide, and the vibrant red hues some Rhodophyta hold, this probably leaves out a great number of less known, but potentially equally promising species. Being phycoerythrin a protein, red seaweeds with reportedly high protein content may look particularly promising to explore as well. Examples of such seaweeds include *Chondrus crispus*, *Osmundea pinnatifida*, *Pterocladia capillacea*, *Pyropia tenera* (formerly *Neopyropia tenera*) and *Pyropia yezoensis*, besides the abovementioned *Palmaria palmata* and *Porphyra* sp. (Pereira 2011, 2016, 2023).

The primary interest in phycobiliproteins lies not only in their high protein yield but also in their easy-to-perform extraction methods. Typically, in macroalgae, phycoerythrin is studied and processed using various methods, which include grinding/maceration (Francavilla et al. 2015; Pereira et al. 2020), often combined with freeze-thaw techniques (Sfriso et al. 2018; Zhao et al. 2020) or liquid nitrogen (Francavilla et al. 2013; Saluri et al. 2020). The main solvents that are often chosen to complement these techniques are phosphate buffer (Ismail and Osman 2016; Nguyen et al. 2017; Pereira et al. 2020; Sano et al. 2020) and distilled water (Lee et al. 2017; Zhao et al. 2020). Less commonly applied extraction methods include ultrasounds (Le Guillard et al. 2015; Mittal et al. 2017) and enzymatic hydrolysis (Fleurence 2003). Separation and purification of the extracted phycoerythrin are usually performed through chromatography techniques (Niu et al. 2010; Gu et al. 2018; Saluri et al. 2020; Zhao et al. 2020) or gel electrophoresis (MacColl et al. 1996; Galland-Irmouli et al. 2000; Malairaj et al. 2016).

Phycocyanin is the phycobiliprotein that holds the largest market and shares the same properties and applications of phycoerythrin. This brilliant blue colored pigment presents remarkable fluorescent abilities, and it can be processed into fluorescent reagents, probes, and tracers. These are then applied in the context of biomedical research and biological engineering, namely in medical diagnosis and immunology trials (Liu et al. 2016). Phycocyanin also stands out as the most used natural blue pigment in the food industry, being employed to color various products, such as desserts, with a hardly comparable color, since interestingly, there are limited alternatives approved as natural blue food colorants (Brauch 2016). One key advantage and distinctive feature of phycocyanin, apart from its role as a food colorant, is its potential to promote health, being therefore labeled as a pharmaceutically active phyco-pigment (Vinothkanna and Sekar 2020). Phycobiliprotein has an attested nutritional value (Farag et al. 2016), nutraceutical, therapeutic (Piniella-Matamoros et al. 2021) (113), and bioactive potential (Liu et al. 2016), especially as anticancer agent (Jiang et al. 2017; Braune et al. 2021), and shows, as well, remote-sensing abilities (Ogashawara 2020).

Phycocyanin is primarily obtained from the Cyanobacteria *Arthrospira platensis*, which is by far the main source for this pigment, probably in part due to being a highly researched and known organism (Sahin 2018; Wollina et al. 2018; Marková et al. 2020; Araujo et al. 2021; Ragusa et al. 2021), but also due to its cosmopolitan distribution on water and earth (Kannaujiya et al. 2021), thus being easy to obtain. However, the microalgae *Cyanidium caldarium* (Eisele et al. 2000) and *Galdieria sulphuraria* (Chini Zittelli et al. 2023) have also been recently considered for the same purpose. There is an outstanding number of published research and reviews regarding this pigment in the literature (de Morais et al. 2018; Prado et al. 2018; Pagels et al. 2019; Morocho-Jácome et al. 2020; Braune et al. 2021; Cottas et al. 2021; Jaeschke et al. 2021; Patel et al. 2022).

In macroalgae, the Bangiophyceae species such as *Pyropia haitanensis* (as *Neoporphyra haitanensis*) (Liu et al. 2015) and *Bangia atropurpurea* (Chang et al. 2011) have provided B-phycocyanin that demonstrates promising capabilities as an antiallergic agent. Additionally, B-phycocyanin isolated from *Porphyra* sp. exhibits potential as an antioxidant agent (Huang et al. 2021). As part of an effort to enhance our understanding of R-phycocyanin's structure and function in red macroalgae, R-phycocyanin from *Polysiphonia stricta* was isolated, purified, and thoroughly studied (Wang et al. 2014). A mix of several well-known and less-known red seaweed species was also recently evaluated for phycocyanin content (Freitas et al. 2022).

Extraction and purification methods that target phycocyanin are common to those applied to phycoerythrin. However, they are seldom applied or optimized as seaweeds are outpaced by Cyanobacteria, which remains the predominant source of phycocyanin for the industry. Consequently, dedicated studies focused on phycocyanin derived from macroalgae may face challenges in gaining recognition, traction, or support in the coming times. There are few studies use apply phosphate buffer (Lüder et al. 2001; Wang et al. 2014; Ismail and Osman 2016) to extract phycocyanin from red macroalgae, that can be purified by chromatography (Kuddus

et al. 2013; Wang et al. 2014; Huang et al. 2021) and electrophoresis (Huang et al. 2021).

Compared to either phycoerythrin or phycocyanin, allophycocyanin is not extensively studied, regardless of the organism. However, its distinctive blue-green color is almost unparalleled by any other natural pigment (Mysliwa-Kurdziel and Solymosi 2016), which would likely enhance its value as a truly unique compound. Again, cyanobacteria are the prime source of this pigment in academic settings (Chen et al. 2016; Soulier and Bryant 2021), and focus is given to understand structural mechanisms (Dagnino-Leone et al. 2017) and synthesis (Dagnino-Leone et al. 2020; Guo et al. 2020). In seaweeds, allophycocyanin been successfully extracted from various Rhodophyta species using phosphate buffer (Lüder et al. 2001; Ismail and Osman 2016). Efforts have also been made to produce high-quality recombinant allophycocyanin in *Escherichia coli* from *Gracilaria chilensis*, intended for biotechnological and biomedical applications (Dagnino-Leone et al. 2020).

Examples of phycobiliprotein commercialization can be found at a commercial level. Some companies profit from phycobiliprotein-derived natural dyes, with microalgae being prominently featured as the source for their products. Several companies promote their microalgae-based natural dyes for use in cosmetic products. Notably, phycocyanin from *Arthrospira* sp. and phycoerythrin from *Porphyridium* sp. are used in this context. Moreover, R-Phycoerythrin is distributed as a laboratory consumable, sourced from *Pyropia tenera* (as *Neopyropia tenera*) or *Neogastroclonium subarticulatum*, specifically for biotechnological and biomedical research purposes. Research on these pigments, obtained from macroalgae, is still scarce. Recent studies focused on the optimization of culture conditions to manipulate phycobiliprotein content and production of *Colaconema* sp. (Lee et al. 2021b), *Halymenia floresii* (Godínez-Ortega et al. 2008), *Halymenia durvillei* (Rula et al. 2021), *Gracilaria caudata*, and *Laurencia catarinensis* (Souza et al. 2019). Such endeavors have, however, progressed little beyond the academic context, which may be partly due to the challenges inherent in extraction procedures, discussed below.

#### 13.1.3.4 Current Challenges and Perspectives

One of the primary challenges in exploring pigments derived from seaweed sources lies in the differing cultural perspectives on seaweeds themselves. Throughout history, seaweeds have held a significant place in the cultures and traditions of Eastern countries, serving various purposes beyond human consumption and health, as extensively documented in the literature (Pereira 2011, 2016, 2018, 2023; Abreu et al. 2015; Carvalho and Pereira 2015; Wells et al. 2017; Leandro et al. 2020; Pereira and Valado 2021; Morais et al. 2021; Kalasariya et al. 2022). On the other hand, the Western part of the world still tends to embrace a lifestyle that emphasizes the abundance and diversity of available food options (Pereira 2023). However, this diversity often includes highly unhealthy choices, such as the widely prevalent “fast food,” which has become a response to the fast-paced lifestyle in the West. These processed foods are high in calories and unhealthy fats, artificially flavored with

synthetic additives, while lacking nutritional value and appeal. Consequently, in a considerable portion of the Western world, food is primarily viewed and consumed as a necessity for survival, with a number of exceptions such as countries following a Mediterranean diet, for example. In the East, on the other hand, food consumption and preparation are integral to the traditions of many cultures, and the act of eating is often considered a revered and ceremonious activity.

It is no surprise that seaweeds have gained widespread recognition in Eastern cultures, while the Western world still holds reservations about them. In many shore-side Western countries, seaweeds were once consumed as a last resort in times of strife, such as warfare and poverty, so they may now be held as a gloomy reminder of such difficult times back then. Only a few Western countries incorporate seaweeds into their cultural practices (Pérez-Lloréns et al. 2020), and in most places, they are considered a relatively new and unexplored addition to a healthy diet. Nonetheless, extensive research has already been conducted, particularly in academic settings, but the full transition to integrating seaweeds into the mainstream industry and making them commonly available in grocery stores is yet to be accomplished.

Seaweeds, as a food source, have not yet captured the interest of the typical Western society, which often prefers to stick with familiar options rather than explore new alternatives, coupled with an inherent lack of skill, dare, or imagination, in incorporating seaweeds to their daily diet. The lack of interest leads to minimal demand, making industries hesitant to invest in seaweed products when it seems people do care little about them yet. However, recently, both Eastern and Western societies have started to reflect on their lifestyle and the potential consequences for their health and the well-being of future generations. People have become more conscious of the quality of their food, clothing, and other mundane choices and are now making smarter decisions that consider not only personal health but also the environment. There is a growing demand for higher-quality products in the market, and individuals are actively seeking alternatives for both food and materials, reflecting a shift toward a more mindful and sustainable way of living.

Seaweeds exemplify this kind of resource. In contemporary times, although encountering skepticism, particularly from individuals entrenched in traditional customs, seaweeds are conveniently accessible, at the very least, in large retail outlets and commercial spaces. Naturally, there exists a potential downside to this situation, centered around the apprehension of endangering the excessive use of native seaweed populations. However, this issue can be mitigated by implementing effective resource management strategies and practicing sustainable cultivation of the desired species. Besides all their benefits, numerous seaweed species have the added advantage that can be sustainably cultivated, allowing the preservation of natural populations, either in controlled, indoor settings or in outdoor, shored settings. Naturally, challenges remain regarding process sustainability, cost-effectiveness, and economic viability. The diversity of the natural pigments obtained from seaweeds determines their stability against a range of external conditions, such as environmental or those applied in technological settings (Cserhádi 2006).

There are challenges also inherent to the recovery of pigments, or any other compound, from a biological matrix as challenging as that of a seaweed. Their extracellular material hinders the full recovery and yield of chlorophylls, whereas microalgae pose a significantly easier endeavor (Chen et al. 2017a). Then, there are the challenges pertaining the pigments themselves. Natural pigments are highly unstable, being particularly sensitive to temperature and light, and the biomass quickly adjusts its pigment composition to the external conditions. While this may present an advantage regarding the manipulation of culture conditions to obtain the desired pigment, a hardly overlooked disadvantage lies in the fact that it is quite challenging to preserve the quality and stability of the metabolites as soon as they are extracted from the biomass. Processes have always taken this into consideration, but process scale-up efforts are challenging.

The isolation of carotenoids can be performed by conventional processing technologies, such as solvent extraction. However, such methods present several limitations, such as high solvent consumption and time-consuming steps, which also result in poor efficiency and selectivity of the end product (Poojary et al. 2016). Certain precautions need to be taken during carotene extraction to minimize degradation and isomerization. Factors such as exposure to light, heat, and oxygen can considerably reduce the efficiency of extraction. Therefore, it is essential to handle and process the samples promptly (Rodriguez-Amaya and Kimura 2004; Rosso and de Rosso and Mercadante 2007). Certain methodologies also have proven to be quite costly, such as the supercritical fluid extraction methodology, or cause carotene degradation, such as ultrasound-assisted extraction and microwave-assisted extraction, that involves the use of high temperatures during the process (Poojary et al. 2016). Alternatives to such sensitive techniques are also highly desired, and to isolate carotenoids from micro- and macroalgae novel techniques such as microwaves, ultrasounds, high-pressure homogenization, pulsed electric fields, liquid pressurization, supercritical fluids, and subcritical fluids, have been recently considered (Poojary et al. 2016). Chemical synthesis of carotenoids is currently commercially made for astaxanthin, and possible to be performed for fucoxanthin although for the latter pigment, such process is quite expensive, and therefore, the standardization of the extraction and purification methods targeting algae-sourced fucoxanthin is a fairly appealing endeavor (Pereira et al. 2021).

Phycobiliproteins are applied in the industry in its water-soluble protein form, and its commercial uses heavily rely on comprehensive knowledge and advanced technology, which are still relatively limited (Mysliwa-Kurdziel and Solymosi 2016). To begin with, efforts have been made to achieve success in culture settings in order to obtain not only macroalgae, but also cyanobacteria, as the source material to extract pigments, particularly regarding achieving a balance between biomass growth rates and phycobiliprotein productivity (Dagnino-Leone et al. 2022). Then, there is also the fact that the majority of innovative applications involving phycobiliproteins are currently only disclosed in patents (Sekar and Chandramohan 2008; Mysliwa-Kurdziel and Solymosi 2016). Currently, the commercialization of phycobiliproteins is hindered not only by their chemical instability, which reduces their shelf life, but also by the high level of purity that is required for pharmaceutical

applications, which involves several steps. These steps increase both production time and costs (Chini Zittelli et al. 2023) and may compromise the pigment quality due to manipulation alone. The low yields often obtained during production also limit implementation and setting in the food and cosmetic industries. Additionally, these compounds have limited chemical stability, particularly under heat and light conditions, making them susceptible to denaturation.

To address these issues, researchers have compared and reviewed strategies to improve phycobiliprotein yields and chemical stability (Hsieh-Lo et al. 2019), although said research has been more focused on phycocyanin and phycoerythrin, and such leaving out allophycocyanin. Most research under this topic also focus on phycobiliproteins obtained from *Spirulina platensis* (Nowruzi et al. 2022), leaving out a wide number of likely promising species, either micro or macroalgae. In the food sector, recent progress reviews the stability of phycobiliproteins under a wide range of the acidic, light, and temperature conditions in food storage. Phycobiliproteins are significantly more stable when coupled with other natural preservatives or encapsulated by using algal materials such as alginates and carrageenans, through nanotechnology (Nowruzi et al. 2022). Although this is still a procedure seldom applied, research focusing on this methodology has been recently published (Braga et al. 2016; Seyed Yagoubi et al. 2017; Patel et al. 2020).

Currently, the purification of phycobiliproteins remains expensive, urging the consideration of more effective and cost-efficient extraction and purification methods, especially on a larger scale (Pereira et al. 2020). Most laboratory protocols share common points, such as meticulous biomass preparation and the use of specialized equipment. However, the subtle variations between extraction protocols make it challenging to establish a universally efficient procedure capable of sustainably process large quantities of algae at a minimal cost. While researchers achieve impressive yields in the laboratory, these results are not directly applicable from a commercial perspective, as there is no industrial-scale viability. To bridge this gap, research must shift focus to larger-scale settings and incorporate industrial parameters to develop a commercial protocol that delivers high yield and purity of the pigment (Beattie et al. 2018; Carlos et al. 2021). This emphasis on industrial-scale viability remains relevant and critical in the current context.

## 13.2 Conclusion

Natural pigments derived from seaweeds exhibit structural diversity and a wide range of vivid colors, while also serving various functions and applications. Chlorophylls, carotenoids, and phycobiliproteins are pivotal components of the seaweed photosynthesis process. They are finely tuned to capture solar energy within specific wavelengths of the light spectrum and convert it into chemical energy, facilitating the synthesis of essential carbohydrates for the organism. Moreover, many of these pigments play a crucial photoprotective role, shielding the seaweed from excessive radiation.

Seaweed-derived pigments are increasingly preferred over synthetic alternatives, reflecting the contemporary society's heightened awareness and concern for health, lifestyle choices, and the long-term impact on both the environment and personal well-being. The manifold benefits offered by chlorophylls, carotenoids, and phycobiliproteins for human health are well established, encompassing a diverse array of bioactivities. Within the realm of biotechnology, these pigments are in high demand across the food, cosmetic, and pharmaceutical industries due to their unique properties.

Nonetheless, challenges persist in the acquisition of these pigments from macroalgae. The ongoing overexploitation of natural seaweed resources underscores the urgency in developing species-specific cultivation techniques. The inherent physiological variations across different seaweed taxa necessitate the refinement of extraction and purification protocols, which are still undergoing optimization to achieve maximum yields at the species level. This optimization is crucial as these processes transition to an industrial scale, while maintaining sustainability and eco-friendliness. These complexities explain why, within the realm of algae, chlorophylls, carotenoids, and phycobiliproteins are primarily sourced from microalgae. These microalgae benefit from well-mastered culture techniques and optimized extraction methods. On the other hand, similar endeavors with macroalgae are mostly confined to research purposes. Nonetheless, ongoing research highlights the remarkable potential of macroalgae as abundant sources of high-quality natural pigments, warranting further thorough exploration.

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## References

- Abreu MH, Pereira R, Sassi J-F (2015) Marine algae and the global food industry. In: Pereira L, Neto JM (eds) Marine algae: biodiversity, taxonomy, environmental assessment, and biotechnology, 1st edn. CRC Press, Boca Raton, pp 300–319
- Aldred EM, Buck C, Vall K (2009) Terpenes. In: Aldred EM (ed) Pharmacology: a handbook for complementary healthcare professionals. Elsevier, Amsterdam, p 362
- Araujo GS, Santiago CS, Moreira RT et al (2021) Nutrient removal by *Arthrospira platensis* cyanobacteria in cassava processing wastewater. J Water Process Eng 40:101826. <https://doi.org/10.1016/j.jwpe.2020.101826>
- Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141:391–396. <https://doi.org/10.1104/pp.106.082040>
- Aziz E, Batool R, Akhtar W et al (2020) Xanthophyll: health benefits and therapeutic insights. Life Sci 240:117104. <https://doi.org/10.1016/j.lfs.2019.117104>
- Balasubramaniam V, June Chelyn L, Vimala S et al (2020) Carotenoid composition and antioxidant potential of *Eucheuma denticulatum*, *Sargassum polycystum* and *Caulerpa lentillifera*. Heliyon 6:e04654. <https://doi.org/10.1016/j.heliyon.2020.e04654>

- Banerjee K, Ghosh R, Homechaudhuri S, Mitra A (2009) Seasonal variation in the biochemical composition of red seaweed (*Catenella repens*) from Gangetic delta, northeast coast of India. *J Earth Syst Sci* 118:497–505. <https://doi.org/10.1007/S12040-009-0045-2>
- Barbosa M, Inácio LG, Afonso C, Maranhão P (2023) The microalga *Dunaliella* and its applications: a review. *Appl Phycol* 4:99–120. <https://doi.org/10.1080/26388081.2023.2222318>
- Basheva D, Moten D, Stoyanov P et al (2018) Content of phycoerythrin, phycocyanin, allophycocyanin and phycoerythrocyanin in some cyanobacterial strains: applications. *Eng Life Sci* 18:861–866. <https://doi.org/10.1002/elsc.201800035>
- Beattie SW, Moranças M, Déléris P et al (2018) Extraction of phycocyanin and phycoerythrin pigments. In: Charrier B, Wichard T, Reddy CRK (eds) *Protocols for macroalgae research*. CRC Press, Boca Raton, pp 249–265
- Becerra MO, Contreras LM, Lo MH et al (2020) Lutein as a functional food ingredient: stability and bioavailability. *J Funct Foods* 66:103771. <https://doi.org/10.1016/j.jff.2019.103771>
- Begum H, Yusoff FMD, Banerjee S et al (2016) Availability and utilization of pigments from microalgae. *Crit Rev Food Sci Nutr* 56:2209–2222. <https://doi.org/10.1080/10408398.2013.764841>
- Bei H, Guang-Ce W, Chen-Kui Z, Zhen-Gang L (2002) The experimental research of R-phycoerythrin subunits on cancer treatment: a new photosensitizer in PDT. *Cancer Biother Radiopharm* 17:35–42. <https://doi.org/10.1089/10849780252824055>
- Bhat I, Haripriya G, Jogi N, Mamatha BS (2021) Carotenoid composition of locally found seaweeds of Dakshina Kannada district in India. *Algal Res* 53:102154. <https://doi.org/10.1016/j.algal.2020.102154>
- Bi Fai P, Grant A, Reid B (2007) Chlorophyll a fluorescence as a biomarker for rapid toxicity assessment. *Environ Toxicol Chem* 26:1520–1531. <https://doi.org/10.1897/06-394R1.1>
- Bohn T, Bonet ML, Borel P et al (2021) Mechanistic aspects of carotenoid health benefits—where are we now? *Nutr Res Rev* 34:276–302. <https://doi.org/10.1017/S0954422421000147>
- Bonanno G, Orlando-Bonaca M (2018) Chemical elements in Mediterranean macroalgae. A review. *Ecotoxicol Environ Saf* 148:44–71. <https://doi.org/10.1016/j.ecoenv.2017.10.013>
- Borovkov AB, Gudvilovich IN, Lelekov AS, Avsiyan AL (2023) Effect of specific irradiance on productivity and pigment and protein production of *Porphyridium purpureum* (Rhodophyta) semi-continuous culture. *Bioresour Technol* 374:128771. <https://doi.org/10.1016/J.BIORTECH.2023.128771>
- Bourdon L, Jensen AA, Kavanagh JM, McClure DD (2021) Microalgal production of zeaxanthin. *Algal Res* 55:102266. <https://doi.org/10.1016/j.algal.2021.102266>
- Braga ARC, Figueira F, da Silveira JT et al (2016) Improvement of thermal stability of C-phycocyanin by nanofiber and preservative agents. *J Food Process Preserv* 40:1264–1269. <https://doi.org/10.1111/jfpp.12711>
- Brasil Silva E, Ferreira Pinto PV, Bamutsha Chretien J et al (2017) Green optical dissolved oxygen sensor based on a chlorophyll–zinc complex extracted from the plant *Brassica oleracea* L. *Appl Opt* 56:9951. <https://doi.org/10.1364/AO.56.009951>
- Brauch JE (2016) Underutilized fruits and vegetables as potential novel pigment sources. In: Carle R, Schweiggert R (eds) *Handbook on natural pigments in food and beverages: industrial applications for improving food color*. Elsevier, Duxford, pp 305–335
- Braune S, Krüger-Genge A, Kammerer S et al (2021) Phycocyanin from *Arthrospira platensis* as potential anti-cancer drug: review of in vitro and in vivo studies. *Life* 11:91. <https://doi.org/10.3390/life11020091>
- Britton G, Liaaen-Jensen S, Pfander H (2004) *Carotenoids*. Birkhäuser Basel, Basel
- Brotosudarmo T, Heriyanto, Shioi Y et al (2018) Composition of the main dominant pigments from potential two edible seaweeds. *Philipp J Sci* 147:47–55
- Carlos TAV, dos Santos Pires Cavalcante KM, de Cássia Evangelista Oliveira F et al (2021) Pressurized extraction of phycobiliproteins from *Arthrospira platensis* and evaluation of its effect on antioxidant and anticancer activities of these biomolecules. *J Appl Phycol* 33:929–938. <https://doi.org/10.1007/s10811-020-02358-z>

- Carpaena M, Caleja C, Pereira E et al (2021) Red seaweeds as a source of nutrients and bioactive compounds: optimization of the extraction. *Chemosensors* 9:132. <https://doi.org/10.3390/chemosensors9060132>
- Carvalho LG, Pereira L (2015) Review of marine algae as source of bioactive metabolites: a marine biotechnological approach. In: Pereira L, Neto JM (eds) *Marine algae: biodiversity, taxonomy, environmental assessment, and biotechnology*. CRC Press, Boca Raton, pp 195–227
- Chaerle L, Hagenbeek D, De Bruyne E et al (2004) Thermal and chlorophyll-fluorescence imaging distinguish plant-pathogen interactions at an early stage. *Plant Cell Physiol* 45:887–896. <https://doi.org/10.1093/PCP/PCH097>
- Chan PT, Matanjun P, Yasir SM, Tan TS (2015) Antioxidant activities and polyphenolics of various solvent extracts of red seaweed, *Gracilaria changii*. *J Appl Phycol* 27:2377–2386. <https://doi.org/10.1007/s10811-014-0493-1>
- Chang CJ, Yang YH, Liang YC et al (2011) A novel phycobiliprotein alleviates allergic airway inflammation by modulating immune responses. *Am J Respir Crit Care Med* 183:15–25. <https://doi.org/10.1164/rccm.201001-0009OC>
- Chapman RL (2013) Algae: the world's most important “plants”—an introduction. *Mitig Adapt Strateg Glob Chang* 18:5–12. <https://doi.org/10.1007/s11027-010-9255-9>
- Chen H, Jiang P (2018) Combinational biosynthesis and characterization of fusion proteins with tandem repeats of allophycocyanin holo- $\alpha$  subunits, and their application as bright fluorescent labels for immunofluorescence assay. *J Biosci Bioeng* 126:778–782. <https://doi.org/10.1016/j.jbiosc.2018.06.004>
- Chen K, Roca M (2019) Cooking effects on bioaccessibility of chlorophyll pigments of the main edible seaweeds. *Food Chem* 295:101–109. <https://doi.org/10.1016/J.FOODCHEM.2019.05.092>
- Chen H, Liu Q, Zhao J, Jiang P (2016) Biosynthesis, spectral properties and thermostability of cyanobacterial allophycocyanin holo- $\alpha$  subunits. *Int J Biol Macromol* 88:88–92. <https://doi.org/10.1016/j.ijbiomac.2016.03.050>
- Chen K, Ríos JJ, Pérez-Gálvez A, Roca M (2017a) Comprehensive chlorophyll composition in the main edible seaweeds. *Food Chem* 228:625–633. <https://doi.org/10.1016/J.FOODCHEM.2017.02.036>
- Chen X, Wu M, Yang Q, Wang S (2017b) Preparation, characterization of food grade phycobiliproteins from *Porphyra haitanensis* and the application in liposome-meat system. *LWT* 77:468–474. <https://doi.org/10.1016/J.LWT.2016.12.005>
- Chen H, Qi H, Xiong P (2022) Phycobiliproteins—a family of algae-derived biliproteins: productions, characterization and pharmaceutical potentials. *Mar Drugs* 20:450. <https://doi.org/10.3390/md20070450>
- Chen K, Ma T, Ding J et al (2023) Effects of straw return with nitrogen fertilizer reduction on rice (*Oryza sativa* L.) morphology, photosynthetic capacity, yield and water–nitrogen use efficiency traits under different water regimes. *Agronomy* 13:133. <https://doi.org/10.3390/AGRONOMY13010133>
- Chini Zittelli G, Lauceri R, Faraloni C et al (2023) Valuable pigments from microalgae: phycobiliproteins, primary carotenoids, and fucoxanthin. *Photochem Photobiol Sci* 22:1733–1789. <https://doi.org/10.1007/S43630-023-00407-3>
- Cian RE, López-Posadas R, Drago SR et al (2012) Immunomodulatory properties of the protein fraction from *Porphyra columbina*. *J Agric Food Chem* 60:8146–8154. <https://doi.org/10.1021/jf300928j>
- Conde E, Moure A, Domínguez H (2015) Supercritical CO<sub>2</sub> extraction of fatty acids, phenolics and fucoxanthin from freeze-dried *Sargassum muticum*. *J Appl Phycol* 27:957–964. <https://doi.org/10.1007/s10811-014-0389-0>
- Cottas AG, Ribeiro EJ, Watanabe EO, Ferreira JDS (2021) Evaluation of extraction methods and purification by aqueous two-phase systems of phycocyanin from *Anabaena variabilis* and *Noctoc* sp. *Braz J Chem Eng* 38:617–627. <https://doi.org/10.1007/s43153-021-00131-4>
- Cserhádi T (2006) *Liquid chromatography of natural pigments and synthetic dyes*, 1st edn. Elsevier Science, Amsterdam

