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REVIEW

Sea grapes (*Caulerpa lentillifera* J. Agardh, Chlorophyta) for human use: Structured review on recent research in cultivation, nutritional value, and post-harvest management

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Abstract

Seaweeds are a major contributor to global marine aquaculture production, with the biomass being mainly used, among others, for human nutrition, pharmaceutics, and cosmetics. However, green seaweeds are severely underrepresented, compared to red and brown macroalgae. *Caulerpa lentillifera* (known as "sea grapes" or "green caviar") is an edible, green seaweed with a distinctive texture and various nutritional benefits. In this review, all articles on sea grapes published between 1900 and October 2022 and found in the scientific citation databases Scopus and Web of Science (search string: "caulerpa" AND "lentillifera") were grouped by research topic and the intended application following the PRISMA approach. 51% of the 130 articles included in the review focused on the topic of "Biochemical composition", followed by "Water treatment" (18%) and "Ecophysiology" (15%). The most prominent application was "Pharmaceutics", followed by "Cultivation" and "Fundamental research". In order to provide a knowledge base to researchers and practitioners of C. lentillifera aquaculture, research that was simultaneously grouped under one of the topics "Biochemical composition", "Water treatment", or "Ecophysiology" and the applications "Cultivation", "Nutritional value" or "Post-harvest" was summarized in more detail. Light management of sea grapes, their use as a high-value co-culture species and the capacity to bioremediate nutrients, as well as their short shelf-life were identified as important areas of research interest. The assessment revealed several knowledge gaps, for example the need for intra-species comparisons of *C. lentillifera* biochemical composition across spatial and temporal scales.

Keywords Chlorophyta · Bioremediation · Co-cultivation · Functional foods · Green caviar · Nutritional value

Introduction

Macroalgae represent > 50% of global marine and coastal aquaculture products (35 million t in 2020, based on wet weight (WW), mainly due to production for human consumption (FAO 2020; Chopin and Tacon 2021). Eight genera of red and brown macroalgae dominate the production, whereas green macroalgae are underrepresented with < 1% (FAO 2020; reviewed by Moreira et al. 2021). However, *Caulerpa* is one genus that is gaining increasing popularity, with the highest mean contribution to global green seaweed cultivation in the years 1950–2019 (annual average of 6404 t WW), but with declining values until 2019 (1090 t WW, Cai et al. 2021a). However, these production values are likely to be underestimated, mainly based on reports from The Philippines. *Caulerpa* species, and especially edible *C. racemosa* and *C. lentillifera* (known as "sea grapes" or "green caviar") are particularly popular in the Indo-Pacific region, where they are consumed fresh or salt-preserved in salads or as a snack (Long et al. 2020b). In particular, the striking texture (Fig. 1A; Zubia et al. 2020), the nutritional benefits, including e.g. the content of bioactive compounds and polyunsaturated fatty acids (PUFA), and the pleasant taste have led to an increasing demand of sea grapes worldwide (de Gaillande et al. 2017; Chen et al. 2019; Zubia et al. 2020). Compared to average seaweeds, sea grapes achieve high market prices (Dobson et al. 2020; Cai et al. 2021a)

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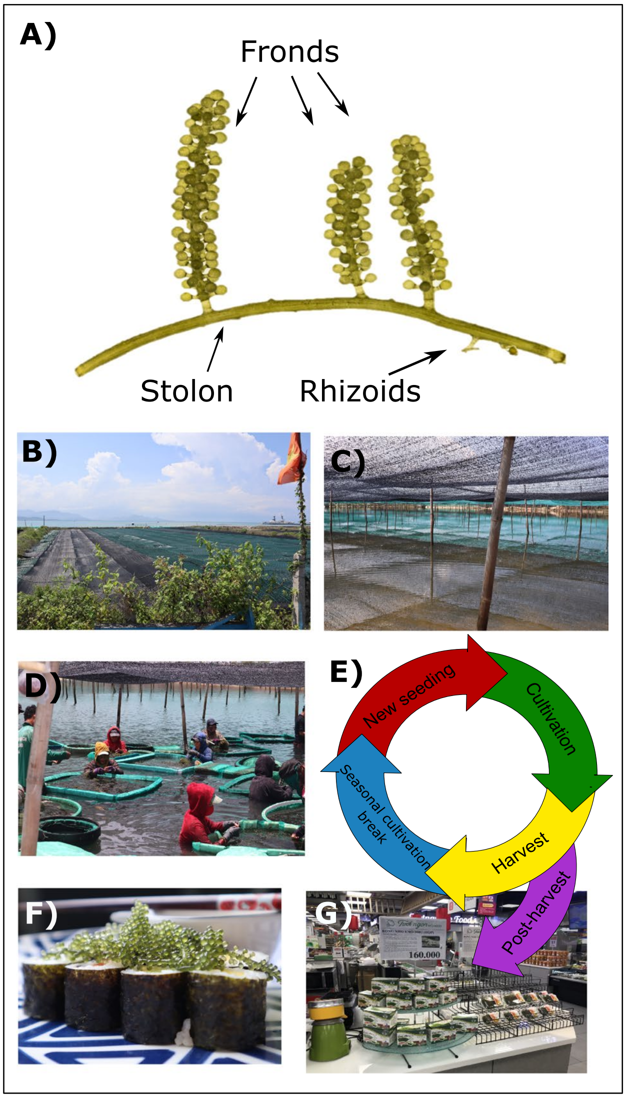

Fig. 1 **A** *Caulerpa lentillifera* consists of upright fronds (assimilators) with grape-like, vesiculate ramuli irregularly arranged around a pedicel, which are attached to creeping stolons with rhizoids (Zubia et al., 2020). The life-cycle of the sea grapes in aquaculture consists of different stages **E**. Seedlings are applied to start the cultivation, which can take place in outdoor, tidal ponds **B** or in land-based systems. The shade-adapted seaweeds are shaded from the sun, e.g. with gauze material **C**. Sea grape fronds reaching harvestable size are continuously harvested during the cultivation season **D** and the harvest is collected at a collection point for cleaning and sorting of the product before retail of the fresh or dehydrated sea grapes **G**. *C. lentillifera* fronds are e.g. served with sushi or as a salad **F**. Pictures were taken at a sea grape farming facility in Vietnam, Khanh Hoa province

and they are proposed as promising functional food ingredient (Syakilla et al. 2022), or certain compounds are being investigated in a pharmaceutical context, e.g. for their antidiabetic and anticancer activities (Daud et al. 2020; Fajriah et al. 2020; Manoppo et al. 2022). However, the species is not yet covered by the Novel food Regulation (EU), which limits the potential customer base (Barbier et al. 2019).

Historically, sea grape cultivation began in Japan (Okinawa) and The Philippines (Trono and Toma 1993; Yap 1999). In The Philippines sea grapes were introduced by accident into fish ponds, but the successful growth of the species ensured its targeted cultivation (Trono and Largo 2019).

As sea grapes can be propagated by fragmentation, they are easy to cultivate without the need for expensive infrastructure or strong expertise (Fig. 1B-F; de Gaillande et al. 2017). Cultivation methods vary according to country and system (Trono and Largo 2019). In The Philippines and Vietnam the algae are grown in perforated plastic trays or nets (tray method) or are planted directly into the sediment in tidal ponds (sowing method; Rabia 2016), sometimes shaded with e.g. gauze material (Fig. 1B,C). In Japan and China, land-based raceway cultures are increasingly used to meet the high demand for sea grapes (de Gaillande et al. 2017). However, sea grapes can also be grown in sheltered coastal areas in nets or trays (Tanduyan et al. 2013). The rapid growth and relatively low habitat requirements of sea grapes have also led to their increased use in integrated aquaculture systems (Paul and de Nys 2008), in order to mitigate the potentially problematic nutrient rich effluent of wastewaters and to provide an additional income from the metabolized biomass (Largo et al. 2016; Bambaranda et al. 2019a, b; Dobson et al. 2020). After harvesting of the edible fronds, they are soaked in tanks with seawater to allow this siphonous alga to heal tissue injuries. Subsequently, the fronds meeting the required quality standards (e.g. bright green colour, size) are stored in plastic containers with moisture sheets for shipment or retail as a fresh product, or for preservation (dehydrated or brine-cured de Gaillande et al. 2017; Terada et al. 2018; Chaiklahan et al. 2020). Biomass that does not meet food quality standards (60–70%) is discarded as waste, but there is potential for its further use (Chaiklahan et al. 2020).

Along with the economic interest, the number of scientific publications seems to be increasing. Recent review articles and book chapters focused on the consumption, nutritional value and farming of the genus *Caulerpa* (de Gaillande et al. 2017), as well as the biology and its use (Zubia et al. 2020) and the nutraceutical and pharmaceutical potential (Darmawan et al. 2020). To our knowledge one review article from 2019 sums up the research on the species *C. lentillifera* (Chen et al. 2019) and one review summarizes the nutrients, phytochemicals and health benefits (Syakilla et al. 2022). The present review article aims to (1) conduct a scientometric analysis of the published literature to identify trends of the different research topics and applications, in order to reveal knowledge gaps and identify future research directions. To achieve this goal, seven research topics (e.g. "Biochemical composition", "Genetics", "Water treatment") and nine research applications (e.g. "Pharmaceutics", "Fundamental research", "Cultivation") were formulated and the articles were grouped in the respective topic and application. In a next step (2), the literature focusing on the aquaculture of *C. lentillifera*, namely the topics of cultivation parameters, nutritional value, and post-harvest applications were summarized in concise manner to provide a structured overview for practitioners in the field and researchers working with this species.