- Dagnino-Leone J, Figueroa M, Mella C et al (2017) Structural models of the different trimers present in the core of phycobilisomes from *Gracilaria chilensis* based on crystal structures and sequences. PLoS One 12:e0177540. <https://doi.org/10.1371/journal.pone.0177540>
- Dagnino-Leone J, Figueroa M, Uribe E et al (2020) Biosynthesis and characterization of a recombinant eukaryotic allophycocyanin using prokaryotic accessory enzymes. Microbiology 9:e989. <https://doi.org/10.1002/mbo3.989>
- Dagnino-Leone J, Figueroa CP, Castañeda ML et al (2022) Phycobiliproteins: structural aspects, functional characteristics, and biotechnological perspectives. Comput Struct Biotechnol J 20:1506–1527. <https://doi.org/10.1016/J.CSBJ.2022.02.016>
- Darvin ME, Sterry W, Lademann J, Vergou T (2011) The role of carotenoids in human skin. Molecules 16:10491. <https://doi.org/10.3390/MOLECULES161210491>
- Dashwood RH (1997) Chlorophylls as anticarcinogens (Review). Int J Oncol 10:721–727. <https://doi.org/10.3892/ijo.10.4.721>
- Davinelli S, Nielsen ME, Scapagnini G (2018) Astaxanthin in skin health, repair, and disease: a comprehensive review. Nutrients 10:522. <https://doi.org/10.3390/nu10040522>
- de Morais MG, da Fontoura Prates D, Moreira JB et al (2018) Phycocyanin from microalgae: properties, extraction and purification, with some recent applications. Ind Biotechnol 14:30–37. <https://doi.org/10.1089/ind.2017.0009>
- de Rosso VV, Mercadante AZ (2007) Identification and quantification of carotenoids, by HPLC-PDA-MS/MS, from Amazonian fruits. J Agric Food Chem 55:5062–5072. <https://doi.org/10.1021/jf0705421>
- Dias MG, Borge GIA, Kljak K et al (2021) European database of carotenoid levels in foods. Factors affecting carotenoid content. Food Secur 10:912. <https://doi.org/10.3390/foods10050912>
- Dufossé L (2016) Current and potential natural pigments from microorganisms (bacteria, yeasts, fungi, microalgae). In: Carle R, Schweiggert RM (eds) Handbook on natural pigments in food and beverages: industrial applications for improving food color. Woodhead Publishing, Amsterdam, pp 337–354
- Dufossé L, Galaup P, Yaron A et al (2005) Microorganisms and microalgae as sources of pigments for food use: a scientific oddity or an industrial reality? Trends Food Sci Technol 16:389–406. <https://doi.org/10.1016/j.tifs.2005.02.006>
- Dumay J, Moranças M (2016) Proteins and pigments. In: Fleurence J, Levine IA (eds) Seaweed in health and disease prevention. Elsevier Academic Press, London, pp 275–318
- Dumay J, Clément N, Moranças M, Fleurence J (2013) Optimization of hydrolysis conditions of *Palmaria palmata* to enhance R-phycoerythrin extraction. Bioresour Technol 131:21–27. <https://doi.org/10.1016/j.biortech.2012.12.146>
- Dumay J, Moranças M, Munier M et al (2014) Phycoerythrins: valuable proteinic pigments in red seaweeds. Adv Bot Res 71:321–343. <https://doi.org/10.1016/B978-0-12-408062-1.00011-1>
- Eggersdorfer M, Wyss A (2018) Carotenoids in human nutrition and health. Arch Biochem Biophys 652:18–26. <https://doi.org/10.1016/j.abb.2018.06.001>
- Eisele LE, Bakhru SH, Liu X et al (2000) Studies on C-phycoerythrin from *Cyanidium caldarium*, a eukaryote at the extremes of habitat. BBA-Bioenergetics 1456:99–107. [https://doi.org/10.1016/S0005-2728\(99\)00110-3](https://doi.org/10.1016/S0005-2728(99)00110-3)
- Eismann AI, Perpetuo Reis R, Ferreira da Silva A, Negrão Cavalcanti D (2020) *Ulva* spp. carotenoids: responses to environmental conditions. Algal Res 48:101916. <https://doi.org/10.1016/j.algal.2020.101916>
- Elbahnaswy S, Elshopakey GE (2023) Recent progress in practical applications of a potential carotenoid astaxanthin in aquaculture industry: a review. Fish Physiol Biochem 2023:1–30. <https://doi.org/10.1007/S10695-022-01167-0>
- Esteban R, Martínez B, Fernández-Marín B et al (2009) Carotenoid composition in Rhodophyta: insights into xanthophyll regulation in *Corallina elongata*. Eur J Phycol 44:221–230. <https://doi.org/10.1080/09670260802439109>
- Fakhri S, Abbaszadeh F, Dargahi L, Jorjani M (2018) Astaxanthin: a mechanistic review on its biological activities and health benefits. Pharmacol Res 136:1–20. <https://doi.org/10.1016/j.phrs.2018.08.012>

- Farag MR, Alagawany M, El-Hack MEA, Dhama K (2016) Nutritional and health aspects of *Spirulina (Arthrospira)* for poultry, animals and human. *Int J Pharmacol* 12:36–51. <https://doi.org/10.3923/ijp.2016.36.51>
- Febbo E, Richard C, Horlin E et al (2012) PAM chlorophyll a fluorometry for monitoring health of corals along the coast of Qatar. Society of Petroleum Engineers – SPE/APPEA Int conference on health, safety and environment in oil and gas exploration and production 2012: protecting people and the environment – evolving challenges 2:1159–1172. <https://doi.org/10.2118/156815-MS>
- Fernández-Rojas B, Hernández-Juárez J, Pedraza-Chaverri J (2014) Nutraceutical properties of Phycocyanin. *J Funct Foods* 11:375–392. <https://doi.org/10.1016/j.jff.2014.10.011>
- Fernández-Sevilla JM, Acien Fernández FG, Molina Grima E (2010) Biotechnological production of lutein and its applications. *Appl Microbiol Biotechnol* 86:27–40. <https://doi.org/10.1007/s00253-009-2420-y>
- Ferreira MS, Resende DISP, Sousa Lobo JM et al (2021) Marine ingredients for sensitive skin: market overview. *Mar Drugs* 19:464. <https://doi.org/10.3390/MD19080464>
- Fiedor J, Burda K (2014) Potential role of carotenoids as antioxidants in human health and disease. *Nutrients* 6:466–488. <https://doi.org/10.3390/nu6020466>
- Firdous AP, Kuttan G, Kuttan R (2015) Anti-inflammatory potential of carotenoid meso-zeaxanthin and its mode of action. *Pharm Biol* 53:961–967. <https://doi.org/10.3109/13880209.2014.950673>
- Fleurence J (2003) R-phycoerythrin from red macroalgae: strategies for extraction and potential application in biotechnology. *Appl Biotechnol Food Sci Policy* 1:1–6
- Francavilla M, Franchi M, Monteleone M, Caroppo C (2013) The red seaweed *Gracilaria gracilis* as a multi products source. *Mar Drugs* 11:3754–3776. <https://doi.org/10.3390/md11103754>
- Francavilla M, Manara P, Kamaterou P et al (2015) Cascade approach of red macroalgae *Gracilaria gracilis* sustainable valorization by extraction of phycobiliproteins and pyrolysis of residue. *Bioresour Technol* 184:305–313. <https://doi.org/10.1016/j.biortech.2014.10.147>
- Freitas MV, Inácio LG, Martins M et al (2022) Primary composition and pigments of 11 red seaweed species from the Center of Portugal. *J Mar Sci Eng* 10:1168. <https://doi.org/10.3390/jmse10091168>
- Frense D, Müller A, Beckmann D (1998) Detection of environmental pollutants using optical biosensor with immobilized algae cells. *Sens Actuators B Chem* 51:256–260. [https://doi.org/10.1016/S0925-4005\(98\)00203-2](https://doi.org/10.1016/S0925-4005(98)00203-2)
- Fujii R, Kita M, Doe M et al (2012) The pigment stoichiometry in a chlorophyll a/c type photosynthetic antenna. *Photosynth Res* 111:165–172. <https://doi.org/10.1007/S11120-011-9698-1/TABLES/2>
- Galland-Irmouli AV, Pons L, Luçon M et al (2000) One-step purification of R-phycoerythrin from the red macroalga *Palmaria palmata* using preparative polyacrylamide gel electrophoresis. *J Chromatogr B: Biomed Sci Appl* 739:117–123
- Gammone MA, Riccioni G, D’Orazio N (2015) Carotenoids: potential allies of cardiovascular health? *Food Nutr Res* 59:26762. <https://doi.org/10.3402/fnr.v59.26762>
- Garcia-Perez P, Lourenço-Lopes C, Silva A et al (2022) Pigment composition of nine brown algae from the Iberian Northwestern coastline: influence of the extraction solvent. *Mar Drugs* 20:113. <https://doi.org/10.3390/MD20020113>
- Gevaert F, Creach A, Davoult D et al (2002) Photo-inhibition and seasonal photosynthetic performance of the seaweed *Laminaria saccharina* during a simulated tidal cycle: chlorophyll fluorescence measurements and pigment analysis. *Plant Cell Environ* 25:859–872. <https://doi.org/10.1046/J.1365-3040.2002.00869.X>
- Glazer AN (1994) Phycobiliproteins – a family of valuable, widely used fluorophores. *J Appl Phycol* 6:105–112. <https://doi.org/10.1007/BF02186064>
- Godínez-Ortega JL, Snoeijs P, Robledo D et al (2008) Growth and pigment composition in the red alga *Halymenia floresii* cultured under different light qualities. *J Appl Phycol* 20:253–260. <https://doi.org/10.1007/S10811-007-9241-0/FIGURES/5>

- Gomes L, Monteiro P, Cotas J et al (2022) Seaweeds' pigments and phenolic compounds with antimicrobial potential. *Biomol Concepts* 13:89–102. <https://doi.org/10.1515/BMC-2022-0003>
- González S, Astner S, An W et al (2003) Dietary lutein/zeaxanthin decreases ultraviolet B-induced epidermal hyperproliferation and acute inflammation in hairless mice. *J Invest Dermatol* 121:399–405. <https://doi.org/10.1046/j.1523-1747.2003.12355.x>
- Gu D, Lazo-Portugal R, Fang C et al (2018) Purification of R-phycoerythrin from *Gracilaria lemaneiformis* by centrifugal precipitation chromatography. *J Chromatogr B Analyt Technol Biomed Life Sci* 1087–1088:138–141. <https://doi.org/10.1016/j.jchromb.2018.04.047>
- Guo Y, Tan J (2015) Recent advances in the application of chlorophyll a fluorescence from photosystem II. *Photochem Photobiol* 91:1–14. <https://doi.org/10.1111/PHP.12362>
- Guo Y, Zang X, Cao X et al (2020) Cloning and expression of Allophycocyanin gene from *Gracilaria lemaneiformis* and studying the binding sites of phycocyanobilin on its  $\alpha$  and  $\beta$  subunits. *J Appl Phycol* 32:2657–2671. <https://doi.org/10.1007/s10811-020-02102-7>
- Han D, Li Y, Hu Q (2013) Astaxanthin in microalgae: pathways, functions and biotechnological implications. *Algae* 28:131–147. <https://doi.org/10.4490/ALGAE.2013.28.2.131>
- Hao S, Li S, Wang J et al (2018) Phycocyanin reduces proliferation of melanoma cells through downregulating GRB2/ERK signaling. *J Agric Food Chem* 66:10921–10929. <https://doi.org/10.1021/acs.jafc.8b03495>
- Hegazi MM, Pérez-Ruzafa A, Almela L, Candela ME (1998) Separation and identification of chlorophylls and carotenoids from *Caulerpa prolifera*, *Jania rubens* and *Padina pavonica* by reversed-phase high-performance liquid chromatography. *J Chromatogr A* 829:153–159. [https://doi.org/10.1016/S0021-9673\(98\)00803-6](https://doi.org/10.1016/S0021-9673(98)00803-6)
- Hemlata, Afreen S, Fatma T (2018) Extraction, purification and characterization of phycoerythrin from *Michrochaete* and its biological activities. *Biocatal Agric Biotechnol* 13:84–89. <https://doi.org/10.1016/j.bcab.2017.11.012>
- Himeshima N, Amao Y (2005) Green process for hydrogen production from cellulose derivative using visible light-harvesting function of Mg chlorophyll-a. *Green Chem* 7:742–746. <https://doi.org/10.1039/B504377H>
- Hsieh-Lo M, Castillo G, Ochoa-Becerra MA, Mojica L (2019) Phycocyanin and phycoerythrin: strategies to improve production yield and chemical stability. *Algal Res* 42:101600. <https://doi.org/10.1016/j.algal.2019.101600>
- Huang Y, Thomson SJ, Molin WT et al (2012) Early detection of soybean plant injury from glyphosate by measuring chlorophyll reflectance and fluorescence. *J Agric Sci* 4:p117. <https://doi.org/10.5539/JAS.V4N5P117>
- Huang C-H, Chen W-C, Gao Y-H et al (2021) Enzyme-assisted method for phycobiliproteins extraction from *Porphyra* and evaluation of their bioactivity. *Processes* 9:560. <https://doi.org/10.3390/pr9030560>
- Husu I, Rodio G, Touloupakis E et al (2013) Insights into photo-electrochemical sensing of herbicides driven by *Chlamydomonas reinhardtii* cells. *Sens Actuators B Chem* 185:321–330. <https://doi.org/10.1016/J.SNB.2013.05.013>
- Ismail MM, Osman MEH (2016) Seasonal fluctuation of photosynthetic pigments of most common red seaweeds species collected from Abu Qir, Alexandria, Egypt. *Rev Biol Mar Oceanogr* 51:515–525. <https://doi.org/10.4067/S0718-19572016000300004>
- Jaesche DP, Teixeira IR, Marczak LDF, Mercali GD (2021) Phycocyanin from *Spirulina*: a review of extraction methods and stability. *Food Res Int* 143:110314. <https://doi.org/10.1016/j.foodres.2021.110314>
- Janarthanan M, Senthil Kumar M (2017) The properties of bioactive substances obtained from seaweeds and their applications in textile industries. *J Ind Text* 48:361–401. <https://doi.org/10.1177/1528083717692596>
- Jesumani V, Du H, Aslam M et al (2019) Potential use of seaweed bioactive compounds in skin-care – a review. *Mar Drugs* 17:688. <https://doi.org/10.3390/MD17120688>
- Jesús VC, Gutiérrez-Rebolledo GA, Hernández-Ortega M et al (2016) Methods for extraction, isolation and purification of C-phycoerythrin: 50 years of research in review. *Int J Food Nutr Sci* 3:275–284. <https://doi.org/10.15436/2377-0619.16.946>

- Jiang L, Wang Y, Yin Q et al (2017) Phycocyanin: a potential drug for cancer treatment. *J Cancer* 8:3416–3429. <https://doi.org/10.7150/jca.21058>
- Kalasaraya HS, Pereira L, Patel NB (2022) Pioneering role of marine macroalgae in cosmeceuticals. *Phycology* 2:172–203. <https://doi.org/10.3390/PHYCOLOGY2010010>
- Kannaujiya VK, Sundaram S, Sinha RP (2017) *Phycobiliproteins: recent developments and future applications*, 1st edn. Springer Singapore, Singapore
- Kannaujiya VK, Kumar D, Singh V, Sinha RP (2021) Advances in phycobiliproteins research: innovations and commercialization. In: Sinha RP, Häder D-P (eds) *Natural bioactive compounds: technological advancements*. Academic Press, London, pp 57–81
- Karpiński TM, Adamczak A (2019) Fucoxanthin—an antibacterial carotenoid. *Antioxidants* 8. [https://doi.org/10.3390/ANTIOX8080239/ANTIOXIDANTS\\_08\\_00239\\_PDF.PDF](https://doi.org/10.3390/ANTIOX8080239/ANTIOXIDANTS_08_00239_PDF.PDF)
- Kasanah N, Ulfah M, Imania O et al (2022) Rhodophyta as potential sources of photoprotectants, anti-photoaging compounds, and hydrogels for cosmeceutical application. *Molecules* 27:7788. <https://doi.org/10.3390/MOLECULES27227788>
- Kato K, Shinoda T, Nagao R et al (2020) Structural basis for the adaptation and function of chlorophyll *f* in photosystem I. *Nat Commun* 11:238. <https://doi.org/10.1038/S41467-019-13898-5>
- Koizumi J, Takatani N, Kobayashi N et al (2018) Carotenoid profiling of a red seaweed *Pyropia yezoensis*: insights into biosynthetic pathways in the order Bangiales. *Mar Drugs* 16:1–14. <https://doi.org/10.3390/md16110426>
- Koo SY, Cha KH, Song DG et al (2012) Optimization of pressurized liquid extraction of zeaxanthin from *Chlorella ellipsoidea*. *J Appl Phycol* 24:725–730. <https://doi.org/10.1007/s10811-011-9691-2>
- Krinsky NI, Johnson EJ (2005) Carotenoid actions and their relation to health and disease. *Mol Asp Med* 26:459–516. <https://doi.org/10.1016/j.mam.2005.10.001>
- Kuddus M, Singh P, Thomas G, Al-Hazimi A (2013) Recent developments in production and biotechnological applications of C-phycocyanin. *Biomed Res Int* 2013:742859. <https://doi.org/10.1155/2013/742859>
- Kulczyński B, Gramza-Michałowska A, Kobus-Cisowska J, Kmiecik D (2017) The role of carotenoids in the prevention and treatment of cardiovascular disease – current state of knowledge. *J Funct Foods* 38:45–65. <https://doi.org/10.1016/j.jff.2017.09.001>
- Lamers PP, Janssen M, De Vos RCH et al (2008) Exploring and exploiting carotenoid accumulation in *Dunaliella salina* for cell-factory applications. *Trends Biotechnol* 26:631–638
- Lanfer-Marquez UM, Barros RMC, Sinnecker P (2005) Antioxidant activity of chlorophylls and their derivatives. *Food Res Int* 38:885–891. <https://doi.org/10.1016/j.foodres.2005.02.012>
- Larkum AWD, Grossman AR, Raven JA (2021) *Photosynthesis in algae: biochemical and physiological mechanisms*. Springer International Publishing, New York
- Le Guillard C, Dumay J, Donnay-Moreno C et al (2015) Ultrasound-assisted extraction of R-phycoerythrin from *Grateloupia turuturu* with and without enzyme addition. *Algal Res* 12:522–528. <https://doi.org/10.1016/j.algal.2015.11.002>
- Leandro A, Pereira L, Gonçalves AMM (2020) Diverse applications of marine macroalgae. *Mar Drugs* 18:1–15. <https://doi.org/10.3390/md18010017>
- Lee D, Nishizawa M, Shimizu Y, Saeki H (2017) Anti-inflammatory effects of dulse (*Palmaria palmata*) resulting from the simultaneous water-extraction of phycobiliproteins and chlorophyll a. *Food Res Int* 100:514–521. <https://doi.org/10.1016/j.foodres.2017.06.040>
- Lee HG, Lu YA, Je JG et al (2021a) Effects of ethanol extracts from *Grateloupia elliptica*, a red seaweed, and its chlorophyll derivative on 3T3-L1 adipocytes: suppression of lipid accumulation through downregulation of adipogenic protein expression. *Mar Drugs* 19:91. <https://doi.org/10.3390/MD19020091>
- Lee MC, Yeh HY, Jhang FJ et al (2021b) Enhancing growth, phycoerythrin production, and pigment composition in the red alga *Colaconema* sp. through optimal environmental conditions in an indoor system. *Bioresour Technol* 333:125199. <https://doi.org/10.1016/J.BIORTECH.2021.125199>

- Lee PT, Yeh HY, Lung WQC et al (2021c) R-phycoerythrin from *Colaconema formosanum* (Rhodophyta), an anti-allergic and collagen promoting material for cosmeceuticals. Appl Sci (Switzerland) 11:9425. <https://doi.org/10.3390/APP11209425>
- Leney AC, Tschanz A, Heck AJR (2018) Connecting color with assembly in the fluorescent B-phycoerythrin protein complex. FEBS J 285:178–187. <https://doi.org/10.1111/febs.14331>
- Li W, Su HN, Pu Y et al (2019a) Phycobiliproteins: molecular structure, production, applications, and prospects. Biotechnol Adv 37:340–353. <https://doi.org/10.1016/j.biotechadv.2019.01.008>
- Li Y, Song H, Zhou L et al (2019b) Tracking chlorophyll fluorescence as an indicator of drought and rewatering across the entire leaf lifespan in a maize field. Agric Water Manag 211:190–201. <https://doi.org/10.1016/j.agwat.2018.09.050>
- Li N, Liu Z, Wang P et al (2022) Effects of sodium hypochlorite treatment on the chlorophyll fluorescence in photosystem II of microalgae. Sci Total Environ 833:155192. <https://doi.org/10.1016/j.scitotenv.2022.155192>
- Lim KC, Yusoff FM, Shariff M, Kamarudin MS (2018) Astaxanthin as feed supplement in aquatic animals. Rev Aquac 10:738–773. <https://doi.org/10.1111/RAQ.12200>
- Lin A, Shen S, Wang G et al (2011) Comparison of chlorophyll and photosynthesis parameters of floating and attached *Ulva prolifera*. J Integr Plant Biol 53:25–34. <https://doi.org/10.1111/j.1744-7909.2010.01002.x>
- Liu Q, Wang Y, Cao M et al (2015) Anti-allergic activity of R-phycoerythrin from *Porphyra haitanensis* in antigen-sensitized mice and mast cells. Int Immunopharmacol 25:465–473. <https://doi.org/10.1016/j.intimp.2015.02.032>
- Liu Q, Huang Y, Zhang R et al (2016) Medical application of *Spirulina platensis* derived C-phycoerythrin. Evid Based Complement Alternat Med 2016. <https://doi.org/10.1155/2016/7803846>
- Liu Z, Sun X, Sun X et al (2019) Fucoxanthin isolated from *Undaria pinnatifida* can interact with *Escherichia coli* and *Lactobacilli* in the intestine and inhibit the growth of pathogenic bacteria. J Ocean Univ China 18:926–932. <https://doi.org/10.1007/s11802-019-4019-y>
- Liu Z, Li W, Xu Z et al (2022) Effects of different nitrogen forms and concentrations on seedling growth traits and physiological characteristics of *Populus simonii* × *P. nigra*. J For Res (Harbin) 33:1593–1606. <https://doi.org/10.1007/S11676-021-01447-0>
- Long JR, Ma GH, Wan YZ et al (2013) Effects of nitrogen fertilizer level on chlorophyll fluorescence characteristics in flag leaf of super hybrid rice at late growth stage. Rice Sci 20:220–228. [https://doi.org/10.1016/S1672-6308\(13\)60138-9](https://doi.org/10.1016/S1672-6308(13)60138-9)
- Lourenço-Lopes C, Carreira-Casais A, Carperna M et al (2023) Emerging technologies to extract fucoxanthin from *Undaria pinnatifida*: microwave vs. ultrasound assisted extractions. Mar Drugs 21:282. <https://doi.org/10.3390/md21050282>
- Lüder UH, Knoetzel J, Wiencke C (2001) Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic antarctic red macroalga *Palmaria decipiens*. Polar Biol 24:231–236. <https://doi.org/10.1007/s003000100260>
- Lumbessy SY, Junaidi M, Diniarti N et al (2021) Identification of chlorophyll pigment on *Gracilaria salicornia* seaweed. IOP Conf Ser Earth Environ Sci 681:12017. <https://doi.org/10.1088/1755-1315/681/1/012017>
- Ma L, Lin XM (2010) Effects of lutein and zeaxanthin on aspects of eye health. J Sci Food Agric 90:2–12. <https://doi.org/10.1002/jsfa.3785>
- Ma J, Hu J, Sha X et al (2022) Phycobiliproteins, the pigment-protein complex form of natural food colorants and bioactive ingredients. Crit Rev Food Sci Nutr 4:1–19. <https://doi.org/10.1080/10408398.2022.2128714>
- MacColl R, Eisele LE, Williams EC, Bowser SS (1996) The discovery of a novel R-phycoerythrin from an Antarctic red alga. J Biol Chem 271:17157–17160. <https://doi.org/10.1074/jbc.271.29.17157>
- Maeda H, Fukuda S, Izumi H, Saga N (2018) Anti-oxidant and fucoxanthin contents of brown alga *Ishimozuku (Sphaerotrichia divaricata)* from the West Coast of Aomori, Japan. Mar Drugs 16:0255. <https://doi.org/10.3390/md16080255>

- Malairaj S, Muthu S, Gopal VB et al (2016) Qualitative and quantitative determination of R-phycoerythrin from *Halymenia floresia* (Clemente) C. Agardh by polyacrylamide gel using electrophoretic elution technique. *J Chromatogr A* 1454:120–126. <https://doi.org/10.1016/j.chroma.2016.05.063>
- Mandal R, Dutta G (2020) From photosynthesis to biosensing: chlorophyll proves to be a versatile molecule. *Sens Int* 1:100058. <https://doi.org/10.1016/j.sintl.2020.100058>
- Manirafasha E, Guo L, Jing K (2020) Nutraceutical and pharmaceutical applications of phycobiliproteins. In: Jacob-Lopes E, Queiroz MI, Zepka LQ (eds) *Pigments from microalgae handbook*. Springer, Cham, pp 577–654
- Maoka T (2009) Recent progress in structural studies of carotenoids in animals and plants. *Arch Biochem Biophys* 483:191–195. <https://doi.org/10.1016/J.ABB.2008.10.019>
- Maoka T (2020) Carotenoids as natural functional pigments. *J Nat Med* 74:1–16. <https://doi.org/10.1007/s11418-019-01364-x>
- Marková I, Koničková R, Vaňková K et al (2020) Anti-angiogenic effects of the blue-green alga *Arthrospira platensis* on pancreatic cancer. *J Cell Mol Med* 24:2402–2415. <https://doi.org/10.1111/jcmm.14922>
- Martins M, Fernandes APM, Torres-Acosta MA et al (2023) Extraction of chlorophyll from wild and farmed *Ulva* spp. using aqueous solutions of ionic liquids. *Sep Purif Technol* 254:117589. <https://doi.org/10.1016/J.SEPPUR.2020.117589>
- Mayne ST (1996) Beta-carotene, carotenoids, and disease prevention in humans. *FASEB J* 10:690–701. <https://doi.org/10.1096/fasebj.10.7.8635686>
- Meléndez-Martínez AJ, Mandić AI, Bantis F et al (2020) A comprehensive review on carotenoids in foods and feeds: status quo, applications, patents, and research needs. *Crit Rev Food Sci Nutr* 5:1–51. <https://doi.org/10.1080/10408398.2020.1867959>
- Méresse S, Fodil M, Fleury F, Chénais B (2020) Fucoxanthin, a marine-derived carotenoid from brown seaweeds and microalgae: a promising bioactive compound for cancer therapy. *Int J Mol Sci* 21:1–27. <https://doi.org/10.3390/ijms21239273>
- Merz D, Geyer M, Moss DA, Ache HJ (1996) Chlorophyll fluorescence biosensor for the detection of herbicides. *Anal Bioanal Chem* 354:299–305. <https://doi.org/10.1007/S0021663540299>
- Miki W (1991) Biological functions and activities of animal carotenoids. *Pure Appl Chem* 63:141–146. <https://doi.org/10.1351/PAC199163010141/MACHINEREADABLECITATION/RIS>
- Ming JX, Wang ZC, Huang Y et al (2021) Fucoxanthin extracted from *Laminaria japonica* inhibits metastasis and enhances the sensitivity of lung cancer to Gefitinib. *J Ethnopharmacol* 265:113302. <https://doi.org/10.1016/j.jep.2020.113302>
- Mittal R, Raghavarao KSMS (2018) Extraction of R-Phycoerythrin from marine macroalgae, *Gelidium pusillum*, employing consortia of enzymes. *Algal Res* 34:1–11. <https://doi.org/10.1016/j.algal.2018.07.002>
- Mittal R, Tavanandi HA, Mantri VA, Raghavarao KSMS (2017) Ultrasound assisted methods for enhanced extraction of phycobiliproteins from marine macro-algae, *Gelidium pusillum* (Rhodophyta). *Ultrason Sonochem* 38:92–103. <https://doi.org/10.1016/j.ultsonch.2017.02.030>
- Mittal R, Sharma R, Raghavarao K (2019) Aqueous two-phase extraction of R-Phycoerythrin from marine macro-algae, *Gelidium pusillum*. *Bioresour Technol* 280:277–286. <https://doi.org/10.1016/j.biortech.2019.02.044>
- Morais T, Cotas J, Pacheco D, Pereira L (2021) Seaweeds compounds: an eco-sustainable source of cosmetic ingredients? *Cosmetics* 8:8. <https://doi.org/10.3390/COSMETICS8010008>
- Morocho-Jácome AL, Ruscinc N, Martinez RM et al (2020) (Bio)Technological aspects of microalgae pigments for cosmetics. *Appl Microbiol Biotechnol* 104:9513–9522. <https://doi.org/10.1007/s00253-020-10936-x>
- Munier M, Jubeau S, Wijaya A et al (2014) Physicochemical factors affecting the stability of two pigments: R-phycoerythrin of *Grateloupia turuturu* and B-phycoerythrin of *Porphyridium cruentum*. *Food Chem* 150:400–407. <https://doi.org/10.1016/j.foodchem.2013.10.113>
- Munier M, Moranchais M, Dumay J et al (2015) One-step purification of R-phycoerythrin from the red edible seaweed *Grateloupia turuturu*. *J Chromatogr B Analyt Technol Biomed Life Sci* 992:23–29. <https://doi.org/10.1016/j.jchromb.2015.04.012>

- Muñoz-Miranda LA, Iñiguez-Moreno M (2023) An extensive review of marine pigments: sources, biotechnological applications, and sustainability. *Aquat Sci* 85:68. <https://doi.org/10.1007/s00027-023-00966-8>
- Muradian Kh, Vaiserman A, Min K-J, Fraifeld VE (2015) Fucoxanthin and lipid metabolism: A minireview. *Nutr Metab Cardiovasc Dis* 25:891–897. <https://doi.org/10.1016/j.numecd.2015.05.010>
- Murillo AG, Hu S, Fernandez ML (2019) Zeaxanthin: metabolism, properties, and antioxidant protection of eyes, heart, liver, and skin. *Antioxidants* 8:390. <https://doi.org/10.3390/antiox8090390>
- Murray MT, Capelli B (2020)  $\beta$ -carotene and other carotenoids. In: *Textbook of natural medicine*, pp 443–450.e2. <https://doi.org/10.1016/B978-0-323-43044-9.00057-1>
- Mysliwa-Kurczel B, Solymosi K (2016) Phycobilins and phycobiliproteins used in food industry and medicine. *Mini-Rev Med Chem* 17:1173–1193. <https://doi.org/10.2174/1389557516666160912180155>
- Nagaraj S, Arulmurugan P, Rajaram MG et al (2012) Hepatoprotective and antioxidative effects of C-phycoerythrin from *Arthrospira maxima* SAG 25780 in CCl<sub>4</sub>-induced hepatic damage rats. *Biomed Prev Nutr* 2:81–85. <https://doi.org/10.1016/j.bionut.2011.12.001>
- Nakano T, Wiegertjes G (2020) Properties of carotenoids in fish fitness: a review. *Mar Drugs* 18. <https://doi.org/10.3390/MD18110568>
- Nawaz A, Chaudhary R, Shah Z et al (2020) An overview on industrial and medical applications of bio-pigments synthesized by marine bacteria. *Microorganisms* 9:1–24. <https://doi.org/10.3390/MICROORGANISMS9010011>
- Nazarudin MF, Isha A, Mastuki SN et al (2020) Chemical composition and evaluation of the  $\alpha$ -glucosidase inhibitory and cytotoxic properties of marine algae *Ulva intestinalis*, *Halimeda macroloba*, and *Sargassum ilicifolium*. *Evid Based Complement Alternat Med* 2020:2753945. <https://doi.org/10.1155/2020/2753945>
- Nguyen HPT, Morançais M, Fleurence J, Dumay J (2017) *Mastocarpus stellatus* as a source of R-phycoerythrin: optimization of enzyme assisted extraction using response surface methodology. *J Appl Phycol* 29:1563–1570. <https://doi.org/10.1007/s10811-016-1024-z>
- Nguyen HPT, Morançais M, Déléris P et al (2020) Purification of R-phycoerythrin from a marine macroalga *Gracilaria gracilis* by anion-exchange chromatography. *J Appl Phycol* 32:553–561. <https://doi.org/10.1007/s10811-019-01947-x>
- Niu JF, Chen ZF, Wang GC, Zhou BC (2010) Purification of phycoerythrin from *Porphyra yezoensis* Ueda (Bangiales, Rhodophyta) using expanded bed absorption. *J Appl Phycol* 22:25–31. <https://doi.org/10.1007/s10811-009-9420-2>
- Niu J, Xu M, Wang G et al (2013) Comprehensive extraction of agar and R-phycoerythrin from *Gracilaria lemaneiformis* (Bangiales, Rhodophyta). *Indian J Mar Sci* 42:21–28
- Nomura M, Kamogawa H, Susanto E et al (2013) Seasonal variations of total lipids, fatty acid composition, and fucoxanthin contents of *Sargassum horneri* (Turner) and *Cystoseira hakodatensis* (Yendo) from the northern seashore of Japan. *J Appl Phycol* 25:1159–1169. <https://doi.org/10.1007/s10811-012-9934-x>
- Noviendri D, Hasrini RF, Subaryono, Marraskuranto E (2022) Biopigments (phycoerythrin, fucoxanthin and siphonaxanthin) from seaweeds and their potential applications as ingredients in cosmeceutical industries: a review. *IOP Conf Ser Earth Environ Sci* 1118:012028. <https://doi.org/10.1088/1755-1315/1118/1/012028>
- Nowruzi B, Konur O, Amir S, Anvar A (2022) The stability of the phycobiliproteins in the adverse environmental conditions relevant to the food storage. *Food Bioprocess Technol* 15:2646–2663. <https://doi.org/10.1007/s11947-022-02855-8>
- O'Connor I, O'Brien N (1998) Modulation of UVA light-induced oxidative stress by beta-carotene, lutein and astaxanthin in cultured fibroblasts. *J Dermatol Sci* 16:226–230. [https://doi.org/10.1016/s0923-1811\(97\)00058-3](https://doi.org/10.1016/s0923-1811(97)00058-3)
- Ogashawara I (2020) Determination of phycocyanin from space—a bibliometric analysis. *Remote Sens* 12:567. <https://doi.org/10.3390/rs12030567>

- Ojulari OV, Gi Lee S, Nam JO (2020) Therapeutic effect of seaweed derived xanthophyl carotenoid on obesity management; overview of the last decade. *Int J Mol Sci* 21:2502. <https://doi.org/10.3390/ijms21072502>
- Online Etymology Dictionary Photosynthesis | Etymology, origin and meaning of photosynthesis by etymonline. <https://www.etymonline.com/word/photosynthesis>. Accessed 13 Apr 2023
- Osório C, Machado S, Peixoto J et al (2020) Pigments content (Chlorophylls, fucoxanthin and phycobiliproteins) of different commercial dried algae. *Separations* 7:1–14. <https://doi.org/10.3390/separations7020033>
- Padhi B, Chauhan G, Kandoi D et al (2021) A comparison of chlorophyll fluorescence transient measurements, using handy pea and fluorpen fluorometers. *Photosynthetica* 59:399–408. <https://doi.org/10.32615/PS.2021.026>
- Pádua D, Rocha E, Gargiulo D, Ramos AA (2015) Bioactive compounds from brown seaweeds: phloroglucinol, fucoxanthin and fucoidan as promising therapeutic agents against breast cancer. *Phytochem Lett* 14:91–98. <https://doi.org/10.1016/j.phytol.2015.09.007>
- Pagels F, Guedes AC, Amaro HM et al (2019) Phycobiliproteins from cyanobacteria: chemistry and biotechnological applications. *Biotechnol Adv* 37:422–443. <https://doi.org/10.1016/j.biotechadv.2019.02.010>
- Pangestuti R, Kim SK (2011a) Neuroprotective effects of marine algae. *Mar Drugs* 9:803–818. <https://doi.org/10.3390/MD9050803>
- Pangestuti R, Kim SK (2011b) Biological activities and health benefit effects of natural pigments derived from marine algae. *J Funct Foods* 3:255–266. <https://doi.org/10.1016/j.jff.2011.07.001>
- Park JJ, Lee WY (2021) Anti-glycation effects of brown algae extracts and its phenolic compounds. *Food Biosci* 41:101042. <https://doi.org/10.1016/J.FBIO.2021.101042>
- Park HJ, Lee MK, Park YB et al (2011) Beneficial effects of *Undaria pinnatifida* ethanol extract on diet-induced-insulin resistance in C57BL/6J mice. *Food Chem Toxicol* 49:727–733. <https://doi.org/10.1016/j.fct.2010.11.032>
- Patel AS, Lakshmi-balasubramaniam SP, Nayak B (2020) Steric stabilization of phycobiliprotein loaded liposome through polyethylene glycol adsorbed cellulose nanocrystals and their impact on the gastrointestinal tract. *Food Hydrocoll* 98:105252. <https://doi.org/10.1016/j.foodhyd.2019.105252>
- Patel SN, Sonani RR, Roy D et al (2022) Exploring the structural aspects and therapeutic perspectives of cyanobacterial phycobiliproteins. *3 Biotech* 12(9):1–15. <https://doi.org/10.1007/S13205-022-03284-2>
- Pattarayan D, Rajarajan D, Ayyanar S et al (2017) C-phycoyanin suppresses transforming growth factor- $\beta$ 1-induced epithelial mesenchymal transition in human epithelial cells. *Pharmacol Rep* 69:426–431. <https://doi.org/10.1016/j.pharep.2016.12.013>
- Peguero-Pina JJ, Morales F, Gil-Pelegrín E (2008) Frost damage in *Pinus sylvestris* L. stems assessed by chlorophyll fluorescence in cortical bark chlorenchyma. *Ann For Sci* 65:813–813. <https://doi.org/10.1051/FOREST:2008068/METRICS>
- Pemberton RM, Amine A, Hart JP (2007) Voltammetric behavior of chlorophyll a at a screen-printed carbon electrode and its potential role as a biomarker for monitoring fecal contamination. *Anal Lett* 37:1625–1643. <https://doi.org/10.1081/AL-120037592>
- Peng J, Yuan JP, Wu CF, Wang JH (2011) Fucoxanthin, a marine carotenoid present in brown seaweeds and diatoms: metabolism and bioactivities relevant to human health. *Mar Drugs* 9:1806–1828. <https://doi.org/10.3390/md9101806>
- Pereira L (2011) A review of the nutrient composition of selected edible seaweeds. In: Pomin VH (ed) *Seaweed: ecology, nutrient composition and medicinal uses*, 1st edn. Nova Science Publishers, Inc., Coimbra, pp 15–47
- Pereira L (2016) *Edible seaweeds of the world*, 1st edn. CRC Press, Boca Raton
- Pereira L (2018) Nutritional composition of the main edible algae. In: Pereira L (ed) *Therapeutic and nutritional uses of algae*. CRC Press, Boca Raton, pp 65–127
- Pereira L (2021) Macroalgae. *Encyclopedia* 1:177–188. <https://doi.org/10.3390/ENCYCLOPEDIA1010017>

- Pereira L (2023) Atlantic algae as food and their extracts. *Explor Foods Foodomics* 1:15–31. <https://doi.org/10.37349/EFF.2023.00003>
- Pereira L, Neto JM (2015) Marine algae – biodiversity, taxonomy, environmental assessment, and biotechnology, 1st edn. CRC Press, Boca Raton
- Pereira L, Valado A (2021) The seaweed diet in prevention and treatment of the neurodegenerative diseases. *Mar Drugs* 19:1–25. <https://doi.org/10.3390/md19030128>
- Pereira T, Barroso S, Mendes S et al (2020) Optimization of phycobiliprotein pigments extraction from red algae *Gracilaria gracilis* for substitution of synthetic food colorants. *Food Chem* 321:126688. <https://doi.org/10.1016/j.foodchem.2020.126688>
- Pereira AG, Otero P, Echave J et al (2021) Xanthophylls from the sea: algae as source of bioactive carotenoids. *Mar Drugs* 19:188. <https://doi.org/10.3390/MD19040188>
- Pérez-Gálvez A, Viera I, Roca M (2020) Carotenoids and chlorophylls as antioxidants. *Antioxidants* 9:505. <https://doi.org/10.3390/antiox9060505>
- Pérez-Lloréns JL, Mouritsen OG, Rhatigan P et al (2020) Seaweeds in mythology, folklore, poetry, and life. *J Appl Phycol* 32:3157–3182. <https://doi.org/10.1007/s10811-020-02133-0>
- Phan MAT, Bucknall M, Arcot J (2018) Interactive effects of  $\beta$ -carotene and anthocyanins on cellular uptake, antioxidant activity and anti-inflammatory activity in vitro and ex vivo. *J Funct Foods* 45:129–137. <https://doi.org/10.1016/j.jff.2018.03.021>
- Piniella-Matamoros B, Marín-Prida J, Pentón-Rol G (2021) Nutraceutical and therapeutic potential of Phycocyanobilin for treating Alzheimer’s disease. *J Biosci* 46:1–16. <https://doi.org/10.1007/s12038-021-00161-7>
- Poojary MM, Barba FJ, Aliakbarian B et al (2016) Innovative alternative technologies to extract carotenoids from microalgae and seaweeds. *Mar Drugs* 14:214. <https://doi.org/10.3390/md14110214>
- Prado JM, Veggi PC, Náthia-Neves G, Meireles MAA (2018) Extraction methods for obtaining natural blue colorants. *Curr Anal Chem* 16:504–532. <https://doi.org/10.2174/1573411014666181115125740>
- Puzorjov A, McCormick AJ (2020) Phycobiliproteins from extreme environments and their potential applications. *J Exp Bot* 71:3827–3842. <https://doi.org/10.1093/JXB/ERAA139>
- Qiang X, Wang L, Niu J et al (2021) Phycobiliprotein as fluorescent probe and photosensitizer: a systematic review. *Int J Biol Macromol* 193:1910–1917. <https://doi.org/10.1016/J.IJBIOMAC.2021.11.022>
- Quitério E, Soares C, Ferraz R et al (2021) Marine health-promoting compounds: recent trends for their characterization and human applications. *Food Secur* 10:3100. <https://doi.org/10.3390/FOODS10123100>
- Ragusa I, Nardone GN, Zanatta S et al (2021) Spirulina for skin care: a bright blue future. *Cosmetics* 8:7. <https://doi.org/10.3390/cosmetics8010007>
- Rapoport A, Guzhova I, Bernetti L et al (2021) Carotenoids and some other pigments from fungi and yeasts. *Metabolites* 11:92. <https://doi.org/10.3390/metabo11020092>
- Resende ACR, Pereira R, Nunes C et al (2023) Photosynthetic pigment and carbohydrate profiling of *Fucus vesiculosus* from an Iberian Coastal Lagoon. *Plants* 12:1324. <https://doi.org/10.3390/plants12061324>
- Robertson RC, Guihéneuf F, Bahar B et al (2015) The anti-inflammatory effect of algae-derived lipid extracts on lipopolysaccharide (LPS)-stimulated human THP-1 macrophages. *Mar Drugs* 13:5402–5424. <https://doi.org/10.3390/md13085402>
- Rodriguez-Amaya DB (2015) Food carotenoids: chemistry, biology and technology. Wiley-Blackwell, Chichester
- Rodriguez-Amaya D, Kimura M (2004) HarvestPlus handbook for carotenoid analysis. HarvestPlus, Washington DC
- Román RB, Álvarez-Pez JM, Fernández FGA, Grima EM (2002) Recovery of pure B-phycoerythrin from the microalga *Porphyridium cruentum*. *J Biotechnol* 93:73–85. [https://doi.org/10.1016/S0168-1656\(01\)00385-6](https://doi.org/10.1016/S0168-1656(01)00385-6)

- Rossano R, Ungaro N, D'Ambrosio A et al (2003) Extracting and purifying R-phycoerythrin from Mediterranean red algae *Corallina elongata* Ellis & Solander. *J Biotechnol* 101:289–293. [https://doi.org/10.1016/S0168-1656\(03\)00002-6](https://doi.org/10.1016/S0168-1656(03)00002-6)
- Rula NAM, Ganzon-Fortes ET, Pante MJR, Trono GC (2021) Influence of light, water motion, and stocking density on the growth and pigment content of *Halymenia durvillei* (Rhodophyceae) under laboratory conditions. *J Appl Phycol* 33:2367–2377. <https://doi.org/10.1007/S10811-021-02474-4/FIGURES/6>
- Saha SK, Ermis H, Murray P (2020) Marine microalgae for potential lutein production. *Appl Sci (Switzerland)* 10:6457. <https://doi.org/10.3390/APP10186457>
- Sahin SC (2018) The potential of *Arthrospira platensis* extract as a tyrosinase inhibitor for pharmaceutical or cosmetic applications. *S Afr J Bot* 119:236–243. <https://doi.org/10.1016/j.sajb.2018.09.004>
- Saiki Y, Amao Y (2002) Visible light induced biohydrogen production from sucrose using the photosensitization of Mg chlorophyll-a. *Bioconjug Chem* 13:898–901. <https://doi.org/10.1021/BC025506G/ASSET/IMAGES/LARGE/BC025506GF00004.JPEG>
- Saini RK, Keum YS (2018) Carotenoid extraction methods: a review of recent developments. *Food Chem* 240:90–103. <https://doi.org/10.1016/j.foodchem.2017.07.099>
- Sajilata MG, Singhal RS, Kamat MY (2008) The carotenoid pigment zeaxanthin – a review. *Compr Rev Food Sci Food Saf* 7:29–49. <https://doi.org/10.1111/j.1541-4337.2007.00028.x>
- Saluri M, Kaldmäe M, Tuvikene R (2019) Extraction and quantification of phycobiliproteins from the red alga *Furcellaria lumbricalis*. *Algal Res* 37:115–123. <https://doi.org/10.1016/j.algal.2018.11.013>
- Saluri M, Kaldmäe M, Tuvikene R (2020) Reliable quantification of R-phycoerythrin from red algal crude extracts. *J Appl Phycol* 32:1421–1428. <https://doi.org/10.1007/s10811-019-01968-6>
- Samarasinghe N, Fernando S, Lacey R, Faulkner WB (2012) Algal cell rupture using high pressure homogenization as a prelude to oil extraction. *Renew Energy* 48:300–308. <https://doi.org/10.1016/J.RENENE.2012.04.039>
- Sanders CA, Rodriguez M, Greenbaum E (2001) Stand-off tissue-based biosensors for the detection of chemical warfare agents using photosynthetic fluorescence induction. *Biosens Bioelectron* 16:439–446. [https://doi.org/10.1016/S0956-5663\(01\)00158-0](https://doi.org/10.1016/S0956-5663(01)00158-0)
- Sano F, Murata K, Niwa K (2020) Identification, growth, and pigment content of a spontaneous green mutant of *Pyropia kinositae* (Bangiales, Rhodophyta). *J Appl Phycol* 32:1983–1994. <https://doi.org/10.1007/S10811-020-02085-5/TABLES/1>
- Schächtl J, Huber G, Maidl FX et al (2005) Laser-induced chlorophyll fluorescence measurements for detecting the nitrogen status of wheat (*Triticum aestivum* L.) canopies. *Precis Agric* 6:143–156. <https://doi.org/10.1007/S11119-004-1031-Y/METRICS>
- Schepers M, Martens N, Tiane A et al (2020) Edible seaweed-derived constituents: an undisclosed source of neuroprotective compounds. *Neural Regen Res* 15:790–795. <https://doi.org/10.4103/1673-5374.268894>
- Schubert N, García-Mendoza E, Pacheco-Ruiz I (2006) Carotenoid composition of marine red algae. *J Phycol* 42:1208–1216. <https://doi.org/10.1111/j.1529-8817.2006.00274.x>
- Schubert D, Currais A, Goldberg J et al (2018) Geroneuroprotectors: effective geroprotectors for the brain. *Trends Pharmacol Sci* 39:1004–1007
- Sekar S, Chandramohan M (2008) Phycobiliproteins as a commodity: trends in applied research, patents and commercialization. *J Appl Phycol* 20:113–136. <https://doi.org/10.1007/s10811-007-9188-1>
- Sen S, Mallick N (2021) Mycosporine-like amino acids: algal metabolites shaping the safety and sustainability profiles of commercial sunscreens. *Algal Res* 58:102425. <https://doi.org/10.1016/J.ALGAL.2021.102425>
- Seyed Yagoubi A, Shahidi F, Mohebbi M et al (2017) Preparation, characterization and evaluation of physicochemical properties of phycocyanin-loaded solid lipid nanoparticles and nanostructured lipid carriers. *J Food Meas Charact* 1:378–385. <https://doi.org/10.1007/S11694-017-9650-Y>

- Sfriso AA, Gallo M, Baldi F (2018) Phycoerythrin productivity and diversity from five red macroalgae. *J Appl Phycol* 30:2523–2531. <https://doi.org/10.1007/s10811-018-1440-3>
- Shi XM, Jiang Y, Chen F (2002) High-yield production of lutein by the green microalga *Chlorella protothecoides* in heterotrophic fed-batch culture. *Biotechnol Prog* 18:723–727. <https://doi.org/10.1021/bp0101987>
- Shih SR, Tsai KN, Li YS et al (2003) Inhibition of enterovirus 71-induced apoptosis by allophycocyanin isolated from a blue-green alga *Spirulina platensis*. *J Med Virol* 70:119–125. <https://doi.org/10.1002/jmv.10363>
- Sies H, Stahl W (2004) Nutritional protection against skin damage from sunlight. *Annu Rev Nutr* 24:173–200. <https://doi.org/10.1146/annurev.nutr.24.012003.132320>
- Silva SC, Ferreira ICFR, Dias MM, Filomena Barreiro M (2020) Microalgae-derived pigments: a 10-year bibliometric review and industry and market trend analysis. *Molecules* 25:3406. <https://doi.org/10.3390/molecules25153406>
- Singh A, Ahmad S, Ahmad A (2015) Green extraction methods and environmental applications of carotenoids—a review. *RSC Adv* 5. <https://doi.org/10.1039/c5ra10243j>
- Solymsi K, Mysliwa-Kurdziel B (2016) Chlorophylls and their derivatives used in food industry and medicine. *Mini-Rev Med Chem* 17:1194–1222. <https://doi.org/10.2174/1389557516666161004161411>
- Sonani RR, Rastogi RP, Patel R, Madamwar D (2016) Recent advances in production, purification and applications of phycobiliproteins. *World J Biol Chem* 7:100. <https://doi.org/10.4331/WJBC.V7.I1.100>
- Sorrenti V, Davinelli S, Scapagnini G et al (2020) Astaxanthin as a putative geroprotector: molecular basis and focus on brain aging. *Mar Drugs* 18:351
- Soulier N, Bryant DA (2021) The structural basis of far-red light absorbance by allophycocyanins. *Photosynth Res* 147:11–26. <https://doi.org/10.1007/s1120-020-00787-y>
- Souza JMC, Castro JZ, Critchley AT, Yokoya NS (2019) Physiological responses of the red algae *Gracilaria caudata* (Gracilariales) and *Laurencia catarinensis* (Ceramiales) following treatment with a commercial extract of the brown alga *Ascophyllum nodosum* (AMPEP). *J Appl Phycol* 31:1883–1888. <https://doi.org/10.1007/S10811-018-1683-Z/FIGURES/4>
- Stahl W, Sies H (2005) Bioactivity and protective effects of natural carotenoids. *Biochim Biophys Acta Mol basis Dis* 1740:101–107. <https://doi.org/10.1016/j.bbadis.2004.12.006>
- Stahl W, Sies H (2012)  $\beta$ -Carotene and other carotenoids in protection from sunlight. *Am J Clin Nutr* 96:1179S–1184S. <https://doi.org/10.3945/AJCN.112.034819>
- Stefanov M, Rashkov G, Borisova P, Apostolova E (2023) Sensitivity of the photosynthetic apparatus in maize and sorghum under different drought levels. *Plants* 12:1863. <https://doi.org/10.3390/plants12091863>
- Sun H, Wang Y, He Y et al (2023) Microalgae-derived pigments for the food industry. *Mar Drugs* 21:82. <https://doi.org/10.3390/MD21020082>
- Swapnil P, Meena M, Singh SK et al (2021) Vital roles of carotenoids in plants and humans to deteriorate stress with its structure, biosynthesis, metabolic engineering and functional aspects. *Curr Plant Biol* 26:100203. <https://doi.org/10.1016/j.cpb.2021.100203>
- Takahashi S, Murata N (2008) How do environmental stresses accelerate photoinhibition? *Trends Plant Sci* 13:178–182. <https://doi.org/10.1016/j.tplants.2008.01.005>
- Takaichi S (2011) Carotenoids in algae: distributions, biosyntheses and functions. *Mar Drugs* 9:1101–1118. <https://doi.org/10.3390/md9061101>
- Takaichi S, Yokoyama A, Mochimaru M et al (2016) Carotenogenesis diversification in phylogenetic lineages of Rhodophyta. *J Phycol* 52:329–338. <https://doi.org/10.1111/jpy.12411>
- Takeuchi Y, Amao Y (2005) Biohydrogen production from sucrose using the light-harvesting function of zinc chlorophyll-a. *Bull Chem Soc Jpn* 78:622–625. <https://doi.org/10.1246/BCSJ.78.622>
- Talarico L, Maranzana G (2000) Light and adaptive responses in red macroalgae: an overview. *J Photochem Photobiol B* 56:1–11. [https://doi.org/10.1016/S1011-1344\(00\)00046-4](https://doi.org/10.1016/S1011-1344(00)00046-4)
- Thompson CC, Kruger RH, Thompson FL (2017) Unlocking marine biotechnology in the developing world. *Trends Biotechnol* 35:1119–1121. <https://doi.org/10.1016/J.TIBTECH.2017.08.005>

- Tomonou Y, Amao Y (2002) Visible light induced hydrogen production with Mg chlorophyll-a from spirulina and colloidal platinum. *Biometals* 15:391–395. <https://doi.org/10.1023/A:1020213122186>
- Torres PB, Chow F, Furlan CM et al (2014) Standardization of a protocol to extract and analyze chlorophyll a and carotenoids in *Gracilaria tenuistipitata* var. *liui*. Zhang and Xia (Rhodophyta). *Braz J Oceanogr* 62:57–63. <https://doi.org/10.1590/S1679-87592014068106201>
- Tung J, Goodwin PH, Hsiang T (2013) Chlorophyll fluorescence for quantification of fungal foliar infection and assessment of the effectiveness of an induced systemic resistance activator. *Eur J Plant Pathol* 136:301–315. <https://doi.org/10.1007/S10658-012-0164-5/FIGURES/8>
- Urrea-Victoria V, Galdes V, Pinto E, Castellanos L (2023) Photosynthetic pigments and photoprotective metabolites of Colombian pacific marine macroalgae in response to contrasting ultraviolet-index periods. *J Exp Mar Biol Ecol* 564. <https://doi.org/10.1016/J.JEMBE.2023.151908>
- Van Der Weij-De Wit CD, Doust AB, Van Stokkum IHM et al (2006) How energy funnels from the phycoerythrin antenna complex to photosystem I and photosystem II in cryptophyte *Rhodomonas* CS24 cells. *J Phys Chem B* 110:25066–25073. <https://doi.org/10.1021/jp061546w>
- van der Westhuizen MM, Oosterhuis DM, Berner JM, Boogaers N (2020) Chlorophyll a fluorescence as an indicator of heat stress in cotton (*Gossypium hirsutum* L.). *S Afr J Plant Soil* 37:116–119. <https://doi.org/10.1080/02571862.2019.1665721>
- Védrine C, Leclerc JC, Durrieu C, Tran-Minh C (2003) Optical whole-cell biosensor using *Chlorella vulgaris* designed for monitoring herbicides. *Biosens Bioelectron* 18:457–463. [https://doi.org/10.1016/S0956-5663\(02\)00157-4](https://doi.org/10.1016/S0956-5663(02)00157-4)
- Viera I, Pérez-Gálvez A, Roca M (2018) Bioaccessibility of marine carotenoids. *Mar Drugs* 16:397. <https://doi.org/10.3390/md16100397>
- Vílchez C, Forján E, Cuaresma M et al (2011) Marine carotenoids: biological functions and commercial applications. *Mar Drugs* 9:319–333. <https://doi.org/10.3390/md9030319>
- Vinothkanna A, Sekar S (2020) Diagnostic applications of phycobiliproteins. In: *Pigments from microalgae handbook*, pp 585–610. [https://doi.org/10.1007/978-3-030-50971-2\\_24](https://doi.org/10.1007/978-3-030-50971-2_24)
- Wang J, Sun J, Song Y et al (2013) A label-free microfluidic biosensor for activity detection of single microalgae cells based on chlorophyll fluorescence. *Sensors* 13:16075–16089. <https://doi.org/10.3390/S131216075>
- Wang L, Qu Y, Fu X et al (2014) Isolation, purification and properties of an R-phycoerythrin from the phycobilisomes of a marine red macroalga *Polysiphonia urceolata*. *PLoS One* 9:e101724. <https://doi.org/10.1371/journal.pone.0087833>
- Wang Z, Li G, Sun H et al (2018) Effects of drought stress on photosynthesis and photosynthetic electron transport chain in young apple tree leaves. *Biol Open* 7:bio035279. <https://doi.org/10.1242/BIO.035279>
- Wang C, Shen Z, Cui X et al (2020) Response surface optimization of enzyme-assisted extraction of R-phycoerythrin from dry *Pyropia yezoensis*. *J Appl Phycol* 32:1429–1440. <https://doi.org/10.1007/s10811-019-01963-x>
- Wells ML, Potin P, Craigie JS et al (2017) Algae as nutritional and functional food sources: revisiting our understanding. *J Appl Phycol* 29:949–982. <https://doi.org/10.1007/s10811-016-0974-5>
- Willcox DC, Scapagnini G, Willcox BJ (2014) Healthy aging diets other than the Mediterranean: a focus on the Okinawan diet. *Mech Ageing Dev* 136–137:148–162. <https://doi.org/10.1016/j.mad.2014.01.002>
- Wollina U, Voicu C, Gianfaldoni S et al (2018) *Arthrospira platensis* – potential in dermatology and beyond. *Open Access Maced J Med Sci* 6:176–180. <https://doi.org/10.3889/oamjms.2018.033>
- World Intellectual Property Organization (WIPO) (2016) Patent landscape report: microalgae-related technologies. *Patent Landscape Reports*
- World International Property Organization (2021) PATENTSCOPE. In: *Patentscope*. <https://www.wipo.int/patentscope/en/>. Accessed 7 Dec 2021