Material and methods

Literature review

We conducted a systematic literature search using two popular scientific citation databases, namely Web of Science (WoS) and Scopus. The PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) statement was applied (Liberati et al. 2009). In both databases the search string "caulerpa" AND "lentillifera" for the period 1900 to 2022 was used to search within title, keywords and abstract. The search took place on 29 October 2022 and resulted in a total of n = 192 studies (after removal of duplicates, Fig. 2).

Selection criteria

In order to check for eligibility of the studies the following selection criteria were used a) *Caulerpa lentillifera* is a main topic of the article and b) language of the article was English, c) the article was not a review article, d) scientific accuracy was given. This was evaluated by screening the titles and abstracts of the documents. In case the information provided was not sufficient to determine the question, the complete document was screened.

Data extraction

From the studies declared "eligible" according to the criteria (n = 130, Fig. 2), the following information was extracted: (a) publication year, (b) study location, (c) affiliation of the main author, (d) location of the affiliation of the main author, (e) type of article (journal article, review article, book chapter, book, technical report), (f) topic of research (definitions in On-line Appendices I) and (g) application of research (definitions in On-line Appendices II). The topics and applications were defined by the authors after reviewing the existing literature. The search and extraction criteria were tested by a pilot classification, where two authors (BBC and LES) categorized 30 studies and discussed and cross-checked their choices in order to ensure a reliable and homogenized coding. Two papers, namely Stuthmann et al. (2020) and Paul et al. (2014) have been sorted in two categories since they dealt with various topics and/or applications ("Ecophysiology" – "Post-harvest" & "Ecophysiology" – "Cultivation" and "Biochemical composition" – "Nutritional value" & "Water treatment" – "Cultivation", respectively) within each respective article.

This review was set-up on one hand as a scientometric analysis of the existing literature in order to identify research trends and knowledge gaps, and on the other hand as a contextual synopsis of sea grape aquaculture for practitioners and field-researchers. Hence, the review investigated certain combinations of topics and applications in more contextual detail, namely the topics of "Ecophysiology", "Biochemical composition" and "Water treatment" with the respective applications of "Cultivation", "Nutritional value" or "Post-harvest". In a subsequent discussion, first the results of the scientometric analysis were considered and secondly the contextual summary was analysed across topics and applications with a focus on the peculiarities and knowledge gaps identified. The salinity units were reported as they appeared in the respective papers.

Results

Scientometric analysis: Number of publications, research topics and applications

Since 1990, eight review articles on the topic of *C. lentillifera* have been published, but all of them in the period 2019–2022, and six of them focused only on sea grapes. Until the search for this review (October 2022) 130 research articles were published (Fig. 3A). However, since 2018, the annual number of published journal articles about sea grapes was ≥ 10, and in total added up to 86 (66% of total published journal articles). The majority of articles were on the topics of "Biochemical composition" (51%), followed by "Water treatment", "Ecophysiology" and "Genetics", whereas only ≤ 5 articles researched "Microbiome", "Distribution" and "Ethnophycology", respectively (Fig. 3B). In contrast, the application of the research articles was more distributed, with "Pharmaceutics" having the highest and "Feedstock" and "Cosmetics" the lowest count, focusing on the use for bio-oil production (Ong et al. 2019; Wuttilerts et al. 2019) or in creams (Thu et al. 2018; Chang et al. 2021; Fig. 3C). The application as "Animal feed" was also underrepresented with only three studies, using sea grapes as fish (Ilias et al. 2015; Arisa et al. 2020) and shrimp (Putra et al. 2019) feed. The application of "Pharmaceutics" was made up almost exclusively