- Xie X, Lu X, Wang L et al (2020) High light intensity increases the concentrations of  $\beta$ -carotene and zeaxanthin in marine red macroalgae. *Algal Res* 47:101852. <https://doi.org/10.1016/j.algal.2020.101852>
- Xu DP, Li Y, Meng X et al (2017) Natural antioxidants in foods and medicinal plants: extraction, assessment and resources. *Int J Mol Sci* 18:96. <https://doi.org/10.3390/ijms18010096>
- Yabuta Y, Fujimura H, Kwak CS et al (2010) Antioxidant activity of the phycoerythrobilin compound formed from a dried Korean purple laver (*Porphyra* sp.) during *in vitro* digestion. *Food Sci Technol Res* 16:347–352. <https://doi.org/10.3136/fstr.16.347>
- Yabuzaki J (2017) Carotenoids database: structures, chemical fingerprints and distribution among organisms. Database 2017:bax004. <https://doi.org/10.1093/database/bax004>
- Yang EJ, Ham YM, Lee WJ et al (2013) Anti-inflammatory effects of apo-9'-fucoxanthinone from the brown alga, *Sargassum muticum*. *DARU, J Pharm Sci* 21:62. <https://doi.org/10.1186/2008-2231-21-62>
- Yang M, Xuan Z, Wang Q et al (2021) Fucoxanthin has potential for therapeutic efficacy in neurodegenerative disorders by acting on multiple targets. *Nutr Neurosci*:1–14. <https://doi.org/10.1080/1028415X.2021.1926140>
- Ye ZW, Jiang JG, Wu GH (2008) Biosynthesis and regulation of carotenoids in *Dunaliella*: progresses and prospects. *Biotechnol Adv* 26:352–360. <https://doi.org/10.1016/j.biotechadv.2008.03.004>
- Ye KX, Fan TT, Keen LJ, Han BN (2019) A review of pigments derived from marine natural products. *Isr J Chem* 59:327–338. <https://doi.org/10.1002/ijch.201800154>
- Yuan Y, Zhang J, Fan J et al (2018) Microwave assisted extraction of phenolic compounds from four economic brown macroalgae species and evaluation of their antioxidant activities and inhibitory effects on  $\alpha$ -amylase,  $\alpha$ -glucosidase, pancreatic lipase and tyrosinase. *Food Res Int* 113:288–297. <https://doi.org/10.1016/J.FOODRES.2018.07.021>
- Zerres S, Stahl W (2020) Carotenoids in human skin. *Biochim Biophys Acta Mol Cell Biol Lipids* 1865:158588. <https://doi.org/10.1016/J.BBALIP.2019.158588>
- Zhao P, Wang X, Niu J et al (2020) Agar extraction and purification of R-phycoerythrin from *Gracilaria tenuistipitata*, and subsequent wastewater treatment by *Ulva prolifera*. *Algal Res* 47:101862. <https://doi.org/10.1016/j.algal.2020.101862>
- Zhao W, Hu CM, Zhou W et al (2022) Carotenoids participate in adaptation/resistance of daily desiccation in the intertidal red alga *Neopyropia yezoensis* (Bangiales, Rhodophyta). *Algal Res* 61:102606. <https://doi.org/10.1016/j.algal.2021.102606>
- Zhu Z, Wu Q, Di X et al (2017) Multistage recovery process of seaweed pigments: investigation of ultrasound assisted extraction and ultra-filtration performances. *Food Bioprod Process* 104:40–47. <https://doi.org/10.1016/J.FBP.2017.04.008>

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C. R. K. Reddy  
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*Editors*

Nitin Trivedi  
Marine Biotechnology  
Gujarat Biotechnology University  
Gandhinagar, Gujarat, India

C. R. K. Reddy  
Centre for Energy Biosciences  
Institute of Chemical Technology  
Mumbai, India

Alan T. Critchley  
Verschuren Centre  
Sydney, Nova Scotia, Canada

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# Chapter 13

## The Vibrant Spectra of the Oceans: Unravelling the Diversity, Functions, and Applications of Seaweed Pigments



Marta V. Freitas, Clélia Afonso, Leonel Pereira, and Teresa Mouga

**Abstract** Seaweeds are photosynthetic organisms that harvest sunlight and convert it into essential energy through a highly effective biochemical process powered by light, which in turn is captured and directed to the reactive centers by pigments. Seaweed pigments are fundamental to the seaweed photosynthetic process and are also responsible for their current taxonomic classification into three distinct divisions. The Chlorophyta comprises the green seaweeds, which hold high levels of both chlorophyll *a* and *b*, along with lesser amounts of  $\beta$ -carotene and xanthophylls. The Ochrophyta integrates the brown seaweeds (class Phaeophyceae), which are particularly rich in the xanthophyll fucoxanthin, while also showing lower levels of other xanthophylls, chlorophyll *a* and *c*, and  $\beta$ -carotene. The Rhodophyta houses the red seaweeds, which are characterized by holding high levels of phycoerythrin, as well as lower quantities of phycocyanin, chlorophyll *a*,  $\beta$ -carotene, and xanthophylls. However, regardless of their designation, seaweed species exhibit a significant range of colors and hues that go beyond “green,” “brown,” and “red,” rendering them visually unique, due to the relative composition and abundance of each pigment within their living cells. Nowadays, science has unveiled not only the diversity of these pigments, but also their biological function. Targeted extraction methods

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M. V. Freitas (✉)

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network,  
ESTM, Polytechnic of Leiria, Edifício Cetemares, Peniche, Portugal

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network,  
ESTM, Polytechnic of Leiria, Edifício Cetemares, Av. Porto de Pesca,  
Coimbra, Portugal  
e-mail: [marta.freitas@ipleiria.pt](mailto:marta.freitas@ipleiria.pt)

C. Afonso · T. Mouga

MARE-Marine and Environmental Sciences Centre/ARNET-Aquatic Research Network,  
ESTM, Polytechnic of Leiria, Edifício Cetemares, Peniche, Portugal

L. Pereira

CFE - Centre for Functional Ecology: Science for People & Planet, Marine Resources,  
Conservation and Technology - Marine Algae Lab, University of Coimbra, Department of  
Life Sciences, Calçada Martim de Freitas, Coimbra, Portugal

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and potential end-use applications for these pigments have been researched and developed, with the resulting product often designed to protect and promote human health. Today, humankind acknowledges the benefits of natural products obtained from the oceans, including those obtained from seaweed pigments. This chapter aims to supply insight on the diversity, functions, and applications of the pigments found in all the three divisions, thus contributing to a greater understanding of the benefits these functional molecules can provide to humanity.

**Keywords** Photosynthesis · Chlorophylls · Carotenoids · Phycobiliproteins

## 13.1 Introduction

### 13.1.1 *The Role of Pigments in Photosynthesis*

Photosynthesis, from the Greek *photo* (light) and *synthesis* (putting together) (Online Etymology Dictionary 2023), is the process where autotrophic organisms, such as plants, algae, and cyanobacteria, harvest solar energy and convert it into chemical energy to synthesize carbohydrates, essential for growth and development. With this process, the photoautotrophs incorporate carbon dioxide and water and release oxygen to the environment. Therefore, photosynthesis is the vital process that upkeeps the atmospheric oxygen and balances climatic processes, being thus considered the patron process of all life on Earth.

Seaweeds, also known as macroalgae, are photosynthetic aquatic organisms, which, unlike terrestrial plants or seagrass, lack true roots, stems, and leaves, and a vascular system (Pereira 2021). Being primary producers, they are fundamental in upkeeping marine trophic chains, in providing shelter and nursery grounds for marine life (Kasanah et al. 2022). Together with microalgae, macroalgae supply the greatest part of the photosynthetic ability of Earth, being therefore the dominant producers of the oxygen that we all depend on to live (Chapman 2013; Pereira 2021). In seaweeds, the metabolites that are tasked with capturing the light energy and convert it into chemical energy are known as pigments. These pigments are found in the living cells of photosynthetic organisms and are classified as photosynthetic pigments (e.g., chlorophylls) or accessory pigments (e.g., carotenoids and phycobiliproteins).

Seaweeds are found in seawater or brackish water, restrict to depths reachable by sunlight so they can perform photosynthesis, but can colonize a variety of ecological niches (Pereira 2021). Sunlight falls directly on seaweeds at specific times of the day, or it can first interact with sediment, macrophytic components, and the water itself as depth increases before reaching the seaweed tissues. The light spectral composition and irradiance that reaches the seaweed is thus highly diverse and ultimately determines its relative pigment composition, to ensure the photosynthetic process remains effective. Along with a wide range of other secondary metabolites (phenols, sterols, vitamins, among others), pigments are produced by seaweeds as a

quick adaptation response to any abiotic changes in the environment (Talarico and Maranzana 2000). This is a fundamental ability that allows seaweeds to adapt to niches where abiotic changes accompany the tidal flux, such as tide pools (Pereira 2021).

Besides being directly involved in the photosynthetic process, pigments are also particularly effective photoprotective molecules able to shield the seaweed against ultraviolet radiation, which can reach biologically significant depths in aquatic ecosystems and can significantly damage the photosynthetic apparatus and hinder photosynthetic efficiency (Sen and Mallick 2021).

These seaweed pigments hold an amazing chromatic diversity, to which the organism owns the unique colors it displays. Seaweed pigments have also been settling the whole seaweed taxonomy since, at least, the last century (Pereira 2021). Green seaweeds, with pigmentation identical to that of vascular plants, are characterized by high amounts of chlorophyll *a* and *b* and small amounts of  $\beta$ -carotene and xanthophylls (lutein, neoxanthin, violaxanthin, and zeaxanthin) and thus belong to phylum Chlorophyta. Brown seaweeds owe their color to high concentrations of fucoxanthin, but also have low concentrations of chlorophyll *a* and *c*, violaxanthin, and  $\beta$ -carotene and therefore belong to phylum Ochrophyta, class Phaeophyceae. Finally, red seaweeds, which include species that are perfectly adapted to the low light levels, found at high ocean depths, hold high content in phycobilins (in particular R-phycoerythrin and R-phyocyanin), but low content in chlorophyll *a*,  $\beta$ -carotene, and xanthophylls (lutein and zeaxanthin), and thus belong to phylum Rhodophyta (Pereira and Neto 2015; Bonanno and Orlando-Bonaca 2018; Pereira 2021).

## ***13.1.2 Diversity and Function of Pigments in Seaweeds***

### **13.1.2.1 Chlorophylls**

Chlorophylls, whose name comes from the Greek “*khloros*” (green) and “*phullon*” (leaf), are non-polar green pigments that are key players in the photosynthetic process, being specifically involved as light harvesters and in the energy transference and storage processes, functioning as natural solar cells (Mandal and Dutta 2020; Kato et al. 2020).

There are several kinds of chlorophyll, namely, chlorophyll *a*, chlorophyll *b*, chlorophyll *c*<sub>1</sub> and *c*<sub>2</sub>, chlorophyll *d*, and chlorophyll *f*. All chlorophyll types are optimized to efficiently target and use the diverse spectral components of solar energy. Chlorophylls capture light from both ends of the electromagnetic spectrum, namely the blue and the red region, while scattering wavelengths from the green region. While all chlorophylls are able to absorb solar energy, not all are able to follow up, by converting it into chemical energy (Mandal and Dutta 2020). In seaweeds, there are only three types of chlorophylls: chlorophyll *a*, chlorophyll *b*, and chlorophyll *c*.

Chlorophyll *a* is present in all seaweed groups (Pereira 2021), as well as in all oxygenic photosynthetic organisms, being specifically found in the photosystem cores and in the light-harvesting antennas within chloroplasts (Kato et al. 2020). In fact, the reaction center of the photosystem I of all oxygenic photosynthetic organisms only contain this type of chlorophyll, which has its peak absorption at wavelengths 430 and 664 nm (Larkum et al. 2021). Regarding its chemical structure, chlorophyll *a* holds a porphyrin ring with a hetero polycyclic structure that surrounds a central  $Mg^{2+}$  ion. Around this central ion, nitrogen atoms are coordinately positioned, and an ester linkage attaches the polycyclic structure to a long phytol tail, being this a feature shared by all chlorophyll species (Mandal and Dutta 2020).

Chlorophylls *b* and *c* can only be found in green and brown seaweeds, respectively, with chlorophyll *b* being also found in plants. Both pigments are found only in the light-harvesting antennas (Kato et al. 2020). While chlorophyll *b* has its peak absorption at wavelengths 460 and 647 nm, chlorophyll *c* has its peak absorption at wavelengths 442 and 630 nm ( $c_1$ ), and 444 and 630 nm ( $c_2$ ) (Larkum et al. 2021). Chlorophyll *b* shares the same molecular structure of chlorophyll *a*, but while the former contains a methyl group ( $-CH_3$ ) in the second ring, chlorophyll *b* contains an aldehydic group ( $-CHO$ ) instead (Mandal and Dutta 2020). Chlorophylls *d* and *f* are only found in Cyanobacteria. Chlorophyll derivatives such as purpurin-18 *a*, pheophytin *d*, and phytyl-purpurin-18 *a* have been studied within the scope of chlorophyll profile assessment in a number of commercially valuable seaweed species from all taxonomic groups (Chen et al. 2017a).

### 13.1.2.2 Carotenoids

In nature, carotenoids are the most widely distributed pigments, being found in a wide diversity of photosynthetic organisms, namely algae, plants, photosynthetic bacteria, and several archaea and fungi (Koizumi et al. 2018; Maoka 2020). The animal kingdom, on the other hand, lacks the capacity to produce these pigments, likely because of the evolutionary loss of the necessary genes encoding enzymes for carotenoid biosynthesis (Bohn et al. 2021). Carotenoids show warm colors such as yellow, orange, red, and purple. Structurally, carotenoids are tetraterpene pigments, where most consist of eight isoprene units with a 40-carbon skeleton and a general structure of a polyene chain with nine conjugated double bonds and an end group at both ends of the polyene chain (Maoka 2020).

Carotenoids form a crucial component of the light-harvesting antenna complex within the thylakoid membrane of chloroplasts (Koizumi et al. 2018). Carotenoids are essential compounds involved in photosynthesis and photoprotection. In photosynthesis, their primary role is to enhance light absorption in the blue spectrum, effectively extending the range of light absorption (Bohn et al. 2021), as they harvest and transfer light energy to chlorophylls through singlet-singlet transfer. In photoprotection, carotenoids stand as the first line of defense against oxidative damage, by scavenging free radicals through energy transfer and chemical reaction (Zhao et al. 2022). Whenever chlorophylls have any excess energy, carotenoid

photoprotective mechanisms fall in place by absorbing this energy surplus through triplet-triplet transfer and subsequent release by polyene vibration. Carotenoids also have the ability to quench free radicals such as singlet oxygens that are produced by oxygen, light, and the photosynthetic process itself (Schubert et al. 2006; Viera et al. 2018; Maoka 2020; Swapnil et al. 2021).

Carotenoids are divided into two main groups, carotenes and xanthophylls. Carotenes are unsaturated hydrocarbons (Osório et al. 2020), existing about 50 kinds in nature (Britton et al. 2004), being  $\alpha$ -carotene,  $\beta$ -carotene, and lycopene well-known examples (Poojary et al. 2016). Carotenes, essential photosynthetic pigments, play a crucial role in primary light absorption (Aldred et al. 2009) as well as in the photoprotective system of seaweeds (Asada 2006; Takahashi and Murata 2008). Although various carotenes can be detected in seaweeds, depending on the algal species, the presence of  $\beta$ -carotene stands out as one of the major carotenes commonly found (Murray and Capelli 2020). Xanthophylls are similar to carotenes but have, at least, one functional group with oxygen and have a highly diverse structure. These pigments may be present as protein complexes, fatty acid esters, glycosides, and sulfates and are found in a far greater number in nature, with 800 kinds described, until 2018 (Britton et al. 2004; Maoka 2009). Popular examples include lutein, fucoxanthin, astaxanthin, zeaxanthin, and  $\beta$ -cryptoxanthin (Poojary et al. 2016; Pereira et al. 2021). Xanthophylls are essential in photo-inhibition protection, by reducing and dissipating the energy reaching the photosynthetic reaction centers, through non-photochemical quenching (Maoka 2020).

Carotenoids are distinctly distributed across algae taxonomical groups, and their profile can be used for taxonomic classification (Poojary et al. 2016). Green algae have  $\beta$ -carotene, lutein, violaxanthin, neoxanthin, and zeaxanthin (Quitério et al. 2021), and their synthesis share common pathways with those observed in terrestrial plant species (Eismann et al. 2020). Brown seaweeds are especially rich in xanthophylls, with the major compounds being neoxanthins A and B, fucoxanthin, and violaxanthin, but they also have carotenes, especially  $\alpha$ -carotene and  $\beta$ -carotene (Yuan et al. 2018; Park and Lee 2021; Quitério et al. 2021). Fucoxanthin is the main pigment responsible to convey brown algae their color and is one of the most abundant carotenoids in nature (about 10% of natural carotenoid production) (Osório et al. 2020). Red seaweeds usually exhibit a pattern composed of  $\alpha$ -carotene and  $\beta$ -carotene and from one to three xanthophylls: lutein, antheraxanthin, and zeaxanthin (Esteban et al. 2009; Quitério et al. 2021), and differences in carotenoid composition are found between classes within this phylum (Takaichi et al. 2016).

### 13.1.2.3 Phycobiliproteins

Phycobiliproteins are soluble protein pigments, brilliant colored and fluorescent, that are found in the photosynthetic light-harvesting antenna complexes in Rhodophyta macro- and microalgae, and also in Cyanobacteria, Cryptomonads, and Glaucophytes (Chini Zittelli et al. 2023). These natural-soluble pigments are proteins, that exhibit fluorescence emission (Qiang et al. 2021). In most red algae,

distinct types of phycobiliproteins are assembled into supramolecular complexes anchored to the thylakoid membrane of the algae cell, through peptide links. These complexes, known as phycobilisomes, are highly efficient in capturing solar energy and transferring it into photosystems and are also acknowledged for being effective photo-protectors against high radiances, and opportune nutrient reservoirs whenever nitrogen and phosphorus are scarce (Sonani et al. 2016). Phycobilisomes assume distinct forms, being usually bundled, double-barrel-shaped, semicircular, or semiellipsoidal (Qiang et al. 2021).

Phycobiliproteins are grouped into four categories according to their absorption properties, and the distinct color transmitted by the chromophores: phycoerythrin ( $\lambda$  max = 540–570 nm, red-pink), phycocyanin ( $\lambda$  max = 610–625 nm, blue), allophycocyanin ( $\lambda$  max = 650–660 nm, blue-green), and phycoerythrocyanin ( $\lambda$  max = 560–600 nm, magenta) (Sonani et al. 2016; Kannaujiya et al. 2017, 2021; Puzorjov and McCormick 2020). These pigments are further categorized according to their source, namely, C for cyanobacteria, R for Rhodophyta algae, and B for algae from the order Bangiales. With the exception of phycoerythrocyanin, which is exclusive to cyanobacteria (Dagnino-Leone et al. 2022), all abovementioned phycobiliproteins can be found in red algae.

Phycobiliproteins have, as main components, protein subunits  $\alpha$  and  $\beta$  that form monomeric  $\alpha\beta$  units. These units self-assemble and organize themselves on the thylakoid membrane to form phycobilisomes, which are large protein complexes (Chini Zittelli et al. 2023). The phycobiliproteins that compose a phycobilisome are variable within and between biological species (Chini Zittelli et al. 2023), and while red seaweeds have substantial quantities of phycoerythrin, and fair amounts of phycocyanin and allophycocyanin, they do not have phycoerythrocyanin, which is a pigment characteristic of Cyanobacteria (Basheva et al. 2018).

In Rhodophyta, phycobiliproteins comprise up 50% of all water-soluble proteins (Dumay et al. 2014). These molecules are rearranged in an antenna or rod-like structure, with a central allophycocyanin core from where the subunits phycoerythrin, phycocyanin, and allophycocyanin loop outward in an orderly fashion: phycoerythrin (the pigment with the highest energy state) stands placed in the outermost part of the phycobilisome to capture the light energy and transmit it to an adjacent phycocyanin which, in turn, transfer this energy to the allophycocyanin (the pigment with the lowest energy state), placed next to the chlorophyll *a* photosystem reaction center (Qiang et al. 2021; Chini Zittelli et al. 2023). This unidirectional and highly effective energy capture and transport system allows red seaweeds to be remarkably effective in harvesting a wider range of light wavelength and optimizing the whole photosynthetic process, when compared to other seaweed groups (Hsieh-Lo et al. 2019). In the present era, it is recognized that the function of phycobiliproteins goes beyond just light absorption. Phycobilisomes also seemingly play a crucial role as photo-protectors against intense light levels and also serves as a nutrient source during periods of inadequate nitrogen and phosphorus supply (Jesús et al. 2016). In seaweeds, phycoerythrin and phycocyanin are found within the Rhodophyta phyllo (Hsieh-Lo et al. 2019).

Phycoerythrin, the crimson pigment, derives part of its name from the Greek word “erythros” meaning “red,” and it holds the greatest variety of chromophores among phycobiliproteins (Dagnino-Leone et al. 2022). Phycoerythrin serves as a photosynthetic pigment found in red macroalgae (Rossano et al. 2003), red microalgae (Román et al. 2002), and cryptomonads (Van Der Weij-De Wit et al. 2006). As stated before for all phycobiliproteins, the classification of phycoerythrin is determined by its original source, leading to R-Phycoerythrin (phycoerythrin obtained from Rhodophyta, with a peak absorption wavelength of 545–565 nm), C-Phycoerythrin (phycoerythrin obtained from Cyanobacteria, with a peak absorption wavelength of 540–570 nm), and B-Phycoerythrin (phycoerythrin obtained from Bangiales, a specific family of filamentous red macroalgae, with a peak absorption wavelength of 546–565 nm) (Fleurence 2003; Kannaujiya et al. 2021). Additionally, these compounds exhibit slight variations in their absorption characteristics, besides their origin (Mysliwa-Kurdziel and Solymosi 2016). Under conditions of low light but high nutrient load, phycoerythrin stands as the primary soluble protein produced by the cell of red algae (Glazer 1994).

Phycocyanin, the blue pigment, gets part of its name from the word “cyan” in English, which has its origins in the Greek word “kyanos.” Phycoerythrin is categorized based on its source; therefore, R-Phycocyanin is found in Rhodophyta, C-Phycocyanin in Cyanobacteria and Cryptophyta, and B-Phycocyanin in Bangiophyceae (Dumay and Morançais 2016). Besides being from distinct sources, these pigments also exhibit slight variations in their absorption characteristics (Fernández-Rojas et al. 2014; Mysliwa-Kurdziel and Solymosi 2016).

Allophycocyanin, the blue-green pigment, derives its name from the Greek words “allos” (other) and “kyanos” (blue). Within phycobilisomes, allophycocyanin is located at the core, where assembled trimers ( $\alpha\beta$ )<sub>3</sub> and phycocyanobilin bind to an  $\alpha$  or  $\beta$  phycobilisome subunit (Chen and Jiang 2018).

### ***13.1.3 Prospects and Applications of Seaweed Pigments***

Marine biotechnology, or blue biotechnology, pertains to the application of marine resources and tools for a diversity of applications, namely medical, cosmeceutical, environmental, and industrial. Blue biotechnology is a field with amazing potential and promise, as 70% of the planet is covered by ocean, which in turn harbors 90% of all Earth’s organisms (Thompson et al. 2017), and yet a huge slice of this biodiversity remains unexplored. Therefore, there is great potential in unraveling novel natural marine products from the materials, extracts, and molecules the oceans provide (Kasanah et al. 2022), with algae, both micro and macro, being no exception to this. However, regarding the biotechnological application of algae in industry, research endeavors have been mainly focused on microalgae (Dufossé et al. 2005; Begum et al. 2016; Morocho-Jácome et al. 2020; Silva et al. 2020; Chini Zittelli et al. 2023; Sun et al. 2023; Borovkov et al. 2023), although efforts have recently targeted a number of seaweed species from all the three groups, outlined further below.

Seaweeds hold a variety of bioactive compounds with diverse structures, including natural pigments (Osório et al. 2020). Due to their natural properties, there is an increasing demand for these seaweed-derived compounds, as consumers today prefer natural and eco-friendly products and strive for healthier lifestyles. Consequently, markets have started investing in and shifting toward natural-origin products, to replace highly processed and synthetic alternatives. In terms of pigments, synthetic colorants have traditionally been used, due to their accessibility, low cost, high yield, and stable coloring properties (Muñoz-Miranda and Iñiguez-Moreno 2023). However, the development of synthetic colorants involves the inclusion of harmful substances, like heavy metals or dyes in high concentrations, which not only pose risks to the environment but also to human health, potentially leading to cancer occurrences (Nawaz et al. 2020).

On the other hand, natural pigments obtained from seaweeds are known to have biological activities with substantial relevance on a pharmaceutical and biomedical context, such as antioxidant and free-radical scavenging activities. These promote human health (Muñoz-Miranda and Iñiguez-Moreno 2023) and include antioxidant, antimicrobial (Gomes et al. 2022), antitumoral, antimutagenic, antidiabetic, anti-obesity, photoprotective, and neuroprotective activities (Lanfer-Marquez et al. 2005; Stahl and Sies 2012; Chini Zittelli et al. 2023). Due to their notable spectroscopic properties, a number of these natural pigments have also been regarded as a valuable tool in biomedical research, therapeutic science, and clinical diagnosis (Dashwood 1997; Pagels et al. 2019; Li et al. 2019a).

Moreover, these pigments can be applied as substitute of synthetic dyes and colorants, which appeals to the food, cosmetic, and textile industry, among other applications. Examples include the inclusion of these pigments in food products such as bakery, dairy, functional foods, and deserts and in cosmetic products aimed to care and protect the skin against UV radiation and to prevent and treat hair loss (Chini Zittelli et al. 2023).