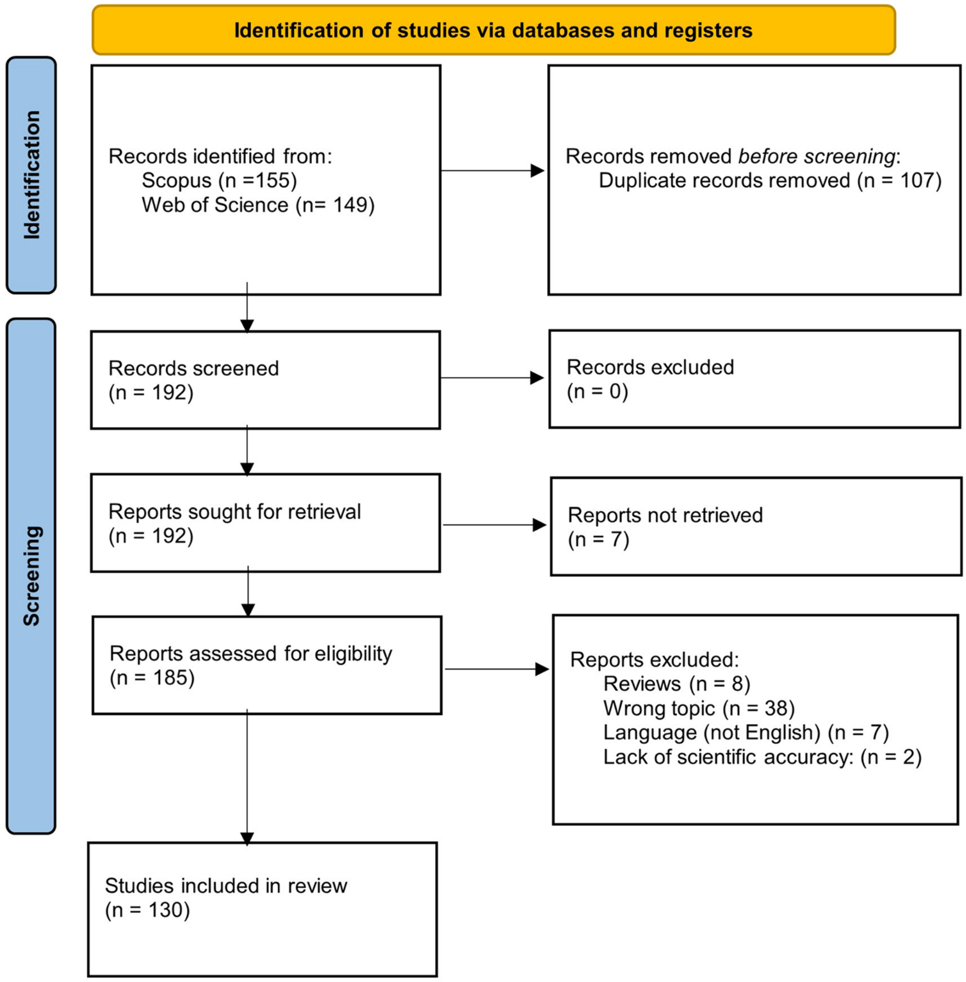

Fig. 2 Flow diagram for the systematic literature review on *Caulerpa lentillifera*. The different stages for the identification, screening, and inclusion of relevant articles are shown. A template of the flow diagram was downloaded from https://www.prisma-statement.org

by articles from the research topic "Biochemical composition", majorly contributing to the high frequency of this topic (Fig. 4) and focusing on various bioactivities of the seaweed's metabolites, including anti-inflammatory (Yoojam et al. 2021), anti-diabetic (Khairuddin et al. 2020) and anti-viral (You et al. 2022). "Industrial effluences" encompassed mainly articles, where *C. lentillifera* biomass was used as a bio-adsorbent for basic dyes (Marungrueng and Pavasant 2006, 2007; Pimol et al. 2008) and heavy metals (Apiratikul and Pavasant 2006, 2008; Pavasant et al. 2006; Apiratikul et al. 2011; Ahamad Zakeri and Abu Bakar 2013; Apiratikul 2017, 2020; Li et al. 2021). The application of "Fundamental research" encompassed all studies of the topics "Genetics" and "Distribution", as well as a few on "Biochemical composition", "Ecophysiology" and "Ethnophycology" (Fig. 4). Studies within the topic of "Genetics" focused e.g. on the alga's chloroplast (Gao et al. 2018), mitochondrial (Zheng et al. 2018; Jia et al. 2019) and complete genome (Arimoto et al. 2019a) and DNA in their pyrenoid core (Miyamura and Hori 1991, 1995), as well as on population genetics (Benzie et al. 1997; Kazi et al. 2013). It accompanied research from the topic "Distribution", reporting on (re)discoveries of *C. lentillifera* in the Gulf of Mannar (Mary et al. 2009) and Gulf of Kutch (Mantri 2004), India and Hainan Island, China (Gao et al. 2020). The topic "Microbiome" encompassed four studies, of which half were on the application of "Post-harvest", namely the effect of season, washing (Pang et al. 2022) and petrifilm aerobic count plate (ACP, Kudaka et al. 2010) and the other half on "Cultivation", dealing with the microbiome of healthy and diseased *C. lentillifera* (Liang et al. 2019; Kopprio et al. 2021).

Scientometric analysis: Research networks

The majority of journal articles were published by first authors who were affiliated with institutions in Asia (Fig. 5), particularly in China (n = 27, 20.8%), Thailand (n = 23; 17.7%), Malaysia (n = 18; 13.8%), Indonesia (n = 12, 9.2%), and Japan (n = 11; 8.5%). Besides, outside of Asia authors with affiliations in Australia (n = 6, 4.6%) and Germany (n = 4; 3.1%) were majorly present. The

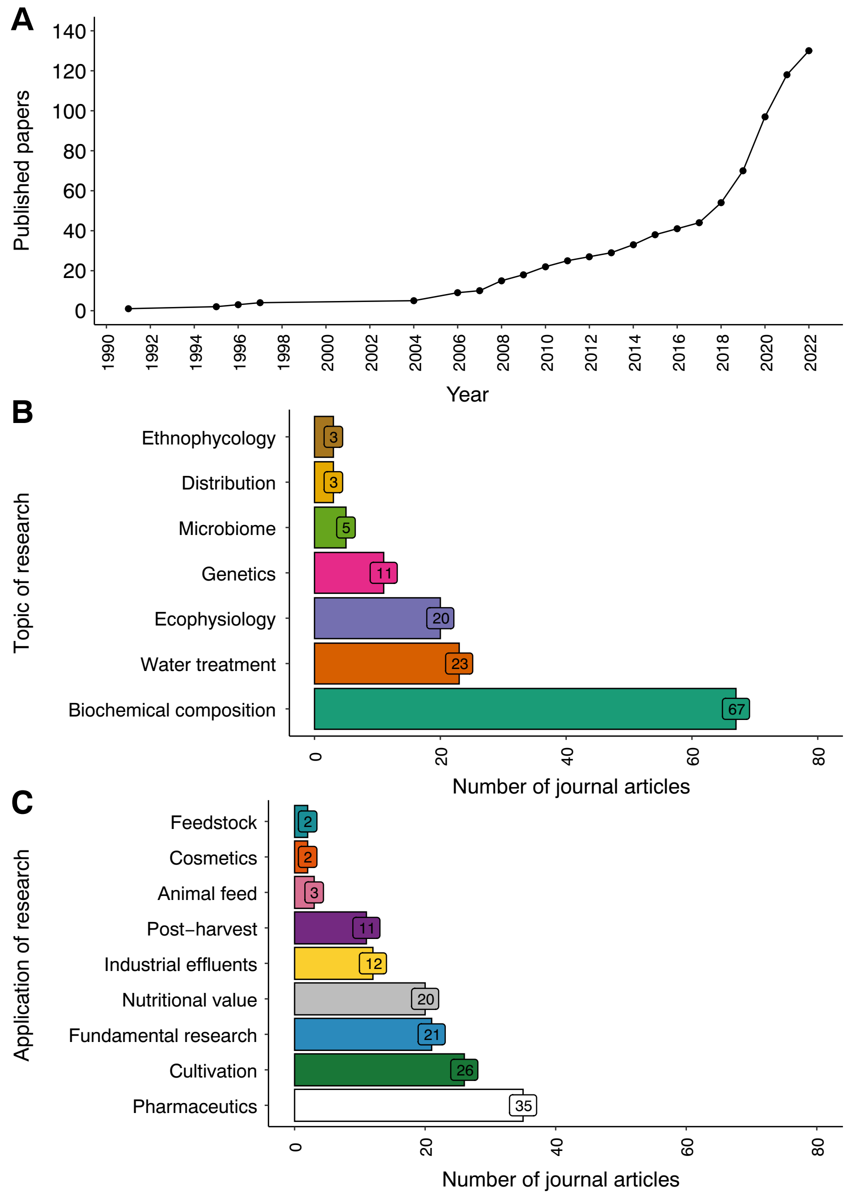

Fig. 3 **A** Cumulative plot of published papers on *Caulerpa lentillifera* (journal articles only) and the respective **B** topics, as well as **C** applications of the research presented in the studies

seven papers that were not included in the study, because they were not written in English were published in Japanese (n = 4), Chinese (n = 2) and Bahasa Indonesia (n = 1).

In the following, the main output articles grouped in the topics of "Ecophysiology", "Biochemical composition" and "Water treatment" with the respective applications of "Cultivation", "Nutritional value" or "Post-harvest" were summarized by topics.

Ecophysiology

A total of 20 papers were grouped under the topic "Ecophysiology" with 17 articles conducting research on the topic of "Ecophysiology" and the application of "Cultivation" (n = 9), followed by "Post-harvest" (n = 6) and "Nutritional value" (n = 2, Figs. 4, 6). The studies focused on the effect of one or more abiotic parameters on the physiology of the alga, and light was the major parameter studied (n = 8, Fig. 6A). The response variables seemed to depend on the application (Fig. 6B), with biomass production, biochemical composition and chlorophyll *a* fluorescence being most commonly used for research in the topic of "Cultivation", whereas studies focusing on "Post-harvest" mainly quantified water content, biochemical composition and colour/ pictures (Fig. 6B). Most studies were designed to test the effect of a single factor (n = 13), rather than running a crossed design experiment (n = 4, Fig. 6C).