Techniques to extract pigments from natural sources are nowadays known to be fast and efficient, regarding yield, time, and costs (Muñoz-Miranda and Iñiguez-Moreno 2023). However, these advantages do not seem to be seen yet in protocols designed to obtain pigments from macroalgal biomass. Terrestrial plants, fungi, yeasts, bacteria, and microalgae are yet the prime providers of pigments (Dufossé 2016; Muñoz-Miranda and Iñiguez-Moreno 2023), especially carotenoids and phycocyanins, on an industrial scale (Dufossé 2016). These pigments have been applied mostly on the cosmetic and human nutrition sectors (World Intellectual Property Organization (WIPO) 2016), and patents are regularly developed that focus especially on chlorophylls and carotenoids (World International Property Organization 2021). Specifically, regarding seaweeds, the most valuable cultivated species from where pigments may be extracted are the green seaweeds *Ulva clathrata*, *Monostroma nitidum*, and *Caulerpa* sp., the brown seaweeds *Saccharina japonica*, *Undaria pinnatifida*, and *Sargassum fusiforme*, and the red seaweeds *Porphyra* sp., *Eucheuma* sp., *Kappaphycus alvarezii*, and *Gracilaria* sp. (Muñoz-Miranda and Iñiguez-Moreno 2023).

### 13.1.3.1 Prospects and Applications of Chlorophylls

The ability of chlorophyll to act as a solar power cell, by harvesting light energy and store it as chemical energy, has inspired scientists to study and harness the process to obtain chemical fuel from solar energy through chlorophyll centric technologies, namely for hydrogen production (Mandal and Dutta 2020). The chlorophyll used to explore this venue was chlorophyll *a*, although it is not obtained from seaweeds, but rather from microalgae of the genus *Spirulina* (Saiki and Amao 2002; Tomonou and Amao 2002; Himeshima and Amao 2005; Takeuchi and Amao 2005).

The activity of chlorophylls involves not only solar energy, but also electromagnetic radiation within the visible range (Mandal and Dutta 2020) and fluorescence properties (Padhi et al. 2021). This means this pigment has unique properties and is an excellent and versatile biomaterial that must be considered to the benefit of humankind.

The biological activities and health benefit effects of natural chlorophylls present in seaweeds have been recently studied. However, studies focusing on the qualitative and quantitative characterization of their chlorophyll profile are yet scarce (Chen et al. 2017a). Chlorophyll is known for its antioxidant and antibacterial activities (Lanfer-Marquez et al. 2005; Pérez-Gálvez et al. 2020). Additionally, chlorophylls have been clinically applied for years in photodynamic therapy of tumors and their chemo-preventive properties are well acknowledged. Chlorophylls also show antimutagenic activity in genotoxicity assays and are able to protect against cancer biomarkers (Dashwood 1997).

Chlorophyll has been tested as a biomarker to screen plant health and physiological condition and detect diseases, mostly on crops relevant to agriculture (Chaerle et al. 2004; Tung et al. 2013; Guo and Tan 2015), but also to measure coral reef health (Febbo et al. 2012) and survey macroalgal blooms (Lin et al. 2011). Chlorophyll markers were also used to test the effects of environmental stress upon plants (Peguero-Pina et al. 2008; Wang et al. 2018; Li et al. 2019b; van der Westhuizen et al. 2020; Stefanov et al. 2023), to monitor nutrient levels in crops (Schächtl et al. 2005; Long et al. 2013; Liu et al. 2022; Chen et al. 2023) and herbicide levels both in soil (Huang et al. 2012) and water samples (Bi Fai et al. 2007).

Due to their significant fluorescent ability, chlorophylls have been considered in the development of optical and electrochemical biosensors. Devised applications include chlorophyll-based biosensors to assess microalgal cell viability in ballast water (Wang et al. 2013; Li et al. 2022), to detect harmful agents (Merz et al. 1996; Frense et al. 1998; Védrine et al. 2003; Husu et al. 2013), to measure dissolved oxygen in water (Brasil Silva et al. 2017), to detect biological warfare agents in gases (Sanders et al. 2001), and to detect chlorophyll levels in fecal matter from livestock (Pemberton et al. 2007). Assessing herbicide levels in the environment is a very popular application for chlorophyll-based optical sensors (Mandal and Dutta 2020).

Additionally, chlorophylls have been clinically applied for years in photodynamic therapy of tumors, and their chemo-preventive properties are acknowledged. Chlorophylls also show antimutagenic activity in genotoxicity assays and show promise as anticancer agents (Dashwood 1997).

Chlorophylls are additionally being considered as a pigment in the textile, cosmetic, and animal feed industries (Solymosi and Mysliwa-Kurdziel 2016; Janarthanan and Senthil Kumar 2017; Jesumani et al. 2019; Morais et al. 2021). A synthetic formulation of chlorophyll, registered as the food additive E140, is extensively used in the food industry to color foods and beverages.

Typically, chlorophyll has predominantly been sourced from microalgae and occasionally from higher plants, in the various applications explored thus far. However, despite not extracting chlorophyll from macroalgae, the abovementioned examples are still referenced to illustrate the diverse array of potential applications for chlorophylls. In seaweeds, chlorophylls and chlorophyll derivatives have been extracted essentially for research purposes, namely from the green seaweeds *Boodleopsis verticillata*, *Cladophora graminea* (Urrea-Victoria et al. 2023), *Halimeda macroloba* (Nazarudin et al. 2020), *Rhizoclonium riparium* (Urrea-Victoria et al. 2023), *Ulva* spp. (formerly *Enteromorpha* spp.) (Chen et al. 2017a), and *Ulva* spp. (Lin et al. 2011; Zhu et al. 2017; Chen et al. 2017a; Nazarudin et al. 2020), the brown seaweeds *Cladosiphon okamuranus* (Fujii et al. 2012), *Sargassum ilicifolium* (Nazarudin et al. 2020), *Laminaria ochroleuca*, and *Undaria pinnatifida* (Chen et al. 2017a), and the red seaweeds *Bostrychia* spp., *Catenella impudica* (Urrea-Victoria et al. 2023), *Chondrus crispus* (Robertson et al. 2015), *Gracilaria salicornia* (Lumbessy et al. 2021), *Gracilaria tenuistipitata* (Torres et al. 2014), *Grateloupia elliptica* (Lee et al. 2021a), *Kappaphycus alvarezii* (Brotosudarmo et al. 2018), *Palmaria palmata* (Robertson et al. 2015), and *Porphyra* spp. (Robertson et al. 2015; Chen et al. 2017a), to cite a few examples. Chlorophyll *a* from red seaweeds, identified chemically as CAS 479-61-8, has received the endorsement of the European Food Safety Authority (EFSA) for inclusion in food processing. Concurrently, it remains under ongoing scrutiny as a potential pigment for various sectors including textiles, animal feed, and cosmetics (Ferreira et al. 2021; Muñoz-Miranda and Iñiguez-Moreno 2023).

There are two primary methods commonly used to extract chlorophylls from seaweeds. The first method involves the use of organic solvents, such as alcoholic or acetone-based solutions, while the second method utilizes cell disruption techniques, such as mechanical or ultrasonication methods. There is, as well, a growing interest in adopting innovative and environmentally friendly approaches to extract chlorophyll from seaweeds. Some of these promising “green” techniques include microwave-assisted extraction and green solvent extraction methods (Samarasinghe et al. 2012; Zhu et al. 2017; Chen and Roca 2019; Martins et al. 2023).

### 13.1.3.2 Prospects and Applications of Carotenoids

Carotenoids have been the focus of investigation since the early nineteenth century (Takaichi 2011). Today, we know these pigments are crucial for our body, but must be acquired from dietary sources as, since as mentioned, the animal kingdom cannot synthesize them (Gammone et al. 2015). Fruits, vegetables, and their processed variants are the most popular sources to obtain this compound (Darvin et al. 2011;

Gammone et al. 2015). Carotenoids also enrich the nutritional content of various other natural food sources, such as eggs, fish, algae, fungi, and yeasts (Meléndez-Martínez et al. 2020; Rapoport et al. 2021). In the human diet, approximately 50 different carotenoids can be identified (Gammone et al. 2015).

Carotenoids have undergone extensive research and are recognized for their significant biological activities, particularly their potent antioxidant properties in scavenging free radicals as their main acting mechanism (Krinsky and Johnson 2005; Pangestuti and Kim 2011a). Consequently, carotenoids have been extensively used as nutraceuticals and cosmeceuticals. Carotenoids hold significant recognition in the cosmetic industry, contributing to improved skin health by bolstering dermal defense against UV radiation (Swapnil et al. 2021), and recent research suggests that carotenoids also influence skin moisture, texture, and elasticity as well (Zerres and Stahl 2020). As antioxidant agents, they work synergistically with other reducing agents like polyphenols and vitamins (C and E) (Chan et al. 2015). Carotenoids also play a crucial role in enhancing immune defenses and reducing the risk of chronic diseases and age-related ailments, including inflammatory diseases, cardiovascular disorders, bone/skin/eye conditions, diabetes, and cancer (Fiedor and Burda 2014; Gammone et al. 2015; Kulczyński et al. 2017; Eggersdorfer and Wyss 2018; Viera et al. 2018; Ojulari et al. 2020; Dias et al. 2021; Swapnil et al. 2021; Pereira et al. 2021). Moreover, they promote mental and metabolic well-being during pregnancy and early life (Dias et al. 2021). However, the most noteworthy biological role carotenoids have is their innate role as a provitamin A, rendering them effective in preventing vitamin A deficiencies (Maeda et al. 2018; Meléndez-Martínez et al. 2020; Quitério et al. 2021). Additionally, carotenoids serve as sources of color, odor, and taste in various contexts (Yabuzaki 2017).

Also, carotenoids have been used as feed supplements in aquaculture (Vílchez et al. 2011; Lim et al. 2018; Nakano and Wiegertjes 2020; Elbahnaswy and Elshopakey 2023), and vastly considered as a natural alternative pigment as food colorant (Poojary et al. 2016). However, the current major commercial carotenoids are chemically synthesized (Rodríguez-Amaya 2015), instead of being obtained from natural sources, which have raised concerns regarding public health, safety, and environment burden, among consumers. Consequently, current market trend is to grow toward the commercialization of natural carotenoid-based products (Poojary et al. 2016).

Terrestrial plants are one of the primary sources of natural-based carotenoids; however, the possibility of obtained carotenoids from algae instead has garnered attention from industry due to the advantages they offer regarding cost, scale, time, and yield (Poojary et al. 2016). Extensive research has already been published, which focus either on macroalgae carotenoids in general (Schubert et al. 2006), or focus in specific *taxa* or species, such as the green seaweeds *Caulerpa prolifera* (Hegazi et al. 1998), *Caulerpa lentillifera* (Balasubramaniam et al. 2020), the brown seaweeds *Padina australis* (Brotosudarmo et al. 2018), *Padina pavonica* (Hegazi et al. 1998), *Saccharina latissima* (Gevaert et al. 2002), and *Sargassum polycystum* (Balasubramaniam et al. 2020), and the red seaweeds *Euchema denticulatum* (Balasubramaniam et al. 2020), *Gracilaria tenuistipitata* (Torres et al. 2014), *Jania*

*rubens* (Hegazi et al. 1998), *Kappaphycus alvarezii* (Brotosudarmo et al. 2018), and *Neopyropia yezoensis* (Koizumi et al. 2018; Xie et al. 2020). It has also been suggested to cultivate *Ulva* sp., a green macroalga with a wide array of commercial purposes, to obtain raw material for carotenoid enrichment and production, to strategically improve its nutritional value (Eismann et al. 2020).

Various methods have been employed for carotenoid extraction, with liquid-liquid extraction being the most common approach, followed recently by alternative extraction procedures such as ultrasound-assisted extraction, microwave-assisted extraction, enzymatically assisted extraction, pressurized liquid extraction, extraction methods based on electrotechnology and supercritical/subcritical fluid extraction (Singh et al. 2015; Poojary et al. 2016; Xu et al. 2017; Saini and Keum 2018). By having a high degree of hydrophobicity, carotenoids are effectively extracted with non-polar solvents such as *n*-hexane, diethyl ether, dimethyl ether, dichloromethane, or mixtures of organic solvents such as acetone and octane, or green/food-grade solvents such as ethanol, limonene, and solutions of water and organic solvents (Poojary et al. 2016). The analysis of carotenoids in seaweeds is conducted using high-performance liquid chromatography (HPLC), in which identification is achieved by comparing their retention times and absorption spectra with authentic standards (Hegazi et al. 1998; Koizumi et al. 2018). Carotenoids that are extensively researched and are worth mentioning further below are the well-known  $\beta$ -carotene for its ubiquitous presence in seaweeds, and the xanthophylls fucoxanthin, for its high presence in brown seaweeds, and astaxanthin, for its reportedly strong activity, particularly when sourced from algae. Lutein and zeaxanthin will also be briefly mentioned.

$\beta$ -Carotene is possibly the most well-known carotene, holding several well-documented benefits for human health, such as antioxidant, anti-inflammatory, anticancer, and antiaging (Mayne 1996; Sies and Stahl 2004; Stahl and Sies 2012; Carpena et al. 2021). This carotene has, therefore, an outstanding potential and applicability in the food, cosmetic, and pharmaceutical industries (Phan et al. 2018; Carpena et al. 2021). In seaweeds, research has shown that it is possible to manipulate  $\beta$ -carotene yields in the red seaweed *Neopyropia yezoensis* (Xie et al. 2020). However, to date, the most efficient source to obtain  $\beta$ -carotene is the green microalgae *Dunaliella salina* (Barbosa et al. 2023), provided its production is properly induced by manipulation of culture conditions (Lamers et al. 2008). Nevertheless, the majority of its industrial production results from chemical synthesis (Ye et al. 2008).

Fucoxanthin, a brown pigment, is one of the most abundant marine carotenoids, is effortlessly found in brown seaweeds (Pereira et al. 2021) and has a wide range of benefits for human health. Fucoxanthin is renowned for its ability to modulate processes in the central nervous system. Additionally, it exhibits antioxidant, antibacterial (Karpinski and Adamczak 2019; Liu et al. 2019), antiphotodamage (Noviendri et al. 2022), antiallergic, anticancer (Pádua et al. 2015; Méresse et al. 2020; Ming et al. 2021), anti-inflammatory (Yang et al. 2013), antidiabetic (Park et al. 2011), antiobese (Ojulari et al. 2020), antiangiogenic (Pereira 2016), and antiobesity activities, while also showing potential for treating neurodegenerative diseases (Schepers

et al. 2020; Yang et al. 2021), which makes this pigment particularly sought out by the pharmaceutical, cosmetic, and food industries (Peng et al. 2011; Aziz et al. 2020; Ojulari et al. 2020). The main algal provider of fucoxanthin is the brown seaweed *Undaria pinnatifida*, that which produce this pigment in high quantities (Liu et al. 2019; Garcia-Perez et al. 2022; Lourenço-Lopes et al. 2023), but other brown species have also been looked at, such as *Fucus* spp. (Garcia-Perez et al. 2022; Resende et al. 2023), *Laminaria* spp. (Ming et al. 2021; Garcia-Perez et al. 2022), *Ascophyllum nodosum*, *Bifurcaria bifurcata*, *Himanthalia elongata*, *Pelvetia canaliculata* (Garcia-Perez et al. 2022), *Sargassum* spp. (Yang et al. 2013; Nomura et al. 2013; Conde et al. 2015; Garcia-Perez et al. 2022), and *Sphaerotrichia divaricata* (Maeda et al. 2018). Additionally, brown algae from the genus *Alaria*, *Ascophyllum*, *Carpophyllum*, *Cladosiphon*, *Cystophora*, *Cystoseira*, *Dictyota*, *Ecklonia*, *Ectocarpus*, *Eisenia*, *Himanthalia*, *Ishige*, *Kjellmaniella*, *Myagropsis*, *Padina*, *Pelvetia*, *Petalonia*, *Saccharina*, *Sargassum*, *Scytosiphon*, *Sporochnus*, and *Turbinaria* have been targeted as well (Muradian et al. 2015), and their commercial exploration could be an hypothesis to put forward, provided such can be done sustainably by, for example, cultivating the required biomass if possible.

Astaxanthin, a red pigment, is worth mention as it has an antioxidant activity 10 times stronger than a number of other carotenoids such as  $\beta$ -carotene, lutein, and zeaxanthin (O'Connor and O'Brien 1998). This pigment is known for being able to suppress free radical production and inhibit the cellular toxicity induced by reactive oxygen species, which thus labels it as being a super vitamin E (Miki 1991). Astaxanthin has also great potential as a novel geroneuroprotector (compound that slow the rate of biological aging) due to its chemical-physical properties (Schubert et al. 2018; Sorrenti et al. 2020). Additionally, it shares many of the health benefits previously mentioned for other carotenoid classes, namely as a promoter of cardiovascular health, immune response, cancer prevention, and skin health (Davinelli et al. 2018; Fakhri et al. 2018) This renders this pigment particularly interesting, as astaxanthin, when extracted from algae, reportedly has the strongest biological activity when compared to that obtained from other biological sources (Ye et al. 2019). Such has been the key factor triggering the global demand for this pigment on an aquaculture context, as astaxanthin targets a wide range of aquatic animal health conditions, improves their survival, growth, fitness, and reproductivity, and dramatically improves their coloration, thus boosting their market value (Lim et al. 2018; Elbahnaswy and Elshopekey 2023). In seaweeds, research has shown that the content of astaxanthin changes according to season in the red seaweed *Catenella caespitosa* (Banerjee et al. 2009). Brown seaweeds, such as *Undaria pinnatifida*, *Saccharina japonica* (formerly *Laminaria japonica*), and *Sargassum fusiforme* (formerly *Hizikia fusiformis*), are rich in astaxanthin and fucoxanthin; these seaweeds feature in the traditional Okinawan diet, known for its healthy aging properties (Willcox et al. 2014). However, the main source of astaxanthin among algae, besides the commercially produced chemical counterpart, has been the green microalgae *Haematococcus lacustris* (formerly *Haematococcus pluviialis*) and *Chromochloris zofingiensis* (formerly *Chlorella zofingiensis*) (Han et al. 2013).

Lutein and zeaxanthin are carotenoids whose biotechnological potential has been studied. Being stored in the eye macula (Murillo et al. 2019; Gomes et al. 2022), both carotenoids have proven their usefulness as antitumoral compounds (Firdous et al. 2015), as photoprotective agents (González et al. 2003), and as eye health promoters (Stahl and Sies 2005; Ma and Lin 2010; Murillo et al. 2019; Saha et al. 2020; Becerra et al. 2020), and therefore are explored in food, cosmetics, and pharmaceutical industries (Shi et al. 2002; Fernández-Sevilla et al. 2010; Saha et al. 2020; Becerra et al. 2020). Either one of these carotenoids has been studied from macroalgae such as the red seaweeds *Corallina officinalis* (Sajilata et al. 2008; Koo et al. 2012), *Gracilaria corticata*, *Grateloupia filicina* (Bhat et al. 2021), and *Neophyropia yezoensis* (Xie et al. 2020). However, and again similarly to other carotenoids, the production of these pigments, namely zeaxanthin, using microalgae instead remains an attractive venue (Becerra et al. 2020; Bourdon et al. 2021).

### 13.1.3.3 Prospects and Applications of Phycobiliproteins

Phycobiliproteins exhibit remarkable spectroscopic properties, including high absorption coefficient, excitation and emission spectra, quantum yield, low interference, quenching stability, and water solubility (Niu et al. 2013; Kannaujiya et al. 2017, 2021). These exceptional properties have led to their widespread application and documentation in various fields, such as biomedical research, clinical diagnostics, therapeutic science, and the cosmeceutical and pharmaceutical industries (Pagels et al. 2019; Li et al. 2019a; Dagnino-Leone et al. 2020; Chini Zittelli et al. 2023). Notably, these pigments have found extensive use as photosynthesizers in cancer therapy (Bei et al. 2002) and fluorescent sensors in flow cytometry and immunofluorescence microscopy (Leney et al. 2018).

The primary reason for the significant commercial interest in phycobiliproteins lies in the health benefits they offer, acting as antioxidants and free-radical scavengers (Yabuta et al. 2010; Pangestuti and Kim 2011b; Nagaraj et al. 2012; Hemlata et al. 2018), with therapeutic and nutraceutical effects (Fernández-Rojas et al. 2014; Manirafasha et al. 2020; Dagnino-Leone et al. 2022). Moreover, they have demonstrated effectiveness in neuroprotection, antibacterial (Hemlata et al. 2018), antiviral (Shih et al. 2003), anti-inflammatory (Lee et al. 2017), antiallergic (Lee et al. 2021c), antitumoral (Pattarayan et al. 2017; Hao et al. 2018; Hemlata et al. 2018), antiaging (Lee et al. 2021c) and have shown promise as agents for combating Alzheimer's disease. Additionally, they have been found to provide hepatoprotective and immunomodulatory benefits (Nagaraj et al. 2012; Cian et al. 2012) and are considered as potential hypocholesterolemia agents (Sonani et al. 2016; Kannaujiya et al. 2021).

Phycobiliproteins are considered the primary food colorants and preservatives obtained from algae and highly regarded as an excellent green alternative to their chemical counterparts (Chen et al. 2017b; Nowruzi et al. 2022; Dagnino-Leone et al. 2022). Phycoerythrin has extensive applications as a natural dye in the food and cosmetic sectors (Mysliwa-Kurdział and Solymosi 2016; Kannaujiya et al.

2021; Ma et al. 2022; Chen et al. 2022). For example, phycoerythrin extracted from the microalgae *Porphyridium* sp. has garnered significant attention and research due to its ability to emit a vibrant yellow fluorescence. This unique characteristic has led to its thorough exploration and experimentation in the creation of food products with singular visual effects. These include visually captivating cake decorations, soft drinks, and alcoholic beverages that exhibit fluorescence under ultraviolet light or when subjected to specific pH levels (Dufossé et al. 2005).

The potential application and market value of phycobiliproteins is determined by their purity level, specifically the ratio of  $A_{\max} \text{ PBP}/A_{280}$ , and consequently, the potential application from all the possibilities listed above. When this ratio is greater than or equal to 0.7, it is considered food grade, for ratios between 0.7 and 3.9, it is categorized as reagent grade, and lastly a ratio of  $A_{\max} \text{ PBP}/A_{280}$  equal to or greater than 4.0 indicates analytical grade. Both reagent and analytical grade phycobiliproteins are priced higher than food-grade phycobiliproteins (Hsieh-Lo et al. 2019; Qiang et al. 2021).

Within macroalgae, phycoerythrin has been studied not only from the highly acknowledged red seaweeds *Gelidium* sp. (Mittal and Raghavarao 2018; Mittal et al. 2019), *Gracilaria* spp. (Nguyen et al. 2020; Pereira et al. 2020; Zhao et al. 2020), *Grateloupia turuturu* (Munier et al. 2014, 2015; Le Guillard et al. 2015), *Palmaria palmata* (Dumay et al. 2013; Lee et al. 2017), and *Porphyra/Pyropia* sp. (Wang et al. 2020; Sano et al. 2020; Huang et al. 2021), but also from several other non-commercial or otherwise less-known species (Ismail and Osman 2016; Malairaj et al. 2016; Sfriso et al. 2018; Saluri et al. 2019; Freitas et al. 2022). However, considering the amazing diversity of red seaweeds worldwide, and the vibrant red hues some Rhodophyta hold, this probably leaves out a great number of less known, but potentially equally promising species. Being phycoerythrin a protein, red seaweeds with reportedly high protein content may look particularly promising to explore as well. Examples of such seaweeds include *Chondrus crispus*, *Osmundea pinnatifida*, *Pterocladia capillacea*, *Pyropia tenera* (formerly *Neopyropia tenera*) and *Pyropia yezoensis*, besides the abovementioned *Palmaria palmata* and *Porphyra* sp. (Pereira 2011, 2016, 2023).

The primary interest in phycobiliproteins lies not only in their high protein yield but also in their easy-to-perform extraction methods. Typically, in macroalgae, phycoerythrin is studied and processed using various methods, which include grinding/maceration (Francavilla et al. 2015; Pereira et al. 2020), often combined with freeze-thaw techniques (Sfriso et al. 2018; Zhao et al. 2020) or liquid nitrogen (Francavilla et al. 2013; Saluri et al. 2020). The main solvents that are often chosen to complement these techniques are phosphate buffer (Ismail and Osman 2016; Nguyen et al. 2017; Pereira et al. 2020; Sano et al. 2020) and distilled water (Lee et al. 2017; Zhao et al. 2020). Less commonly applied extraction methods include ultrasounds (Le Guillard et al. 2015; Mittal et al. 2017) and enzymatic hydrolysis (Fleurence 2003). Separation and purification of the extracted phycoerythrin are usually performed through chromatography techniques (Niu et al. 2010; Gu et al. 2018; Saluri et al. 2020; Zhao et al. 2020) or gel electrophoresis (MacColl et al. 1996; Galland-Irmouli et al. 2000; Malairaj et al. 2016).

Phycocyanin is the phycobiliprotein that holds the largest market and shares the same properties and applications of phycoerythrin. This brilliant blue colored pigment presents remarkable fluorescent abilities, and it can be processed into fluorescent reagents, probes, and tracers. These are then applied in the context of biomedical research and biological engineering, namely in medical diagnosis and immunology trials (Liu et al. 2016). Phycocyanin also stands out as the most used natural blue pigment in the food industry, being employed to color various products, such as desserts, with a hardly comparable color, since interestingly, there are limited alternatives approved as natural blue food colorants (Brauch 2016). One key advantage and distinctive feature of phycocyanin, apart from its role as a food colorant, is its potential to promote health, being therefore labeled as a pharmaceutically active phyco-pigment (Vinothkanna and Sekar 2020). Phycobiliprotein has an attested nutritional value (Farag et al. 2016), nutraceutical, therapeutic (Piniella-Matamoros et al. 2021) (113), and bioactive potential (Liu et al. 2016), especially as anticancer agent (Jiang et al. 2017; Braune et al. 2021), and shows, as well, remote-sensing abilities (Ogashawara 2020).

Phycocyanin is primarily obtained from the Cyanobacteria *Arthrospira platensis*, which is by far the main source for this pigment, probably in part due to being a highly researched and known organism (Sahin 2018; Wollina et al. 2018; Marková et al. 2020; Araujo et al. 2021; Ragusa et al. 2021), but also due to its cosmopolitan distribution on water and earth (Kannaujiya et al. 2021), thus being easy to obtain. However, the microalgae *Cyanidium caldarium* (Eisele et al. 2000) and *Galdieria sulphuraria* (Chini Zittelli et al. 2023) have also been recently considered for the same purpose. There is an outstanding number of published research and reviews regarding this pigment in the literature (de Morais et al. 2018; Prado et al. 2018; Pagels et al. 2019; Morocho-Jácome et al. 2020; Braune et al. 2021; Cottas et al. 2021; Jaeschke et al. 2021; Patel et al. 2022).

In macroalgae, the Bangiophyceae species such as *Pyropia haitanensis* (as *Neoporphyra haitanensis*) (Liu et al. 2015) and *Bangia atropurpurea* (Chang et al. 2011) have provided B-phycocyanin that demonstrates promising capabilities as an antiallergic agent. Additionally, B-phycocyanin isolated from *Porphyra* sp. exhibits potential as an antioxidant agent (Huang et al. 2021). As part of an effort to enhance our understanding of R-phycocyanin's structure and function in red macroalgae, R-phycocyanin from *Polysiphonia stricta* was isolated, purified, and thoroughly studied (Wang et al. 2014). A mix of several well-known and less-known red seaweed species was also recently evaluated for phycocyanin content (Freitas et al. 2022).

Extraction and purification methods that target phycocyanin are common to those applied to phycoerythrin. However, they are seldom applied or optimized as seaweeds are outpaced by Cyanobacteria, which remains the predominant source of phycocyanin for the industry. Consequently, dedicated studies focused on phycocyanin derived from macroalgae may face challenges in gaining recognition, traction, or support in the coming times. There are few studies use apply phosphate buffer (Lüder et al. 2001; Wang et al. 2014; Ismail and Osman 2016) to extract phycocyanin from red macroalgae, that can be purified by chromatography (Kuddus

et al. 2013; Wang et al. 2014; Huang et al. 2021) and electrophoresis (Huang et al. 2021).

Compared to either phycoerythrin or phycocyanin, allophycocyanin is not extensively studied, regardless of the organism. However, its distinctive blue-green color is almost unparalleled by any other natural pigment (Mysliwa-Kurdziel and Solymosi 2016), which would likely enhance its value as a truly unique compound. Again, cyanobacteria are the prime source of this pigment in academic settings (Chen et al. 2016; Soulier and Bryant 2021), and focus is given to understand structural mechanisms (Dagnino-Leone et al. 2017) and synthesis (Dagnino-Leone et al. 2020; Guo et al. 2020). In seaweeds, allophycocyanin been successfully extracted from various Rhodophyta species using phosphate buffer (Lüder et al. 2001; Ismail and Osman 2016). Efforts have also been made to produce high-quality recombinant allophycocyanin in *Escherichia coli* from *Gracilaria chilensis*, intended for biotechnological and biomedical applications (Dagnino-Leone et al. 2020).