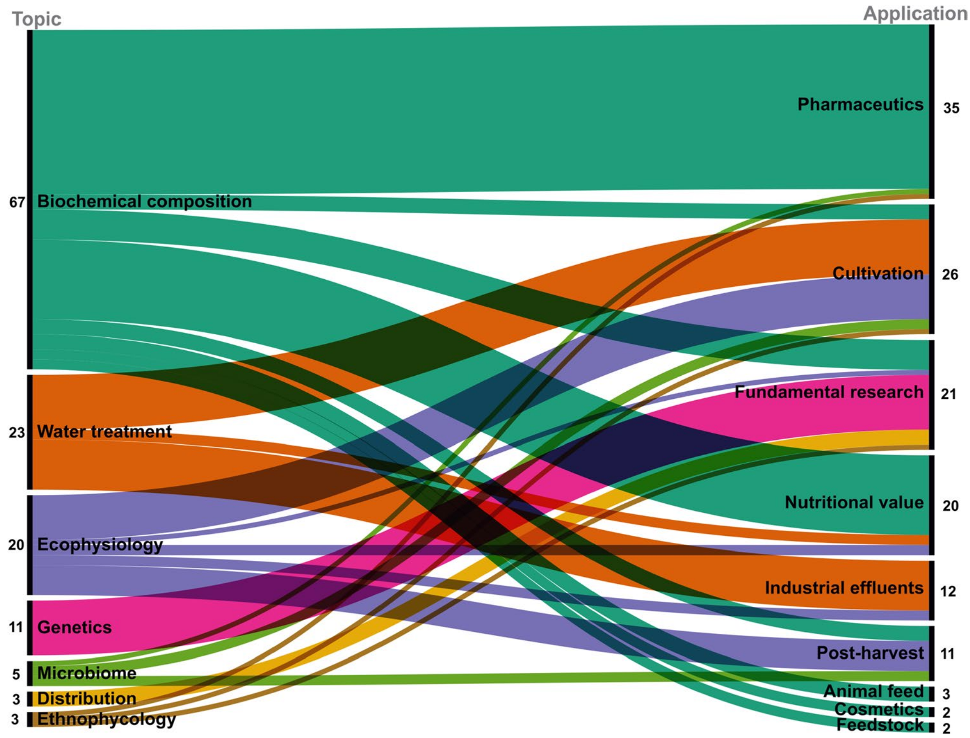

Fig. 4 Sankey-plot visualizing the distribution of *Caulerpa lentillifera* related articles by topics (left) and applications (right). The numbers represent the articles included in the respective category. In total, 130 articles were included. Two papers were sorted in two categories since the articles dealt with various topics and/or applications

Cultivation

Biomass production (n = 6) and the biochemical composition (n = 6), including especially pigment (Guo et al. 2015a, b; Kang et al. 2020; Cai et al. 2021b), protein (Long et al. 2020b; Cai et al. 2021b) or fatty acid content and pattern (Long et al. 2020b), were the most frequently used response variables (Fig. 6B, On-line Appendices III), whereas light was majorly used as an experimental parameter (n = 5, Fig. 6A). The shade-adapted sea grapes showed highest biomass productions at photosynthetically active radiations (PAR) of 40 and 100 µmol photons m^{-2} s^{-1}, compared to 20 and 100 µmol photons m^{-2} s^{-1} (Guo et al. 2015b) and 50 and 150 µmol photons m^{-2} s^{-1} (1Blue, 5Red light emitting diodes/LED; Kang et al. 2020), respectively. However, irradiances of ≥ 100 µmol photons m^{-2} s^{-1} were reported to cause physiological stress (Guo et al. 2015b; Kang et al. 2020; Stuthmann et al. 2020).

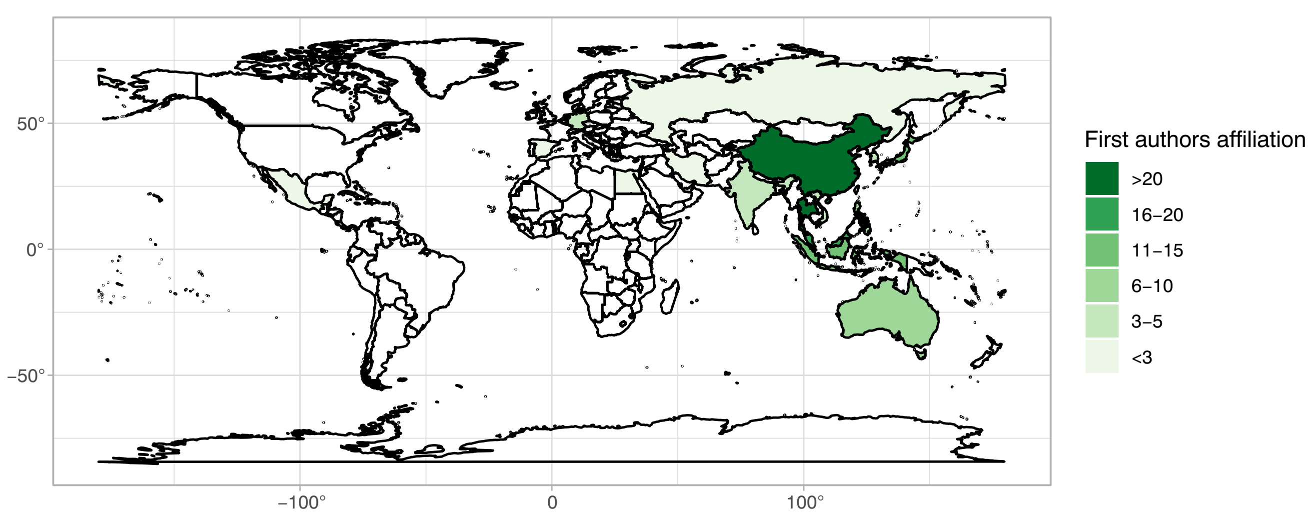

Fig. 5 Affiliations of first authors, who have published *Caulerpa lentillifera* related articles. The countries were grouped by the number of appearances

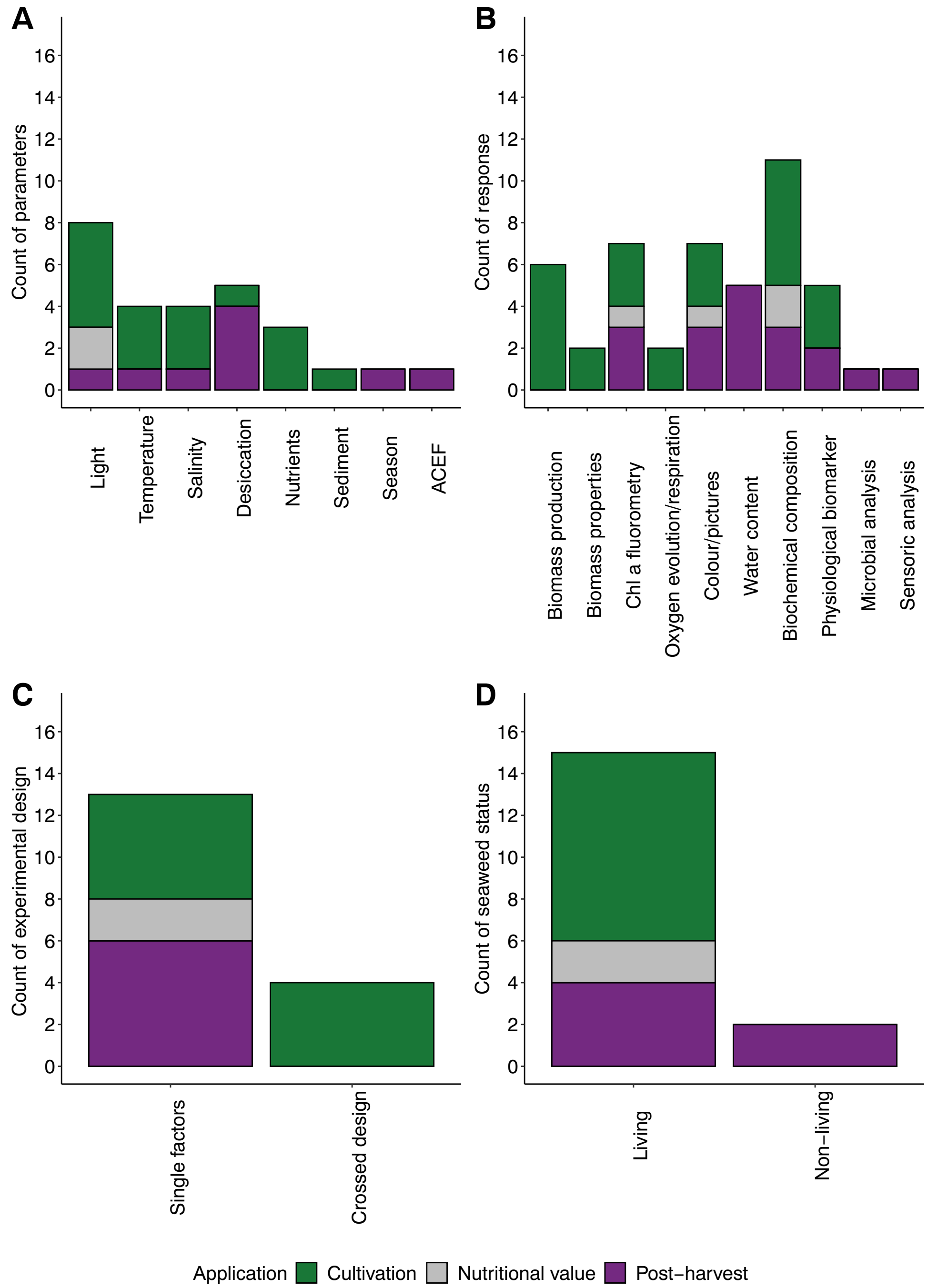

Fig. 6 Count of **A** experimental parameters tested, with alternating current electric field abbreviated as ACEF, **B** response variables quantified, **C** experimental design and **D** seaweed status performed in papers in the topic of "Ecophysiology", "Nutritional value" and "Post-harvest", grouped by the different applications (Count of papers: Cultivation (n=9), Nutritional value (n=2), Post-harvest (n=6))