Examples of phycobiliprotein commercialization can be found at a commercial level. Some companies profit from phycobiliprotein-derived natural dyes, with microalgae being prominently featured as the source for their products. Several companies promote their microalgae-based natural dyes for use in cosmetic products. Notably, phycocyanin from *Arthrospira* sp. and phycoerythrin from *Porphyridium* sp. are used in this context. Moreover, R-Phycoerythrin is distributed as a laboratory consumable, sourced from *Pyropia tenera* (as *Neopyropia tenera*) or *Neogastroclonium subarticulatum*, specifically for biotechnological and biomedical research purposes. Research on these pigments, obtained from macroalgae, is still scarce. Recent studies focused on the optimization of culture conditions to manipulate phycobiliprotein content and production of *Colaconema* sp. (Lee et al. 2021b), *Halymenia floresii* (Godínez-Ortega et al. 2008), *Halymenia durvillei* (Rula et al. 2021), *Gracilaria caudata*, and *Laurencia catarinensis* (Souza et al. 2019). Such endeavors have, however, progressed little beyond the academic context, which may be partly due to the challenges inherent in extraction procedures, discussed below.

#### 13.1.3.4 Current Challenges and Perspectives

One of the primary challenges in exploring pigments derived from seaweed sources lies in the differing cultural perspectives on seaweeds themselves. Throughout history, seaweeds have held a significant place in the cultures and traditions of Eastern countries, serving various purposes beyond human consumption and health, as extensively documented in the literature (Pereira 2011, 2016, 2018, 2023; Abreu et al. 2015; Carvalho and Pereira 2015; Wells et al. 2017; Leandro et al. 2020; Pereira and Valado 2021; Morais et al. 2021; Kalasariya et al. 2022). On the other hand, the Western part of the world still tends to embrace a lifestyle that emphasizes the abundance and diversity of available food options (Pereira 2023). However, this diversity often includes highly unhealthy choices, such as the widely prevalent “fast food,” which has become a response to the fast-paced lifestyle in the West. These processed foods are high in calories and unhealthy fats, artificially flavored with

synthetic additives, while lacking nutritional value and appeal. Consequently, in a considerable portion of the Western world, food is primarily viewed and consumed as a necessity for survival, with a number of exceptions such as countries following a Mediterranean diet, for example. In the East, on the other hand, food consumption and preparation are integral to the traditions of many cultures, and the act of eating is often considered a revered and ceremonious activity.

It is no surprise that seaweeds have gained widespread recognition in Eastern cultures, while the Western world still holds reservations about them. In many shore-side Western countries, seaweeds were once consumed as a last resort in times of strife, such as warfare and poverty, so they may now be held as a gloomy reminder of such difficult times back then. Only a few Western countries incorporate seaweeds into their cultural practices (Pérez-Lloréns et al. 2020), and in most places, they are considered a relatively new and unexplored addition to a healthy diet. Nonetheless, extensive research has already been conducted, particularly in academic settings, but the full transition to integrating seaweeds into the mainstream industry and making them commonly available in grocery stores is yet to be accomplished.

Seaweeds, as a food source, have not yet captured the interest of the typical Western society, which often prefers to stick with familiar options rather than explore new alternatives, coupled with an inherent lack of skill, dare, or imagination, in incorporating seaweeds to their daily diet. The lack of interest leads to minimal demand, making industries hesitant to invest in seaweed products when it seems people do care little about them yet. However, recently, both Eastern and Western societies have started to reflect on their lifestyle and the potential consequences for their health and the well-being of future generations. People have become more conscious of the quality of their food, clothing, and other mundane choices and are now making smarter decisions that consider not only personal health but also the environment. There is a growing demand for higher-quality products in the market, and individuals are actively seeking alternatives for both food and materials, reflecting a shift toward a more mindful and sustainable way of living.

Seaweeds exemplify this kind of resource. In contemporary times, although encountering skepticism, particularly from individuals entrenched in traditional customs, seaweeds are conveniently accessible, at the very least, in large retail outlets and commercial spaces. Naturally, there exists a potential downside to this situation, centered around the apprehension of endangering the excessive use of native seaweed populations. However, this issue can be mitigated by implementing effective resource management strategies and practicing sustainable cultivation of the desired species. Besides all their benefits, numerous seaweed species have the added advantage that can be sustainably cultivated, allowing the preservation of natural populations, either in controlled, indoor settings or in outdoor, shored settings. Naturally, challenges remain regarding process sustainability, cost-effectiveness, and economic viability. The diversity of the natural pigments obtained from seaweeds determines their stability against a range of external conditions, such as environmental or those applied in technological settings (Cserhádi 2006).

There are challenges also inherent to the recovery of pigments, or any other compound, from a biological matrix as challenging as that of a seaweed. Their extracellular material hinders the full recovery and yield of chlorophylls, whereas microalgae pose a significantly easier endeavor (Chen et al. 2017a). Then, there are the challenges pertaining the pigments themselves. Natural pigments are highly unstable, being particularly sensitive to temperature and light, and the biomass quickly adjusts its pigment composition to the external conditions. While this may present an advantage regarding the manipulation of culture conditions to obtain the desired pigment, a hardly overlooked disadvantage lies in the fact that it is quite challenging to preserve the quality and stability of the metabolites as soon as they are extracted from the biomass. Processes have always taken this into consideration, but process scale-up efforts are challenging.

The isolation of carotenoids can be performed by conventional processing technologies, such as solvent extraction. However, such methods present several limitations, such as high solvent consumption and time-consuming steps, which also result in poor efficiency and selectivity of the end product (Poojary et al. 2016). Certain precautions need to be taken during carotene extraction to minimize degradation and isomerization. Factors such as exposure to light, heat, and oxygen can considerably reduce the efficiency of extraction. Therefore, it is essential to handle and process the samples promptly (Rodriguez-Amaya and Kimura 2004; Rosso and de Rosso and Mercadante 2007). Certain methodologies also have proven to be quite costly, such as the supercritical fluid extraction methodology, or cause carotene degradation, such as ultrasound-assisted extraction and microwave-assisted extraction, that involves the use of high temperatures during the process (Poojary et al. 2016). Alternatives to such sensitive techniques are also highly desired, and to isolate carotenoids from micro- and macroalgae novel techniques such as microwaves, ultrasounds, high-pressure homogenization, pulsed electric fields, liquid pressurization, supercritical fluids, and subcritical fluids, have been recently considered (Poojary et al. 2016). Chemical synthesis of carotenoids is currently commercially made for astaxanthin, and possible to be performed for fucoxanthin although for the latter pigment, such process is quite expensive, and therefore, the standardization of the extraction and purification methods targeting algae-sourced fucoxanthin is a fairly appealing endeavor (Pereira et al. 2021).

Phycobiliproteins are applied in the industry in its water-soluble protein form, and its commercial uses heavily rely on comprehensive knowledge and advanced technology, which are still relatively limited (Mysliwa-Kurdziel and Solymosi 2016). To begin with, efforts have been made to achieve success in culture settings in order to obtain not only macroalgae, but also cyanobacteria, as the source material to extract pigments, particularly regarding achieving a balance between biomass growth rates and phycobiliprotein productivity (Dagnino-Leone et al. 2022). Then, there is also the fact that the majority of innovative applications involving phycobiliproteins are currently only disclosed in patents (Sekar and Chandramohan 2008; Mysliwa-Kurdziel and Solymosi 2016). Currently, the commercialization of phycobiliproteins is hindered not only by their chemical instability, which reduces their shelf life, but also by the high level of purity that is required for pharmaceutical

applications, which involves several steps. These steps increase both production time and costs (Chini Zittelli et al. 2023) and may compromise the pigment quality due to manipulation alone. The low yields often obtained during production also limit implementation and setting in the food and cosmetic industries. Additionally, these compounds have limited chemical stability, particularly under heat and light conditions, making them susceptible to denaturation.

To address these issues, researchers have compared and reviewed strategies to improve phycobiliprotein yields and chemical stability (Hsieh-Lo et al. 2019), although said research has been more focused on phycocyanin and phycoerythrin, and such leaving out allophycocyanin. Most research under this topic also focus on phycobiliproteins obtained from *Spirulina platensis* (Nowruzi et al. 2022), leaving out a wide number of likely promising species, either micro or macroalgae. In the food sector, recent progress reviews the stability of phycobiliproteins under a wide range of the acidic, light, and temperature conditions in food storage. Phycobiliproteins are significantly more stable when coupled with other natural preservatives or encapsulated by using algal materials such as alginates and carrageenans, through nanotechnology (Nowruzi et al. 2022). Although this is still a procedure seldom applied, research focusing on this methodology has been recently published (Braga et al. 2016; Seyed Yagoubi et al. 2017; Patel et al. 2020).

Currently, the purification of phycobiliproteins remains expensive, urging the consideration of more effective and cost-efficient extraction and purification methods, especially on a larger scale (Pereira et al. 2020). Most laboratory protocols share common points, such as meticulous biomass preparation and the use of specialized equipment. However, the subtle variations between extraction protocols make it challenging to establish a universally efficient procedure capable of sustainably process large quantities of algae at a minimal cost. While researchers achieve impressive yields in the laboratory, these results are not directly applicable from a commercial perspective, as there is no industrial-scale viability. To bridge this gap, research must shift focus to larger-scale settings and incorporate industrial parameters to develop a commercial protocol that delivers high yield and purity of the pigment (Beattie et al. 2018; Carlos et al. 2021). This emphasis on industrial-scale viability remains relevant and critical in the current context.

## 13.2 Conclusion

Natural pigments derived from seaweeds exhibit structural diversity and a wide range of vivid colors, while also serving various functions and applications. Chlorophylls, carotenoids, and phycobiliproteins are pivotal components of the seaweed photosynthesis process. They are finely tuned to capture solar energy within specific wavelengths of the light spectrum and convert it into chemical energy, facilitating the synthesis of essential carbohydrates for the organism. Moreover, many of these pigments play a crucial photoprotective role, shielding the seaweed from excessive radiation.

Seaweed-derived pigments are increasingly preferred over synthetic alternatives, reflecting the contemporary society's heightened awareness and concern for health, lifestyle choices, and the long-term impact on both the environment and personal well-being. The manifold benefits offered by chlorophylls, carotenoids, and phycobiliproteins for human health are well established, encompassing a diverse array of bioactivities. Within the realm of biotechnology, these pigments are in high demand across the food, cosmetic, and pharmaceutical industries due to their unique properties.

Nonetheless, challenges persist in the acquisition of these pigments from macroalgae. The ongoing overexploitation of natural seaweed resources underscores the urgency in developing species-specific cultivation techniques. The inherent physiological variations across different seaweed taxa necessitate the refinement of extraction and purification protocols, which are still undergoing optimization to achieve maximum yields at the species level. This optimization is crucial as these processes transition to an industrial scale, while maintaining sustainability and eco-friendliness. These complexities explain why, within the realm of algae, chlorophylls, carotenoids, and phycobiliproteins are primarily sourced from microalgae. These microalgae benefit from well-mastered culture techniques and optimized extraction methods. On the other hand, similar endeavors with macroalgae are mostly confined to research purposes. Nonetheless, ongoing research highlights the remarkable potential of macroalgae as abundant sources of high-quality natural pigments, warranting further thorough exploration.

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## References

- Abreu MH, Pereira R, Sassi J-F (2015) Marine algae and the global food industry. In: Pereira L, Neto JM (eds) Marine algae: biodiversity, taxonomy, environmental assessment, and biotechnology, 1st edn. CRC Press, Boca Raton, pp 300–319
- Aldred EM, Buck C, Vall K (2009) Terpenes. In: Aldred EM (ed) Pharmacology: a handbook for complementary healthcare professionals. Elsevier, Amsterdam, p 362
- Araujo GS, Santiago CS, Moreira RT et al (2021) Nutrient removal by *Arthrospira platensis* cyanobacteria in cassava processing wastewater. J Water Process Eng 40:101826. <https://doi.org/10.1016/j.jwpe.2020.101826>
- Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141:391–396. <https://doi.org/10.1104/pp.106.082040>
- Aziz E, Batool R, Akhtar W et al (2020) Xanthophyll: health benefits and therapeutic insights. Life Sci 240:117104. <https://doi.org/10.1016/j.lfs.2019.117104>
- Balasubramaniam V, June Chelyn L, Vimala S et al (2020) Carotenoid composition and antioxidant potential of *Eucheuma denticulatum*, *Sargassum polycystum* and *Caulerpa lentillifera*. Heliyon 6:e04654. <https://doi.org/10.1016/j.heliyon.2020.e04654>

- Banerjee K, Ghosh R, Homechaudhuri S, Mitra A (2009) Seasonal variation in the biochemical composition of red seaweed (*Catenella repens*) from Gangetic delta, northeast coast of India. *J Earth Syst Sci* 118:497–505. <https://doi.org/10.1007/S12040-009-0045-2>
- Barbosa M, Inácio LG, Afonso C, Maranhão P (2023) The microalga *Dunaliella* and its applications: a review. *Appl Phycol* 4:99–120. <https://doi.org/10.1080/26388081.2023.2222318>
- Basheva D, Moten D, Stoyanov P et al (2018) Content of phycoerythrin, phycocyanin, allophycocyanin and phycoerythrocyanin in some cyanobacterial strains: applications. *Eng Life Sci* 18:861–866. <https://doi.org/10.1002/elsc.201800035>
- Beattie SW, Moranças M, Délérís P et al (2018) Extraction of phycocyanin and phycoerythrin pigments. In: Charrier B, Wichard T, Reddy CRK (eds) *Protocols for macroalgae research*. CRC Press, Boca Raton, pp 249–265
- Becerra MO, Contreras LM, Lo MH et al (2020) Lutein as a functional food ingredient: stability and bioavailability. *J Funct Foods* 66:103771. <https://doi.org/10.1016/j.jff.2019.103771>
- Begum H, Yusoff FMD, Banerjee S et al (2016) Availability and utilization of pigments from microalgae. *Crit Rev Food Sci Nutr* 56:2209–2222. <https://doi.org/10.1080/10408398.2013.764841>
- Bei H, Guang-Ce W, Chen-Kui Z, Zhen-Gang L (2002) The experimental research of R-phycoerythrin subunits on cancer treatment: a new photosensitizer in PDT. *Cancer Biother Radiopharm* 17:35–42. <https://doi.org/10.1089/10849780252824055>
- Bhat I, Haripriya G, Jogi N, Mamatha BS (2021) Carotenoid composition of locally found seaweeds of Dakshina Kannada district in India. *Algal Res* 53:102154. <https://doi.org/10.1016/j.algal.2020.102154>
- Bi Fai P, Grant A, Reid B (2007) Chlorophyll a fluorescence as a biomarker for rapid toxicity assessment. *Environ Toxicol Chem* 26:1520–1531. <https://doi.org/10.1897/06-394R1.1>
- Bohn T, Bonet ML, Borel P et al (2021) Mechanistic aspects of carotenoid health benefits—where are we now? *Nutr Res Rev* 34:276–302. <https://doi.org/10.1017/S0954422421000147>
- Bonanno G, Orlando-Bonaca M (2018) Chemical elements in Mediterranean macroalgae. A review. *Ecotoxicol Environ Saf* 148:44–71. <https://doi.org/10.1016/j.ecoenv.2017.10.013>
- Borovkov AB, Gudvilovich IN, Lelekov AS, Avsiyan AL (2023) Effect of specific irradiance on productivity and pigment and protein production of *Porphyridium purpureum* (Rhodophyta) semi-continuous culture. *Bioresour Technol* 374:128771. <https://doi.org/10.1016/J.BIORTECH.2023.128771>
- Bourdon L, Jensen AA, Kavanagh JM, McClure DD (2021) Microalgal production of zeaxanthin. *Algal Res* 55:102266. <https://doi.org/10.1016/j.algal.2021.102266>
- Braga ARC, Figueira F, da Silveira JT et al (2016) Improvement of thermal stability of C-phycocyanin by nanofiber and preservative agents. *J Food Process Preserv* 40:1264–1269. <https://doi.org/10.1111/jfpp.12711>
- Brasil Silva E, Ferreira Pinto PV, Bamutsha Chretien J et al (2017) Green optical dissolved oxygen sensor based on a chlorophyll–zinc complex extracted from the plant *Brassica oleracea* L. *Appl Opt* 56:9951. <https://doi.org/10.1364/AO.56.009951>
- Brauch JE (2016) Underutilized fruits and vegetables as potential novel pigment sources. In: Carle R, Schweiggert R (eds) *Handbook on natural pigments in food and beverages: industrial applications for improving food color*. Elsevier, Duxford, pp 305–335
- Braune S, Krüger-Genge A, Kammerer S et al (2021) Phycocyanin from *Arthrospira platensis* as potential anti-cancer drug: review of in vitro and in vivo studies. *Life* 11:91. <https://doi.org/10.3390/life11020091>
- Britton G, Liaaen-Jensen S, Pfander H (2004) *Carotenoids*. Birkhäuser Basel, Basel
- Brotosudarmo T, Heriyanto, Shioi Y et al (2018) Composition of the main dominant pigments from potential two edible seaweeds. *Philipp J Sci* 147:47–55
- Carlos TAV, dos Santos Pires Cavalcante KM, de Cássia Evangelista Oliveira F et al (2021) Pressurized extraction of phycobiliproteins from *Arthrospira platensis* and evaluation of its effect on antioxidant and anticancer activities of these biomolecules. *J Appl Phycol* 33:929–938. <https://doi.org/10.1007/s10811-020-02358-z>

- Carpaena M, Caleja C, Pereira E et al (2021) Red seaweeds as a source of nutrients and bioactive compounds: optimization of the extraction. *Chemosensors* 9:132. <https://doi.org/10.3390/chemosensors9060132>
- Carvalho LG, Pereira L (2015) Review of marine algae as source of bioactive metabolites: a marine biotechnological approach. In: Pereira L, Neto JM (eds) *Marine algae: biodiversity, taxonomy, environmental assessment, and biotechnology*. CRC Press, Boca Raton, pp 195–227
- Chaerle L, Hagenbeek D, De Bruyne E et al (2004) Thermal and chlorophyll-fluorescence imaging distinguish plant-pathogen interactions at an early stage. *Plant Cell Physiol* 45:887–896. <https://doi.org/10.1093/PCP/PCH097>
- Chan PT, Matanjun P, Yasir SM, Tan TS (2015) Antioxidant activities and polyphenolics of various solvent extracts of red seaweed, *Gracilaria changii*. *J Appl Phycol* 27:2377–2386. <https://doi.org/10.1007/s10811-014-0493-1>
- Chang CJ, Yang YH, Liang YC et al (2011) A novel phycobiliprotein alleviates allergic airway inflammation by modulating immune responses. *Am J Respir Crit Care Med* 183:15–25. <https://doi.org/10.1164/rccm.201001-0009OC>
- Chapman RL (2013) Algae: the world's most important “plants”—an introduction. *Mitig Adapt Strateg Glob Chang* 18:5–12. <https://doi.org/10.1007/s11027-010-9255-9>
- Chen H, Jiang P (2018) Combinational biosynthesis and characterization of fusion proteins with tandem repeats of allophycocyanin holo- $\alpha$  subunits, and their application as bright fluorescent labels for immunofluorescence assay. *J Biosci Bioeng* 126:778–782. <https://doi.org/10.1016/j.jbiosc.2018.06.004>
- Chen K, Roca M (2019) Cooking effects on bioaccessibility of chlorophyll pigments of the main edible seaweeds. *Food Chem* 295:101–109. <https://doi.org/10.1016/J.FOODCHEM.2019.05.092>
- Chen H, Liu Q, Zhao J, Jiang P (2016) Biosynthesis, spectral properties and thermostability of cyanobacterial allophycocyanin holo- $\alpha$  subunits. *Int J Biol Macromol* 88:88–92. <https://doi.org/10.1016/j.ijbiomac.2016.03.050>
- Chen K, Ríos JJ, Pérez-Gálvez A, Roca M (2017a) Comprehensive chlorophyll composition in the main edible seaweeds. *Food Chem* 228:625–633. <https://doi.org/10.1016/J.FOODCHEM.2017.02.036>
- Chen X, Wu M, Yang Q, Wang S (2017b) Preparation, characterization of food grade phycobiliproteins from *Porphyra haitanensis* and the application in liposome-meat system. *LWT* 77:468–474. <https://doi.org/10.1016/J.LWT.2016.12.005>
- Chen H, Qi H, Xiong P (2022) Phycobiliproteins—a family of algae-derived biliproteins: productions, characterization and pharmaceutical potentials. *Mar Drugs* 20:450. <https://doi.org/10.3390/md20070450>
- Chen K, Ma T, Ding J et al (2023) Effects of straw return with nitrogen fertilizer reduction on rice (*Oryza sativa* L.) morphology, photosynthetic capacity, yield and water–nitrogen use efficiency traits under different water regimes. *Agronomy* 13:133. <https://doi.org/10.3390/AGRONOMY13010133>
- Chini Zittelli G, Lauceri R, Faraloni C et al (2023) Valuable pigments from microalgae: phycobiliproteins, primary carotenoids, and fucoxanthin. *Photochem Photobiol Sci* 22:1733–1789. <https://doi.org/10.1007/S43630-023-00407-3>
- Cian RE, López-Posadas R, Drago SR et al (2012) Immunomodulatory properties of the protein fraction from *Porphyra columbina*. *J Agric Food Chem* 60:8146–8154. <https://doi.org/10.1021/jf300928j>
- Conde E, Moure A, Domínguez H (2015) Supercritical CO<sub>2</sub> extraction of fatty acids, phenolics and fucoxanthin from freeze-dried *Sargassum muticum*. *J Appl Phycol* 27:957–964. <https://doi.org/10.1007/s10811-014-0389-0>
- Cottas AG, Ribeiro EJ, Watanabe EO, Ferreira JDS (2021) Evaluation of extraction methods and purification by aqueous two-phase systems of phycocyanin from *Anabaena variabilis* and *Noctoc* sp. *Braz J Chem Eng* 38:617–627. <https://doi.org/10.1007/s43153-021-00131-4>
- Cserhádi T (2006) *Liquid chromatography of natural pigments and synthetic dyes*, 1st edn. Elsevier Science, Amsterdam

- Dagnino-Leone J, Figueroa M, Mella C et al (2017) Structural models of the different trimers present in the core of phycobilisomes from *Gracilaria chilensis* based on crystal structures and sequences. PLoS One 12:e0177540. <https://doi.org/10.1371/journal.pone.0177540>
- Dagnino-Leone J, Figueroa M, Uribe E et al (2020) Biosynthesis and characterization of a recombinant eukaryotic allophycocyanin using prokaryotic accessory enzymes. Microbiology 9:e989. <https://doi.org/10.1002/mbo3.989>
- Dagnino-Leone J, Figueroa CP, Castañeda ML et al (2022) Phycobiliproteins: structural aspects, functional characteristics, and biotechnological perspectives. Comput Struct Biotechnol J 20:1506–1527. <https://doi.org/10.1016/J.CSBJ.2022.02.016>
- Darvin ME, Sterry W, Lademann J, Vergou T (2011) The role of carotenoids in human skin. Molecules 16:10491. <https://doi.org/10.3390/MOLECULES161210491>
- Dashwood RH (1997) Chlorophylls as anticarcinogens (Review). Int J Oncol 10:721–727. <https://doi.org/10.3892/ijo.10.4.721>
- Davinelli S, Nielsen ME, Scapagnini G (2018) Astaxanthin in skin health, repair, and disease: a comprehensive review. Nutrients 10:522. <https://doi.org/10.3390/nu10040522>
- de Morais MG, da Fontoura Prates D, Moreira JB et al (2018) Phycocyanin from microalgae: properties, extraction and purification, with some recent applications. Ind Biotechnol 14:30–37. <https://doi.org/10.1089/ind.2017.0009>
- de Rosso VV, Mercadante AZ (2007) Identification and quantification of carotenoids, by HPLC-PDA-MS/MS, from Amazonian fruits. J Agric Food Chem 55:5062–5072. <https://doi.org/10.1021/jf0705421>
- Dias MG, Borge GIA, Kljak K et al (2021) European database of carotenoid levels in foods. Factors affecting carotenoid content. Food Secur 10:912. <https://doi.org/10.3390/foods10050912>
- Dufossé L (2016) Current and potential natural pigments from microorganisms (bacteria, yeasts, fungi, microalgae). In: Carle R, Schweiggert RM (eds) Handbook on natural pigments in food and beverages: industrial applications for improving food color. Woodhead Publishing, Amsterdam, pp 337–354
- Dufossé L, Galaup P, Yaron A et al (2005) Microorganisms and microalgae as sources of pigments for food use: a scientific oddity or an industrial reality? Trends Food Sci Technol 16:389–406. <https://doi.org/10.1016/j.tifs.2005.02.006>
- Dumay J, Moranças M (2016) Proteins and pigments. In: Fleurence J, Levine IA (eds) Seaweed in health and disease prevention. Elsevier Academic Press, London, pp 275–318
- Dumay J, Clément N, Moranças M, Fleurence J (2013) Optimization of hydrolysis conditions of *Palmaria palmata* to enhance R-phycoerythrin extraction. Bioresour Technol 131:21–27. <https://doi.org/10.1016/j.biortech.2012.12.146>
- Dumay J, Moranças M, Munier M et al (2014) Phycoerythrins: valuable proteinic pigments in red seaweeds. Adv Bot Res 71:321–343. <https://doi.org/10.1016/B978-0-12-408062-1.00011-1>
- Eggersdorfer M, Wyss A (2018) Carotenoids in human nutrition and health. Arch Biochem Biophys 652:18–26. <https://doi.org/10.1016/j.abb.2018.06.001>
- Eisele LE, Bakhru SH, Liu X et al (2000) Studies on C-phycoerythrin from *Cyanidium caldarium*, a eukaryote at the extremes of habitat. BBA-Bioenergetics 1456:99–107. [https://doi.org/10.1016/S0005-2728\(99\)00110-3](https://doi.org/10.1016/S0005-2728(99)00110-3)
- Eismann AI, Perpetuo Reis R, Ferreira da Silva A, Negrão Cavalcanti D (2020) *Ulva* spp. carotenoids: responses to environmental conditions. Algal Res 48:101916. <https://doi.org/10.1016/j.algal.2020.101916>
- Elbahnaswy S, Elshopakey GE (2023) Recent progress in practical applications of a potential carotenoid astaxanthin in aquaculture industry: a review. Fish Physiol Biochem 2023:1–30. <https://doi.org/10.1007/S10695-022-01167-0>
- Esteban R, Martínez B, Fernández-Marín B et al (2009) Carotenoid composition in Rhodophyta: insights into xanthophyll regulation in *Corallina elongata*. Eur J Phycol 44:221–230. <https://doi.org/10.1080/09670260802439109>
- Fakhri S, Abbaszadeh F, Dargahi L, Jorjani M (2018) Astaxanthin: a mechanistic review on its biological activities and health benefits. Pharmacol Res 136:1–20. <https://doi.org/10.1016/j.phrs.2018.08.012>

- Farag MR, Alagawany M, El-Hack MEA, Dhama K (2016) Nutritional and health aspects of *Spirulina (Arthrospira)* for poultry, animals and human. *Int J Pharmacol* 12:36–51. <https://doi.org/10.3923/ijp.2016.36.51>
- Febbo E, Richard C, Horlin E et al (2012) PAM chlorophyll a fluorometry for monitoring health of corals along the coast of Qatar. Society of Petroleum Engineers – SPE/APPEA Int conference on health, safety and environment in oil and gas exploration and production 2012: protecting people and the environment – evolving challenges 2:1159–1172. <https://doi.org/10.2118/156815-MS>
- Fernández-Rojas B, Hernández-Juárez J, Pedraza-Chaverri J (2014) Nutraceutical properties of Phycocyanin. *J Funct Foods* 11:375–392. <https://doi.org/10.1016/j.jff.2014.10.011>
- Fernández-Sevilla JM, Acien Fernández FG, Molina Grima E (2010) Biotechnological production of lutein and its applications. *Appl Microbiol Biotechnol* 86:27–40. <https://doi.org/10.1007/s00253-009-2420-y>
- Ferreira MS, Resende DISP, Sousa Lobo JM et al (2021) Marine ingredients for sensitive skin: market overview. *Mar Drugs* 19:464. <https://doi.org/10.3390/MD19080464>
- Fiedor J, Burda K (2014) Potential role of carotenoids as antioxidants in human health and disease. *Nutrients* 6:466–488. <https://doi.org/10.3390/nu6020466>
- Firdous AP, Kuttan G, Kuttan R (2015) Anti-inflammatory potential of carotenoid meso-zeaxanthin and its mode of action. *Pharm Biol* 53:961–967. <https://doi.org/10.3109/13880209.2014.950673>
- Fleurence J (2003) R-phycoerythrin from red macroalgae: strategies for extraction and potential application in biotechnology. *Appl Biotechnol Food Sci Policy* 1:1–6
- Francavilla M, Franchi M, Monteleone M, Caroppo C (2013) The red seaweed *Gracilaria gracilis* as a multi products source. *Mar Drugs* 11:3754–3776. <https://doi.org/10.3390/md11103754>
- Francavilla M, Manara P, Kamaterou P et al (2015) Cascade approach of red macroalgae *Gracilaria gracilis* sustainable valorization by extraction of phycobiliproteins and pyrolysis of residue. *Bioresour Technol* 184:305–313. <https://doi.org/10.1016/j.biortech.2014.10.147>
- Freitas MV, Inácio LG, Martins M et al (2022) Primary composition and pigments of 11 red seaweed species from the Center of Portugal. *J Mar Sci Eng* 10:1168. <https://doi.org/10.3390/jmse10091168>
- Frense D, Müller A, Beckmann D (1998) Detection of environmental pollutants using optical biosensor with immobilized algae cells. *Sens Actuators B Chem* 51:256–260. [https://doi.org/10.1016/S0925-4005\(98\)00203-2](https://doi.org/10.1016/S0925-4005(98)00203-2)
- Fujii R, Kita M, Doe M et al (2012) The pigment stoichiometry in a chlorophyll a/c type photosynthetic antenna. *Photosynth Res* 111:165–172. <https://doi.org/10.1007/S11120-011-9698-1/TABLES/2>
- Galland-Irmouli AV, Pons L, Luçon M et al (2000) One-step purification of R-phycoerythrin from the red macroalga *Palmaria palmata* using preparative polyacrylamide gel electrophoresis. *J Chromatogr B: Biomed Sci Appl* 739:117–123
- Gammone MA, Riccioni G, D’Orazio N (2015) Carotenoids: potential allies of cardiovascular health? *Food Nutr Res* 59:26762. <https://doi.org/10.3402/fnr.v59.26762>
- Garcia-Perez P, Lourenço-Lopes C, Silva A et al (2022) Pigment composition of nine brown algae from the Iberian Northwestern coastline: influence of the extraction solvent. *Mar Drugs* 20:113. <https://doi.org/10.3390/MD20020113>
- Gevaert F, Creach A, Davoult D et al (2002) Photo-inhibition and seasonal photosynthetic performance of the seaweed *Laminaria saccharina* during a simulated tidal cycle: chlorophyll fluorescence measurements and pigment analysis. *Plant Cell Environ* 25:859–872. <https://doi.org/10.1046/J.1365-3040.2002.00869.X>
- Glazer AN (1994) Phycobiliproteins – a family of valuable, widely used fluorophores. *J Appl Phycol* 6:105–112. <https://doi.org/10.1007/BF02186064>
- Godínez-Ortega JL, Snoeijs P, Robledo D et al (2008) Growth and pigment composition in the red alga *Halymenia floresii* cultured under different light qualities. *J Appl Phycol* 20:253–260. <https://doi.org/10.1007/S10811-007-9241-0/FIGURES/5>

- Gomes L, Monteiro P, Cotas J et al (2022) Seaweeds' pigments and phenolic compounds with antimicrobial potential. *Biomol Concepts* 13:89–102. <https://doi.org/10.1515/BMC-2022-0003>
- González S, Astner S, An W et al (2003) Dietary lutein/zeaxanthin decreases ultraviolet B-induced epidermal hyperproliferation and acute inflammation in hairless mice. *J Invest Dermatol* 121:399–405. <https://doi.org/10.1046/j.1523-1747.2003.12355.x>
- Gu D, Lazo-Portugal R, Fang C et al (2018) Purification of R-phycoerythrin from *Gracilaria lemaneiformis* by centrifugal precipitation chromatography. *J Chromatogr B Analyt Technol Biomed Life Sci* 1087–1088:138–141. <https://doi.org/10.1016/j.jchromb.2018.04.047>
- Guo Y, Tan J (2015) Recent advances in the application of chlorophyll a fluorescence from photosystem II. *Photochem Photobiol* 91:1–14. <https://doi.org/10.1111/PHP.12362>
- Guo Y, Zang X, Cao X et al (2020) Cloning and expression of Allophycocyanin gene from *Gracilaria lemaneiformis* and studying the binding sites of phycocyanobilin on its  $\alpha$  and  $\beta$  subunits. *J Appl Phycol* 32:2657–2671. <https://doi.org/10.1007/s10811-020-02102-7>
- Han D, Li Y, Hu Q (2013) Astaxanthin in microalgae: pathways, functions and biotechnological implications. *Algae* 28:131–147. <https://doi.org/10.4490/ALGAE.2013.28.2.131>
- Hao S, Li S, Wang J et al (2018) Phycocyanin reduces proliferation of melanoma cells through downregulating GRB2/ERK signaling. *J Agric Food Chem* 66:10921–10929. <https://doi.org/10.1021/acs.jafc.8b03495>
- Hegazi MM, Pérez-Ruzafa A, Almela L, Candela ME (1998) Separation and identification of chlorophylls and carotenoids from *Caulerpa prolifera*, *Jania rubens* and *Padina pavonica* by reversed-phase high-performance liquid chromatography. *J Chromatogr A* 829:153–159. [https://doi.org/10.1016/S0021-9673\(98\)00803-6](https://doi.org/10.1016/S0021-9673(98)00803-6)
- Hemlata, Afreen S, Fatma T (2018) Extraction, purification and characterization of phycoerythrin from *Microchaete* and its biological activities. *Biocatal Agric Biotechnol* 13:84–89. <https://doi.org/10.1016/j.bcab.2017.11.012>
- Himeshima N, Amao Y (2005) Green process for hydrogen production from cellulose derivative using visible light-harvesting function of Mg chlorophyll-a. *Green Chem* 7:742–746. <https://doi.org/10.1039/B504377H>
- Hsieh-Lo M, Castillo G, Ochoa-Becerra MA, Mojica L (2019) Phycocyanin and phycoerythrin: strategies to improve production yield and chemical stability. *Algal Res* 42:101600. <https://doi.org/10.1016/j.algal.2019.101600>
- Huang Y, Thomson SJ, Molin WT et al (2012) Early detection of soybean plant injury from glyphosate by measuring chlorophyll reflectance and fluorescence. *J Agric Sci* 4:p117. <https://doi.org/10.5539/JAS.V4N5P117>
- Huang C-H, Chen W-C, Gao Y-H et al (2021) Enzyme-assisted method for phycobiliproteins extraction from *Porphyra* and evaluation of their bioactivity. *Processes* 9:560. <https://doi.org/10.3390/pr9030560>
- Husu I, Rodio G, Touloupakis E et al (2013) Insights into photo-electrochemical sensing of herbicides driven by *Chlamydomonas reinhardtii* cells. *Sens Actuators B Chem* 185:321–330. <https://doi.org/10.1016/J.SNB.2013.05.013>
- Ismail MM, Osman MEH (2016) Seasonal fluctuation of photosynthetic pigments of most common red seaweeds species collected from Abu Qir, Alexandria, Egypt. *Rev Biol Mar Oceanogr* 51:515–525. <https://doi.org/10.4067/S0718-19572016000300004>
- Jaeschke DP, Teixeira IR, Marczak LDF, Mercali GD (2021) Phycocyanin from *Spirulina*: a review of extraction methods and stability. *Food Res Int* 143:110314. <https://doi.org/10.1016/j.foodres.2021.110314>
- Janarthanan M, Senthil Kumar M (2017) The properties of bioactive substances obtained from seaweeds and their applications in textile industries. *J Ind Text* 48:361–401. <https://doi.org/10.1177/1528083717692596>
- Jesumani V, Du H, Aslam M et al (2019) Potential use of seaweed bioactive compounds in skin-care – a review. *Mar Drugs* 17:688. <https://doi.org/10.3390/MD17120688>
- Jesús VC, Gutiérrez-Rebolledo GA, Hernández-Ortega M et al (2016) Methods for extraction, isolation and purification of C-phycoerythrin: 50 years of research in review. *Int J Food Nutr Sci* 3:275–284. <https://doi.org/10.15436/2377-0619.16.946>

- Jiang L, Wang Y, Yin Q et al (2017) Phycocyanin: a potential drug for cancer treatment. *J Cancer* 8:3416–3429. <https://doi.org/10.7150/jca.21058>
- Kalasaraya HS, Pereira L, Patel NB (2022) Pioneering role of marine macroalgae in cosmeceuticals. *Phycology* 2:172–203. <https://doi.org/10.3390/PHYCOLOGY2010010>
- Kannaujiya VK, Sundaram S, Sinha RP (2017) *Phycobiliproteins: recent developments and future applications*, 1st edn. Springer Singapore, Singapore
- Kannaujiya VK, Kumar D, Singh V, Sinha RP (2021) Advances in phycobiliproteins research: innovations and commercialization. In: Sinha RP, Häder D-P (eds) *Natural bioactive compounds: technological advancements*. Academic Press, London, pp 57–81
- Karpiński TM, Adamczak A (2019) Fucoxanthin—an antibacterial carotenoid. *Antioxidants* 8. [https://doi.org/10.3390/ANTIOX8080239/ANTIOXIDANTS\\_08\\_00239\\_PDF.PDF](https://doi.org/10.3390/ANTIOX8080239/ANTIOXIDANTS_08_00239_PDF.PDF)
- Kasanah N, Ulfah M, Imania O et al (2022) Rhodophyta as potential sources of photoprotectants, anti-photoaging compounds, and hydrogels for cosmeceutical application. *Molecules* 27:7788. <https://doi.org/10.3390/MOLECULES27227788>
- Kato K, Shinoda T, Nagao R et al (2020) Structural basis for the adaptation and function of chlorophyll *f* in photosystem I. *Nat Commun* 11:238. <https://doi.org/10.1038/S41467-019-13898-5>
- Koizumi J, Takatani N, Kobayashi N et al (2018) Carotenoid profiling of a red seaweed *Pyropia yezoensis*: insights into biosynthetic pathways in the order Bangiales. *Mar Drugs* 16:1–14. <https://doi.org/10.3390/md16110426>
- Koo SY, Cha KH, Song DG et al (2012) Optimization of pressurized liquid extraction of zeaxanthin from *Chlorella ellipsoidea*. *J Appl Phycol* 24:725–730. <https://doi.org/10.1007/s10811-011-9691-2>
- Krinsky NI, Johnson EJ (2005) Carotenoid actions and their relation to health and disease. *Mol Asp Med* 26:459–516. <https://doi.org/10.1016/j.mam.2005.10.001>
- Kuddus M, Singh P, Thomas G, Al-Hazimi A (2013) Recent developments in production and biotechnological applications of C-phycocyanin. *Biomed Res Int* 2013:742859. <https://doi.org/10.1155/2013/742859>
- Kulczyński B, Gramza-Michałowska A, Kobus-Cisowska J, Kmiecik D (2017) The role of carotenoids in the prevention and treatment of cardiovascular disease – current state of knowledge. *J Funct Foods* 38:45–65. <https://doi.org/10.1016/j.jff.2017.09.001>
- Lamers PP, Janssen M, De Vos RCH et al (2008) Exploring and exploiting carotenoid accumulation in *Dunaliella salina* for cell-factory applications. *Trends Biotechnol* 26:631–638
- Lanfer-Marquez UM, Barros RMC, Sinnecker P (2005) Antioxidant activity of chlorophylls and their derivatives. *Food Res Int* 38:885–891. <https://doi.org/10.1016/j.foodres.2005.02.012>
- Larkum AWD, Grossman AR, Raven JA (2021) *Photosynthesis in algae: biochemical and physiological mechanisms*. Springer International Publishing, New York
- Le Guillard C, Dumay J, Donnay-Moreno C et al (2015) Ultrasound-assisted extraction of R-phycoerythrin from *Grateloupia turuturu* with and without enzyme addition. *Algal Res* 12:522–528. <https://doi.org/10.1016/j.algal.2015.11.002>
- Leandro A, Pereira L, Gonçalves AMM (2020) Diverse applications of marine macroalgae. *Mar Drugs* 18:1–15. <https://doi.org/10.3390/md18010017>
- Lee D, Nishizawa M, Shimizu Y, Saeki H (2017) Anti-inflammatory effects of dulse (*Palmaria palmata*) resulting from the simultaneous water-extraction of phycobiliproteins and chlorophyll a. *Food Res Int* 100:514–521. <https://doi.org/10.1016/j.foodres.2017.06.040>
- Lee HG, Lu YA, Je JG et al (2021a) Effects of ethanol extracts from *Grateloupia elliptica*, a red seaweed, and its chlorophyll derivative on 3T3-L1 adipocytes: suppression of lipid accumulation through downregulation of adipogenic protein expression. *Mar Drugs* 19:91. <https://doi.org/10.3390/MD19020091>
- Lee MC, Yeh HY, Jhang FJ et al (2021b) Enhancing growth, phycoerythrin production, and pigment composition in the red alga *Colaconema* sp. through optimal environmental conditions in an indoor system. *Bioresour Technol* 333:125199. <https://doi.org/10.1016/J.BIORTECH.2021.125199>

- Lee PT, Yeh HY, Lung WQC et al (2021c) R-phycoerythrin from *Colaconema formosanum* (Rhodophyta), an anti-allergic and collagen promoting material for cosmeceuticals. Appl Sci (Switzerland) 11:9425. <https://doi.org/10.3390/APP11209425>
- Leney AC, Tschanz A, Heck AJR (2018) Connecting color with assembly in the fluorescent B-phycoerythrin protein complex. FEBS J 285:178–187. <https://doi.org/10.1111/febs.14331>
- Li W, Su HN, Pu Y et al (2019a) Phycobiliproteins: molecular structure, production, applications, and prospects. Biotechnol Adv 37:340–353. <https://doi.org/10.1016/j.biotechadv.2019.01.008>
- Li Y, Song H, Zhou L et al (2019b) Tracking chlorophyll fluorescence as an indicator of drought and rewetting across the entire leaf lifespan in a maize field. Agric Water Manag 211:190–201. <https://doi.org/10.1016/j.agwat.2018.09.050>
- Li N, Liu Z, Wang P et al (2022) Effects of sodium hypochlorite treatment on the chlorophyll fluorescence in photosystem II of microalgae. Sci Total Environ 833:155192. <https://doi.org/10.1016/j.scitotenv.2022.155192>
- Lim KC, Yusoff FM, Shariff M, Kamarudin MS (2018) Astaxanthin as feed supplement in aquatic animals. Rev Aquac 10:738–773. <https://doi.org/10.1111/RAQ.12200>
- Lin A, Shen S, Wang G et al (2011) Comparison of chlorophyll and photosynthesis parameters of floating and attached *Ulva prolifera*. J Integr Plant Biol 53:25–34. <https://doi.org/10.1111/j.1744-7909.2010.01002.x>
- Liu Q, Wang Y, Cao M et al (2015) Anti-allergic activity of R-phycoerythrin from *Porphyra haitanensis* in antigen-sensitized mice and mast cells. Int Immunopharmacol 25:465–473. <https://doi.org/10.1016/j.intimp.2015.02.032>
- Liu Q, Huang Y, Zhang R et al (2016) Medical application of *Spirulina platensis* derived C-phycoerythrin. Evid Based Complement Alternat Med 2016. <https://doi.org/10.1155/2016/7803846>
- Liu Z, Sun X, Sun X et al (2019) Fucoxanthin isolated from *Undaria pinnatifida* can interact with *Escherichia coli* and *Lactobacilli* in the intestine and inhibit the growth of pathogenic bacteria. J Ocean Univ China 18:926–932. <https://doi.org/10.1007/s11802-019-4019-y>
- Liu Z, Li W, Xu Z et al (2022) Effects of different nitrogen forms and concentrations on seedling growth traits and physiological characteristics of *Populus simonii* × *P. nigra*. J For Res (Harbin) 33:1593–1606. <https://doi.org/10.1007/S11676-021-01447-0>
- Long JR, Ma GH, Wan YZ et al (2013) Effects of nitrogen fertilizer level on chlorophyll fluorescence characteristics in flag leaf of super hybrid rice at late growth stage. Rice Sci 20:220–228. [https://doi.org/10.1016/S1672-6308\(13\)60138-9](https://doi.org/10.1016/S1672-6308(13)60138-9)
- Lourenço-Lopes C, Carreira-Casais A, Carperna M et al (2023) Emerging technologies to extract fucoxanthin from *Undaria pinnatifida*: microwave vs. ultrasound assisted extractions. Mar Drugs 21:282. <https://doi.org/10.3390/md21050282>
- Lüder UH, Knoetzel J, Wiencke C (2001) Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic antarctic red macroalga *Palmaria decipiens*. Polar Biol 24:231–236. <https://doi.org/10.1007/s003000100260>
- Lumbessy SY, Junaidi M, Diniarti N et al (2021) Identification of chlorophyll pigment on *Gracilaria salicornia* seaweed. IOP Conf Ser Earth Environ Sci 681:12017. <https://doi.org/10.1088/1755-1315/681/1/012017>
- Ma L, Lin XM (2010) Effects of lutein and zeaxanthin on aspects of eye health. J Sci Food Agric 90:2–12. <https://doi.org/10.1002/jsfa.3785>
- Ma J, Hu J, Sha X et al (2022) Phycobiliproteins, the pigment-protein complex form of natural food colorants and bioactive ingredients. Crit Rev Food Sci Nutr 4:1–19. <https://doi.org/10.1080/10408398.2022.2128714>
- MacColl R, Eisele LE, Williams EC, Bowser SS (1996) The discovery of a novel R-phycoerythrin from an Antarctic red alga. J Biol Chem 271:17157–17160. <https://doi.org/10.1074/jbc.271.29.17157>
- Maeda H, Fukuda S, Izumi H, Saga N (2018) Anti-oxidant and fucoxanthin contents of brown alga *Ishimozuku (Sphaerotrichia divaricata)* from the West Coast of Aomori, Japan. Mar Drugs 16:0255. <https://doi.org/10.3390/md16080255>

- Malairaj S, Muthu S, Gopal VB et al (2016) Qualitative and quantitative determination of R-phycoerythrin from *Halymenia floresia* (Clemente) C. Agardh by polyacrylamide gel using electrophoretic elution technique. *J Chromatogr A* 1454:120–126. <https://doi.org/10.1016/j.chroma.2016.05.063>
- Mandal R, Dutta G (2020) From photosynthesis to biosensing: chlorophyll proves to be a versatile molecule. *Sens Int* 1:100058. <https://doi.org/10.1016/j.sintl.2020.100058>
- Manirafasha E, Guo L, Jing K (2020) Nutraceutical and pharmaceutical applications of phycobiliproteins. In: Jacob-Lopes E, Queiroz MI, Zepka LQ (eds) *Pigments from microalgae* handbook. Springer, Cham, pp 577–654
- Maoka T (2009) Recent progress in structural studies of carotenoids in animals and plants. *Arch Biochem Biophys* 483:191–195. <https://doi.org/10.1016/J.ABB.2008.10.019>
- Maoka T (2020) Carotenoids as natural functional pigments. *J Nat Med* 74:1–16. <https://doi.org/10.1007/s11418-019-01364-x>
- Marková I, Koničková R, Vaňková K et al (2020) Anti-angiogenic effects of the blue-green alga *Arthrospira platensis* on pancreatic cancer. *J Cell Mol Med* 24:2402–2415. <https://doi.org/10.1111/jcmm.14922>
- Martins M, Fernandes APM, Torres-Acosta MA et al (2023) Extraction of chlorophyll from wild and farmed *Ulva* spp. using aqueous solutions of ionic liquids. *Sep Purif Technol* 254:117589. <https://doi.org/10.1016/J.SEPPUR.2020.117589>
- Mayne ST (1996) Beta-carotene, carotenoids, and disease prevention in humans. *FASEB J* 10:690–701. <https://doi.org/10.1096/fasebj.10.7.8635686>
- Meléndez-Martínez AJ, Mandić AI, Bantis F et al (2020) A comprehensive review on carotenoids in foods and feeds: status quo, applications, patents, and research needs. *Crit Rev Food Sci Nutr* 5:1–51. <https://doi.org/10.1080/10408398.2020.1867959>
- Méresse S, Fodil M, Fleury F, Chénais B (2020) Fucoxanthin, a marine-derived carotenoid from brown seaweeds and microalgae: a promising bioactive compound for cancer therapy. *Int J Mol Sci* 21:1–27. <https://doi.org/10.3390/ijms21239273>
- Merz D, Geyer M, Moss DA, Ache HJ (1996) Chlorophyll fluorescence biosensor for the detection of herbicides. *Anal Bioanal Chem* 354:299–305. <https://doi.org/10.1007/S0021663540299>
- Miki W (1991) Biological functions and activities of animal carotenoids. *Pure Appl Chem* 63:141–146. <https://doi.org/10.1351/PAC199163010141/MACHINEREADABLECITATION/RIS>
- Ming JX, Wang ZC, Huang Y et al (2021) Fucoxanthin extracted from *Laminaria japonica* inhibits metastasis and enhances the sensitivity of lung cancer to Gefitinib. *J Ethnopharmacol* 265:113302. <https://doi.org/10.1016/j.jep.2020.113302>
- Mittal R, Raghavarao KSMS (2018) Extraction of R-Phycoerythrin from marine macroalgae, *Gelidium pusillum*, employing consortia of enzymes. *Algal Res* 34:1–11. <https://doi.org/10.1016/j.algal.2018.07.002>
- Mittal R, Tavanandi HA, Mantri VA, Raghavarao KSMS (2017) Ultrasound assisted methods for enhanced extraction of phycobiliproteins from marine macro-algae, *Gelidium pusillum* (Rhodophyta). *Ultrason Sonochem* 38:92–103. <https://doi.org/10.1016/j.ultsonch.2017.02.030>
- Mittal R, Sharma R, Raghavarao K (2019) Aqueous two-phase extraction of R-Phycoerythrin from marine macro-algae, *Gelidium pusillum*. *Bioresour Technol* 280:277–286. <https://doi.org/10.1016/j.biortech.2019.02.044>
- Morais T, Cotas J, Pacheco D, Pereira L (2021) Seaweeds compounds: an ecosystem sustainable source of cosmetic ingredients? *Cosmetics* 8:8. <https://doi.org/10.3390/COSMETICS8010008>
- Morocho-Jácome AL, Ruscinc N, Martinez RM et al (2020) (Bio)Technological aspects of microalgae pigments for cosmetics. *Appl Microbiol Biotechnol* 104:9513–9522. <https://doi.org/10.1007/s00253-020-10936-x>
- Munier M, Jubeau S, Wijaya A et al (2014) Physicochemical factors affecting the stability of two pigments: R-phycoerythrin of *Grateloupia turuturu* and B-phycoerythrin of *Porphyridium cruentum*. *Food Chem* 150:400–407. <https://doi.org/10.1016/j.foodchem.2013.10.113>
- Munier M, Moranchais M, Dumay J et al (2015) One-step purification of R-phycoerythrin from the red edible seaweed *Grateloupia turuturu*. *J Chromatogr B Analyt Technol Biomed Life Sci* 992:23–29. <https://doi.org/10.1016/j.jchromb.2015.04.012>

- Muñoz-Miranda LA, Iñiguez-Moreno M (2023) An extensive review of marine pigments: sources, biotechnological applications, and sustainability. *Aquat Sci* 85:68. <https://doi.org/10.1007/s00027-023-00966-8>
- Muradian Kh, Vaiserman A, Min K-J, Fraifeld VE (2015) Fucoxanthin and lipid metabolism: A minireview. *Nutr Metab Cardiovasc Dis* 25:891–897. <https://doi.org/10.1016/j.numecd.2015.05.010>
- Murillo AG, Hu S, Fernandez ML (2019) Zeaxanthin: metabolism, properties, and antioxidant protection of eyes, heart, liver, and skin. *Antioxidants* 8:390. <https://doi.org/10.3390/antiox8090390>
- Murray MT, Capelli B (2020)  $\beta$ -carotene and other carotenoids. In: *Textbook of natural medicine*, pp 443–450.e2. <https://doi.org/10.1016/B978-0-323-43044-9.00057-1>
- Mysliwa-Kurczel B, Solymosi K (2016) Phycobilins and phycobiliproteins used in food industry and medicine. *Mini-Rev Med Chem* 17:1173–1193. <https://doi.org/10.2174/1389557516666160912180155>
- Nagaraj S, Arulmurugan P, Rajaram MG et al (2012) Hepatoprotective and antioxidative effects of C-phycoerythrin from *Arthrospira maxima* SAG 25780 in CCl<sub>4</sub>-induced hepatic damage rats. *Biomed Prev Nutr* 2:81–85. <https://doi.org/10.1016/j.bionut.2011.12.001>
- Nakano T, Wiegertjes G (2020) Properties of carotenoids in fish fitness: a review. *Mar Drugs* 18. <https://doi.org/10.3390/MD18110568>
- Nawaz A, Chaudhary R, Shah Z et al (2020) An overview on industrial and medical applications of bio-pigments synthesized by marine bacteria. *Microorganisms* 9:1–24. <https://doi.org/10.3390/MICROORGANISMS9010011>
- Nazarudin MF, Isha A, Mastuki SN et al (2020) Chemical composition and evaluation of the  $\alpha$ -glucosidase inhibitory and cytotoxic properties of marine algae *Ulva intestinalis*, *Halimeda macroloba*, and *Sargassum ilicifolium*. *Evid Based Complement Alternat Med* 2020:2753945. <https://doi.org/10.1155/2020/2753945>
- Nguyen HPT, Morançais M, Fleurence J, Dumay J (2017) *Mastocarpus stellatus* as a source of R-phycoerythrin: optimization of enzyme assisted extraction using response surface methodology. *J Appl Phycol* 29:1563–1570. <https://doi.org/10.1007/s10811-016-1024-z>
- Nguyen HPT, Morançais M, Déléris P et al (2020) Purification of R-phycoerythrin from a marine macroalga *Gracilaria gracilis* by anion-exchange chromatography. *J Appl Phycol* 32:553–561. <https://doi.org/10.1007/s10811-019-01947-x>
- Niu JF, Chen ZF, Wang GC, Zhou BC (2010) Purification of phycoerythrin from *Porphyra yezoensis* Ueda (Bangiales, Rhodophyta) using expanded bed absorption. *J Appl Phycol* 22:25–31. <https://doi.org/10.1007/s10811-009-9420-2>
- Niu J, Xu M, Wang G et al (2013) Comprehensive extraction of agar and R-phycoerythrin from *Gracilaria lemaneiformis* (Bangiales, Rhodophyta). *Indian J Mar Sci* 42:21–28
- Nomura M, Kamogawa H, Susanto E et al (2013) Seasonal variations of total lipids, fatty acid composition, and fucoxanthin contents of *Sargassum horneri* (Turner) and *Cystoseira hakodatensis* (Yendo) from the northern seashore of Japan. *J Appl Phycol* 25:1159–1169. <https://doi.org/10.1007/s10811-012-9934-x>
- Noviendri D, Hasrini RF, Subaryono, Marraskuranto E (2022) Biopigments (phycoerythrin, fucoxanthin and siphonaxanthin) from seaweeds and their potential applications as ingredients in cosmeceutical industries: a review. *IOP Conf Ser Earth Environ Sci* 1118:012028. <https://doi.org/10.1088/1755-1315/1118/1/012028>
- Nowruzi B, Konur O, Amir S, Anvar A (2022) The stability of the phycobiliproteins in the adverse environmental conditions relevant to the food storage. *Food Bioprocess Technol* 15:2646–2663. <https://doi.org/10.1007/s11947-022-02855-8>
- O'Connor I, O'Brien N (1998) Modulation of UVA light-induced oxidative stress by beta-carotene, lutein and astaxanthin in cultured fibroblasts. *J Dermatol Sci* 16:226–230. [https://doi.org/10.1016/s0923-1811\(97\)00058-3](https://doi.org/10.1016/s0923-1811(97)00058-3)
- Ogashawara I (2020) Determination of phycocyanin from space—a bibliometric analysis. *Remote Sens* 12:567. <https://doi.org/10.3390/rs12030567>

- Ojulari OV, Gi Lee S, Nam JO (2020) Therapeutic effect of seaweed derived xanthophyl carotenoid on obesity management; overview of the last decade. *Int J Mol Sci* 21:2502. <https://doi.org/10.3390/ijms21072502>
- Online Etymology Dictionary Photosynthesis | Etymology, origin and meaning of photosynthesis by etymonline. <https://www.etymonline.com/word/photosynthesis>. Accessed 13 Apr 2023
- Osório C, Machado S, Peixoto J et al (2020) Pigments content (Chlorophylls, fucoxanthin and phycobiliproteins) of different commercial dried algae. *Separations* 7:1–14. <https://doi.org/10.3390/separations7020033>
- Padhi B, Chauhan G, Kandoi D et al (2021) A comparison of chlorophyll fluorescence transient measurements, using handy pea and fluorpen fluorometers. *Photosynthetica* 59:399–408. <https://doi.org/10.32615/PS.2021.026>
- Pádua D, Rocha E, Gargiulo D, Ramos AA (2015) Bioactive compounds from brown seaweeds: phloroglucinol, fucoxanthin and fucoidan as promising therapeutic agents against breast cancer. *Phytochem Lett* 14:91–98. <https://doi.org/10.1016/j.phytol.2015.09.007>
- Pagels F, Guedes AC, Amaro HM et al (2019) Phycobiliproteins from cyanobacteria: chemistry and biotechnological applications. *Biotechnol Adv* 37:422–443. <https://doi.org/10.1016/j.biotechadv.2019.02.010>
- Pangestuti R, Kim SK (2011a) Neuroprotective effects of marine algae. *Mar Drugs* 9:803–818. <https://doi.org/10.3390/MD9050803>
- Pangestuti R, Kim SK (2011b) Biological activities and health benefit effects of natural pigments derived from marine algae. *J Funct Foods* 3:255–266. <https://doi.org/10.1016/j.jff.2011.07.001>
- Park JJ, Lee WY (2021) Anti-glycation effects of brown algae extracts and its phenolic compounds. *Food Biosci* 41:101042. <https://doi.org/10.1016/J.FBIO.2021.101042>
- Park HJ, Lee MK, Park YB et al (2011) Beneficial effects of *Undaria pinnatifida* ethanol extract on diet-induced-insulin resistance in C57BL/6J mice. *Food Chem Toxicol* 49:727–733. <https://doi.org/10.1016/j.fct.2010.11.032>
- Patel AS, Lakshmi-balasubramaniam SP, Nayak B (2020) Steric stabilization of phycobiliprotein loaded liposome through polyethylene glycol adsorbed cellulose nanocrystals and their impact on the gastrointestinal tract. *Food Hydrocoll* 98:105252. <https://doi.org/10.1016/j.foodhyd.2019.105252>
- Patel SN, Sonani RR, Roy D et al (2022) Exploring the structural aspects and therapeutic perspectives of cyanobacterial phycobiliproteins. *3 Biotech* 12(9):1–15. <https://doi.org/10.1007/S13205-022-03284-2>
- Pattarayan D, Rajarajan D, Ayyanar S et al (2017) C-phycoyanin suppresses transforming growth factor- $\beta$ 1-induced epithelial mesenchymal transition in human epithelial cells. *Pharmacol Rep* 69:426–431. <https://doi.org/10.1016/j.pharep.2016.12.013>
- Peguero-Pina JJ, Morales F, Gil-Pelegrín E (2008) Frost damage in *Pinus sylvestris* L. stems assessed by chlorophyll fluorescence in cortical bark chlorenchyma. *Ann For Sci* 65:813–813. <https://doi.org/10.1051/FOREST:2008068/METRICS>
- Pemberton RM, Amine A, Hart JP (2007) Voltammetric behavior of chlorophyll a at a screen-printed carbon electrode and its potential role as a biomarker for monitoring fecal contamination. *Anal Lett* 37:1625–1643. <https://doi.org/10.1081/AL-120037592>
- Peng J, Yuan JP, Wu CF, Wang JH (2011) Fucoxanthin, a marine carotenoid present in brown seaweeds and diatoms: metabolism and bioactivities relevant to human health. *Mar Drugs* 9:1806–1828. <https://doi.org/10.3390/md9101806>
- Pereira L (2011) A review of the nutrient composition of selected edible seaweeds. In: Pomin VH (ed) *Seaweed: ecology, nutrient composition and medicinal uses*, 1st edn. Nova Science Publishers, Inc., Coimbra, pp 15–47
- Pereira L (2016) *Edible seaweeds of the world*, 1st edn. CRC Press, Boca Raton
- Pereira L (2018) Nutritional composition of the main edible algae. In: Pereira L (ed) *Therapeutic and nutritional uses of algae*. CRC Press, Boca Raton, pp 65–127
- Pereira L (2021) Macroalgae. *Encyclopedia* 1:177–188. <https://doi.org/10.3390/ENCYCLOPEDIA1010017>

- Pereira L (2023) Atlantic algae as food and their extracts. *Explor Foods Foodomics* 1:15–31. <https://doi.org/10.37349/EFF.2023.00003>
- Pereira L, Neto JM (2015) Marine algae – biodiversity, taxonomy, environmental assessment, and biotechnology, 1st edn. CRC Press, Boca Raton
- Pereira L, Valado A (2021) The seaweed diet in prevention and treatment of the neurodegenerative diseases. *Mar Drugs* 19:1–25. <https://doi.org/10.3390/md19030128>
- Pereira T, Barroso S, Mendes S et al (2020) Optimization of phycobiliprotein pigments extraction from red algae *Gracilaria gracilis* for substitution of synthetic food colorants. *Food Chem* 321:126688. <https://doi.org/10.1016/j.foodchem.2020.126688>
- Pereira AG, Otero P, Echave J et al (2021) Xanthophylls from the sea: algae as source of bioactive carotenoids. *Mar Drugs* 19:188. <https://doi.org/10.3390/MD19040188>
- Pérez-Gálvez A, Viera I, Roca M (2020) Carotenoids and chlorophylls as antioxidants. *Antioxidants* 9:505. <https://doi.org/10.3390/antiox9060505>
- Pérez-Lloréns JL, Mouritsen OG, Rhatigan P et al (2020) Seaweeds in mythology, folklore, poetry, and life. *J Appl Phycol* 32:3157–3182. <https://doi.org/10.1007/s10811-020-02133-0>
- Phan MAT, Bucknall M, Arcot J (2018) Interactive effects of  $\beta$ -carotene and anthocyanins on cellular uptake, antioxidant activity and anti-inflammatory activity in vitro and ex vivo. *J Funct Foods* 45:129–137. <https://doi.org/10.1016/j.jff.2018.03.021>
- Piniella-Matamoros B, Marín-Prida J, Pentón-Rol G (2021) Nutraceutical and therapeutic potential of Phycocyanobilin for treating Alzheimer’s disease. *J Biosci* 46:1–16. <https://doi.org/10.1007/s12038-021-00161-7>
- Poojary MM, Barba FJ, Aliakbarian B et al (2016) Innovative alternative technologies to extract carotenoids from microalgae and seaweeds. *Mar Drugs* 14:214. <https://doi.org/10.3390/md14110214>
- Prado JM, Veggi PC, Náthia-Neves G, Meireles MAA (2018) Extraction methods for obtaining natural blue colorants. *Curr Anal Chem* 16:504–532. <https://doi.org/10.2174/1573411014666181115125740>
- Puzorjov A, McCormick AJ (2020) Phycobiliproteins from extreme environments and their potential applications. *J Exp Bot* 71:3827–3842. <https://doi.org/10.1093/JXB/ERAA139>
- Qiang X, Wang L, Niu J et al (2021) Phycobiliprotein as fluorescent probe and photosensitizer: a systematic review. *Int J Biol Macromol* 193:1910–1917. <https://doi.org/10.1016/J.IJBIOMAC.2021.11.022>
- Quitério E, Soares C, Ferraz R et al (2021) Marine health-promoting compounds: recent trends for their characterization and human applications. *Food Secur* 10:3100. <https://doi.org/10.3390/FOODS10123100>
- Ragusa I, Nardone GN, Zanatta S et al (2021) Spirulina for skin care: a bright blue future. *Cosmetics* 8:7. <https://doi.org/10.3390/cosmetics8010007>
- Rapoport A, Guzhova I, Bernetti L et al (2021) Carotenoids and some other pigments from fungi and yeasts. *Metabolites* 11:92. <https://doi.org/10.3390/metabo11020092>
- Resende ACR, Pereira R, Nunes C et al (2023) Photosynthetic pigment and carbohydrate profiling of *Fucus vesiculosus* from an Iberian Coastal Lagoon. *Plants* 12:1324. <https://doi.org/10.3390/plants12061324>
- Robertson RC, Guihéneuf F, Bahar B et al (2015) The anti-inflammatory effect of algae-derived lipid extracts on lipopolysaccharide (LPS)-stimulated human THP-1 macrophages. *Mar Drugs* 13:5402–5424. <https://doi.org/10.3390/md13085402>
- Rodriguez-Amaya DB (2015) Food carotenoids: chemistry, biology and technology. Wiley-Blackwell, Chichester
- Rodriguez-Amaya D, Kimura M (2004) HarvestPlus handbook for carotenoid analysis. HarvestPlus, Washington DC
- Román RB, Álvarez-Pez JM, Fernández FGA, Grima EM (2002) Recovery of pure B-phycoerythrin from the microalga *Porphyridium cruentum*. *J Biotechnol* 93:73–85. [https://doi.org/10.1016/S0168-1656\(01\)00385-6](https://doi.org/10.1016/S0168-1656(01)00385-6)

- Rossano R, Ungaro N, D'Ambrosio A et al (2003) Extracting and purifying R-phycoerythrin from Mediterranean red algae *Corallina elongata* Ellis & Solander. *J Biotechnol* 101:289–293. [https://doi.org/10.1016/S0168-1656\(03\)00002-6](https://doi.org/10.1016/S0168-1656(03)00002-6)
- Rula NAM, Ganzon-Fortes ET, Pante MJR, Trono GC (2021) Influence of light, water motion, and stocking density on the growth and pigment content of *Halymenia durvillei* (Rhodophyceae) under laboratory conditions. *J Appl Phycol* 33:2367–2377. <https://doi.org/10.1007/S10811-021-02474-4/FIGURES/6>
- Saha SK, Ermis H, Murray P (2020) Marine microalgae for potential lutein production. *Appl Sci (Switzerland)* 10:6457. <https://doi.org/10.3390/APP10186457>
- Sahin SC (2018) The potential of *Arthrospira platensis* extract as a tyrosinase inhibitor for pharmaceutical or cosmetic applications. *S Afr J Bot* 119:236–243. <https://doi.org/10.1016/j.sajb.2018.09.004>
- Saiki Y, Amao Y (2002) Visible light induced biohydrogen production from sucrose using the photosensitization of Mg chlorophyll-a. *Bioconjug Chem* 13:898–901. <https://doi.org/10.1021/BC025506G/ASSET/IMAGES/LARGE/BC025506GF00004.JPEG>
- Saini RK, Keum YS (2018) Carotenoid extraction methods: a review of recent developments. *Food Chem* 240:90–103. <https://doi.org/10.1016/j.foodchem.2017.07.099>
- Sajilata MG, Singhal RS, Kamat MY (2008) The carotenoid pigment zeaxanthin – a review. *Compr Rev Food Sci Food Saf* 7:29–49. <https://doi.org/10.1111/j.1541-4337.2007.00028.x>
- Saluri M, Kaldmäe M, Tuvikene R (2019) Extraction and quantification of phycobiliproteins from the red alga *Furcellaria lumbricalis*. *Algal Res* 37:115–123. <https://doi.org/10.1016/j.algal.2018.11.013>
- Saluri M, Kaldmäe M, Tuvikene R (2020) Reliable quantification of R-phycoerythrin from red algal crude extracts. *J Appl Phycol* 32:1421–1428. <https://doi.org/10.1007/s10811-019-01968-6>
- Samarasinghe N, Fernando S, Lacey R, Faulkner WB (2012) Algal cell rupture using high pressure homogenization as a prelude to oil extraction. *Renew Energy* 48:300–308. <https://doi.org/10.1016/J.RENENE.2012.04.039>
- Sanders CA, Rodriguez M, Greenbaum E (2001) Stand-off tissue-based biosensors for the detection of chemical warfare agents using photosynthetic fluorescence induction. *Biosens Bioelectron* 16:439–446. [https://doi.org/10.1016/S0956-5663\(01\)00158-0](https://doi.org/10.1016/S0956-5663(01)00158-0)
- Sano F, Murata K, Niwa K (2020) Identification, growth, and pigment content of a spontaneous green mutant of *Pyropia kinositae* (Bangiales, Rhodophyta). *J Appl Phycol* 32:1983–1994. <https://doi.org/10.1007/S10811-020-02085-5/TABLES/1>
- Schächtl J, Huber G, Maidl FX et al (2005) Laser-induced chlorophyll fluorescence measurements for detecting the nitrogen status of wheat (*Triticum aestivum* L.) canopies. *Precis Agric* 6:143–156. <https://doi.org/10.1007/S11119-004-1031-Y/METRICS>
- Schepers M, Martens N, Tiane A et al (2020) Edible seaweed-derived constituents: an undisclosed source of neuroprotective compounds. *Neural Regen Res* 15:790–795. <https://doi.org/10.4103/1673-5374.268894>
- Schubert N, García-Mendoza E, Pacheco-Ruiz I (2006) Carotenoid composition of marine red algae. *J Phycol* 42:1208–1216. <https://doi.org/10.1111/j.1529-8817.2006.00274.x>
- Schubert D, Currais A, Goldberg J et al (2018) Geroneuroprotectors: effective geroprotectors for the brain. *Trends Pharmacol Sci* 39:1004–1007
- Sekar S, Chandramohan M (2008) Phycobiliproteins as a commodity: trends in applied research, patents and commercialization. *J Appl Phycol* 20:113–136. <https://doi.org/10.1007/s10811-007-9188-1>
- Sen S, Mallick N (2021) Mycosporine-like amino acids: algal metabolites shaping the safety and sustainability profiles of commercial sunscreens. *Algal Res* 58:102425. <https://doi.org/10.1016/J.ALGAL.2021.102425>
- Seyed Yagoubi A, Shahidi F, Mohebbi M et al (2017) Preparation, characterization and evaluation of physicochemical properties of phycocyanin-loaded solid lipid nanoparticles and nanostructured lipid carriers. *J Food Meas Charact* 1:378–385. <https://doi.org/10.1007/S11694-017-9650-Y>

- Sfriso AA, Gallo M, Baldi F (2018) Phycoerythrin productivity and diversity from five red macroalgae. *J Appl Phycol* 30:2523–2531. <https://doi.org/10.1007/s10811-018-1440-3>
- Shi XM, Jiang Y, Chen F (2002) High-yield production of lutein by the green microalga *Chlorella protothecoides* in heterotrophic fed-batch culture. *Biotechnol Prog* 18:723–727. <https://doi.org/10.1021/bp0101987>
- Shih SR, Tsai KN, Li YS et al (2003) Inhibition of enterovirus 71-induced apoptosis by allophycocyanin isolated from a blue-green alga *Spirulina platensis*. *J Med Virol* 70:119–125. <https://doi.org/10.1002/jmv.10363>
- Sies H, Stahl W (2004) Nutritional protection against skin damage from sunlight. *Annu Rev Nutr* 24:173–200. <https://doi.org/10.1146/annurev.nutr.24.012003.132320>
- Silva SC, Ferreira ICFR, Dias MM, Filomena Barreiro M (2020) Microalgae-derived pigments: a 10-year bibliometric review and industry and market trend analysis. *Molecules* 25:3406. <https://doi.org/10.3390/molecules25153406>
- Singh A, Ahmad S, Ahmad A (2015) Green extraction methods and environmental applications of carotenoids—a review. *RSC Adv* 5. <https://doi.org/10.1039/c5ra10243j>
- Solymsi K, Mysliwa-Kurdziel B (2016) Chlorophylls and their derivatives used in food industry and medicine. *Mini-Rev Med Chem* 17:1194–1222. <https://doi.org/10.2174/1389557516666161004161411>
- Sonani RR, Rastogi RP, Patel R, Madamwar D (2016) Recent advances in production, purification and applications of phycobiliproteins. *World J Biol Chem* 7:100. <https://doi.org/10.4331/WJBC.V7.I1.100>
- Sorrenti V, Davinelli S, Scapagnini G et al (2020) Astaxanthin as a putative geroprotector: molecular basis and focus on brain aging. *Mar Drugs* 18:351
- Soulier N, Bryant DA (2021) The structural basis of far-red light absorbance by allophycocyanins. *Photosynth Res* 147:11–26. <https://doi.org/10.1007/s1120-020-00787-y>
- Souza JMC, Castro JZ, Critchley AT, Yokoya NS (2019) Physiological responses of the red algae *Gracilaria caudata* (Gracilariales) and *Laurencia catarinensis* (Ceramiales) following treatment with a commercial extract of the brown alga *Ascophyllum nodosum* (AMPEP). *J Appl Phycol* 31:1883–1888. <https://doi.org/10.1007/S10811-018-1683-Z/FIGURES/4>
- Stahl W, Sies H (2005) Bioactivity and protective effects of natural carotenoids. *Biochim Biophys Acta Mol basis Dis* 1740:101–107. <https://doi.org/10.1016/j.bbadis.2004.12.006>
- Stahl W, Sies H (2012)  $\beta$ -Carotene and other carotenoids in protection from sunlight. *Am J Clin Nutr* 96:1179S–1184S. <https://doi.org/10.3945/AJCN.112.034819>
- Stefanov M, Rashkov G, Borisova P, Apostolova E (2023) Sensitivity of the photosynthetic apparatus in maize and sorghum under different drought levels. *Plants* 12:1863. <https://doi.org/10.3390/plants12091863>
- Sun H, Wang Y, He Y et al (2023) Microalgae-derived pigments for the food industry. *Mar Drugs* 21:82. <https://doi.org/10.3390/MD21020082>
- Swapnil P, Meena M, Singh SK et al (2021) Vital roles of carotenoids in plants and humans to deteriorate stress with its structure, biosynthesis, metabolic engineering and functional aspects. *Curr Plant Biol* 26:100203. <https://doi.org/10.1016/j.cpb.2021.100203>
- Takahashi S, Murata N (2008) How do environmental stresses accelerate photoinhibition? *Trends Plant Sci* 13:178–182. <https://doi.org/10.1016/j.tplants.2008.01.005>
- Takaichi S (2011) Carotenoids in algae: distributions, biosyntheses and functions. *Mar Drugs* 9:1101–1118. <https://doi.org/10.3390/md9061101>
- Takaichi S, Yokoyama A, Mochimaru M et al (2016) Carotenogenesis diversification in phylogenetic lineages of Rhodophyta. *J Phycol* 52:329–338. <https://doi.org/10.1111/jpy.12411>
- Takeuchi Y, Amao Y (2005) Biohydrogen production from sucrose using the light-harvesting function of zinc chlorophyll-a. *Bull Chem Soc Jpn* 78:622–625. <https://doi.org/10.1246/BCSJ.78.622>
- Talarico L, Maranzana G (2000) Light and adaptive responses in red macroalgae: an overview. *J Photochem Photobiol B* 56:1–11. [https://doi.org/10.1016/S1011-1344\(00\)00046-4](https://doi.org/10.1016/S1011-1344(00)00046-4)
- Thompson CC, Kruger RH, Thompson FL (2017) Unlocking marine biotechnology in the developing world. *Trends Biotechnol* 35:1119–1121. <https://doi.org/10.1016/J.TIBTECH.2017.08.005>

- Tomonou Y, Amao Y (2002) Visible light induced hydrogen production with Mg chlorophyll-a from spirulina and colloidal platinum. *Biometals* 15:391–395. <https://doi.org/10.1023/A:1020213122186>
- Torres PB, Chow F, Furlan CM et al (2014) Standardization of a protocol to extract and analyze chlorophyll a and carotenoids in *Gracilaria tenuistipitata* var. *liui*. Zhang and Xia (Rhodophyta). *Braz J Oceanogr* 62:57–63. <https://doi.org/10.1590/S1679-87592014068106201>
- Tung J, Goodwin PH, Hsiang T (2013) Chlorophyll fluorescence for quantification of fungal foliar infection and assessment of the effectiveness of an induced systemic resistance activator. *Eur J Plant Pathol* 136:301–315. <https://doi.org/10.1007/S10658-012-0164-5/FIGURES/8>
- Urrea-Victoria V, Gerales V, Pinto E, Castellanos L (2023) Photosynthetic pigments and photoprotective metabolites of Colombian pacific marine macroalgae in response to contrasting ultraviolet-index periods. *J Exp Mar Biol Ecol* 564. <https://doi.org/10.1016/J.JEMBE.2023.151908>
- Van Der Weij-De Wit CD, Doust AB, Van Stokkum IHM et al (2006) How energy funnels from the phycoerythrin antenna complex to photosystem I and photosystem II in cryptophyte *Rhodomonas* CS24 cells. *J Phys Chem B* 110:25066–25073. <https://doi.org/10.1021/jp061546w>
- van der Westhuizen MM, Oosterhuis DM, Berner JM, Boogaers N (2020) Chlorophyll a fluorescence as an indicator of heat stress in cotton (*Gossypium hirsutum* L.). *S Afr J Plant Soil* 37:116–119. <https://doi.org/10.1080/02571862.2019.1665721>
- Védrine C, Leclerc JC, Durrieu C, Tran-Minh C (2003) Optical whole-cell biosensor using *Chlorella vulgaris* designed for monitoring herbicides. *Biosens Bioelectron* 18:457–463. [https://doi.org/10.1016/S0956-5663\(02\)00157-4](https://doi.org/10.1016/S0956-5663(02)00157-4)
- Viera I, Pérez-Gálvez A, Roca M (2018) Bioaccessibility of marine carotenoids. *Mar Drugs* 16:397. <https://doi.org/10.3390/md16100397>
- Vílchez C, Forján E, Cuaresma M et al (2011) Marine carotenoids: biological functions and commercial applications. *Mar Drugs* 9:319–333. <https://doi.org/10.3390/md9030319>
- Vinothkanna A, Sekar S (2020) Diagnostic applications of phycobiliproteins. In: *Pigments from microalgae handbook*, pp 585–610. [https://doi.org/10.1007/978-3-030-50971-2\\_24](https://doi.org/10.1007/978-3-030-50971-2_24)
- Wang J, Sun J, Song Y et al (2013) A label-free microfluidic biosensor for activity detection of single microalgae cells based on chlorophyll fluorescence. *Sensors* 13:16075–16089. <https://doi.org/10.3390/S131216075>
- Wang L, Qu Y, Fu X et al (2014) Isolation, purification and properties of an R-phycoerythrin from the phycobilisomes of a marine red macroalga *Polysiphonia urceolata*. *PLoS One* 9:e101724. <https://doi.org/10.1371/journal.pone.0087833>
- Wang Z, Li G, Sun H et al (2018) Effects of drought stress on photosynthesis and photosynthetic electron transport chain in young apple tree leaves. *Biol Open* 7:bio035279. <https://doi.org/10.1242/BIO.035279>
- Wang C, Shen Z, Cui X et al (2020) Response surface optimization of enzyme-assisted extraction of R-phycoerythrin from dry *Pyropia yezoensis*. *J Appl Phycol* 32:1429–1440. <https://doi.org/10.1007/s10811-019-01963-x>
- Wells ML, Potin P, Craigie JS et al (2017) Algae as nutritional and functional food sources: revisiting our understanding. *J Appl Phycol* 29:949–982. <https://doi.org/10.1007/s10811-016-0974-5>
- Willcox DC, Scapagnini G, Willcox BJ (2014) Healthy aging diets other than the Mediterranean: a focus on the Okinawan diet. *Mech Ageing Dev* 136–137:148–162. <https://doi.org/10.1016/j.mad.2014.01.002>
- Wollina U, Voicu C, Gianfaldoni S et al (2018) *Arthrospira platensis* – potential in dermatology and beyond. *Open Access Maced J Med Sci* 6:176–180. <https://doi.org/10.3889/oamjms.2018.033>
- World Intellectual Property Organization (WIPO) (2016) Patent landscape report: microalgae-related technologies. *Patent Landscape Reports*
- World International Property Organization (2021) PATENTSCOPE. In: *Patentscope*. <https://www.wipo.int/patentscope/en/>. Accessed 7 Dec 2021

- Xie X, Lu X, Wang L et al (2020) High light intensity increases the concentrations of  $\beta$ -carotene and zeaxanthin in marine red macroalgae. *Algal Res* 47:101852. <https://doi.org/10.1016/j.algal.2020.101852>
- Xu DP, Li Y, Meng X et al (2017) Natural antioxidants in foods and medicinal plants: extraction, assessment and resources. *Int J Mol Sci* 18:96. <https://doi.org/10.3390/ijms18010096>
- Yabuta Y, Fujimura H, Kwak CS et al (2010) Antioxidant activity of the phycoerythrobilin compound formed from a dried Korean purple laver (*Porphyra* sp.) during *in vitro* digestion. *Food Sci Technol Res* 16:347–352. <https://doi.org/10.3136/fstr.16.347>
- Yabuzaki J (2017) Carotenoids database: structures, chemical fingerprints and distribution among organisms. Database 2017:bax004. <https://doi.org/10.1093/database/bax004>
- Yang EJ, Ham YM, Lee WJ et al (2013) Anti-inflammatory effects of apo-9'-fucoxanthinone from the brown alga, *Sargassum muticum*. *DARU, J Pharm Sci* 21:62. <https://doi.org/10.1186/2008-2231-21-62>
- Yang M, Xuan Z, Wang Q et al (2021) Fucoxanthin has potential for therapeutic efficacy in neurodegenerative disorders by acting on multiple targets. *Nutr Neurosci*:1–14. <https://doi.org/10.1080/1028415X.2021.1926140>
- Ye ZW, Jiang JG, Wu GH (2008) Biosynthesis and regulation of carotenoids in *Dunaliella*: progresses and prospects. *Biotechnol Adv* 26:352–360. <https://doi.org/10.1016/j.biotechadv.2008.03.004>
- Ye KX, Fan TT, Keen LJ, Han BN (2019) A review of pigments derived from marine natural products. *Isr J Chem* 59:327–338. <https://doi.org/10.1002/ijch.201800154>
- Yuan Y, Zhang J, Fan J et al (2018) Microwave assisted extraction of phenolic compounds from four economic brown macroalgae species and evaluation of their antioxidant activities and inhibitory effects on  $\alpha$ -amylase,  $\alpha$ -glucosidase, pancreatic lipase and tyrosinase. *Food Res Int* 113:288–297. <https://doi.org/10.1016/J.FOODRES.2018.07.021>
- Zerres S, Stahl W (2020) Carotenoids in human skin. *Biochim Biophys Acta Mol Cell Biol Lipids* 1865:158588. <https://doi.org/10.1016/J.BBALIP.2019.158588>
- Zhao P, Wang X, Niu J et al (2020) Agar extraction and purification of R-phycoerythrin from *Gracilaria tenuistipitata*, and subsequent wastewater treatment by *Ulva prolifera*. *Algal Res* 47:101862. <https://doi.org/10.1016/j.algal.2020.101862>
- Zhao W, Hu CM, Zhou W et al (2022) Carotenoids participate in adaptation/resistance of daily desiccation in the intertidal red alga *Neopyropia yezoensis* (Bangiales, Rhodophyta). *Algal Res* 61:102606. <https://doi.org/10.1016/j.algal.2021.102606>
- Zhu Z, Wu Q, Di X et al (2017) Multistage recovery process of seaweed pigments: investigation of ultrasound assisted extraction and ultra-filtration performances. *Food Bioprod Process* 104:40–47. <https://doi.org/10.1016/J.FBP.2017.04.008>