Besides the level of irradiances, which also impacted sea grapes´ morphology (Guo et al. 2015b; Fakhrulddin et al. 2021), the photoperiod and the light spectrum had profound effects on the physiology of sea grapes, resulting in different biomass productivities, pigment contents and bioactivities (Kang et al. 2020). Blue light triggered phytoene desaturase (PDS) expression and antioxidant activities, whereas red light rather enhanced biomass production. Hence, authors recommended a spectrum of 1B5R (16.7% blue + 83.3% red) and a photoperiod of 12 h light and 12 h darkness for the indoor cultivation of sea grapes (Kang et al. 2020). UV light is known to induce oxidative stress in seaweeds (Dring 2005) and a reaction of *C. lentillifera* to different exposure scenarios is to be expected. However, only low absorbance in the UV-spectrum was recorded for sea grapes (Tanaka et al. 2020) and the effect of UV light on the ecophysiology of *C. lentillifera* has not yet been investigated. Despite light being the main experimental stressor, the studies were only running for 7 days until 4 weeks and only one article focused on shorter exposure times (< 72 h, On-line Appendices III; Terada et al. 2021).

Three studies focused on the effects of temperature, salinity, and nutrients on the physiology of *C. lentillifera*, respectively (Fig. 6A, Table 1). Temperature and salinity had profound effects on the biomass production of sea grapes, with highest growth rates at 27 °C and 27.5 °C (at 60 and 40 µmol photons m^{-2} s^{-1}, respectively; Guo et al. 2015b; Cai et al. 2021b) and 35 PSU (Guo et al. 2015a; Tanaka et al. 2020). Temperatures and salinities outside of the optimal conditions caused not only a decrease in biomass production, but also changes in the photosynthetic efficiency F_v/F_m, photosynthesis vs. irradiance curve parameters, enzymatic antioxidant expression (catalase/CAT, superoxide dismutase/SOD) and pigment content (Table 1). With regards to nutrients, the effect of nitrate (Guo et al. 2015a; Cai et al. 2021b) and phosphate levels (Guo et al. 2015a), as well as different fertilizers (Fakhrulddin et al. 2021) on the physiology and growth of sea grapes were tested. Nitrate levels did not affect the growth rates of sea grapes at phosphate levels of 10, 29, and 400 µmol L^{-1} (Guo et al. 2015a; Cai et al. 2021b), respectively; whereas an effect was reported at 100 µmol L^{-1} of phosphate (Guo et al. 2015a). Consequently, the presence of commercial fertilizers did result in higher biomass production, compared to the control with natural sea water (Fakhrulddin et al. 2021). Increasing nitrogen (N) levels lead to ascending chlorophyll *a*, carotenoid and soluble protein concentrations (Guo et al. 2015a; Cai et al. 2021b), which might however also depend on the prevailing phosphate concentrations (Guo et al. 2015a). Nutrient accumulation of *C. lentillifera* seemed also influenced by the presence of bottom sediment, which caused an increase in ash, mineral elements and heavy metals, and changes in the amino acid composition; but decreased the content of PUFAs and carbohydrates (Long et al. 2020b). Five studies investigated the effect of a single parameter, while four quantified cross effects (Fig. 6C, Table 1). Interactive effects of light and temperature (Guo et al. 2015b; Terada et al. 2021), phosphorous (P) and N concentrations (Guo et al. 2015a), and N levels and temperature (Cai et al. 2021b) were studied. For instance, effects on photosynthesis and respiration of *C. lentillifera* caused by temperature were reversed by increases in the nitrate level, implicating that eutrophication and climate change could have interactive effects on sea grapes during cultivation (Cai et al. 2021b).

Post-harvest

Six papers investigated the ecophysiology of *C. lentillifera* with a focus on their post-harvest. Four of these focused on the post-harvest storage of the fresh seaweed product in different packaging environments, where desiccation was the main stressor. Therefore, the authors most frequently chose water content as the essential response variable (Fig. 6A, B; Terada et al. 2018; Stuthmann et al. 2020; Liang et al. 2021; Sulaimana et al. 2021).

Desiccation of *C. lentillifera* fronds, independent of the different packaging materials and experimental setups, resulted in varying degrees of water loss over different experimental runs, from ~ 5% after 5 days (Liang et al. 2021), to ~ 25–40% after 9 days (Sulaimana et al. 2021) and ~ 9 to 72% water loss after 12 days (Table 1; Terada et al. 2018; Stuthmann et al. 2020). Desiccation induced oxidative stress, quantified by decreasing F_v/F_m values (Terada et al. 2018; Stuthmann et al. 2020; Liang et al. 2021), increasing levels of stress biomarkers, including malondialdehyde (MDA), superoxide anion, hydrogen peroxide, peroxidase, proline and antioxidant enzymes (CAT, SOD, peroxidase/PER) (Liang et al. 2021; Sulaimana et al. 2021), as well as decreases in chlorophyll *a*, *b* and soluble protein content (Liang et al. 2021; Sulaimana et al. 2021). However, when sea grapes were rehydrated after desiccation, a recovery, e.g. by increasing photosynthetic efficiency values (F_v/F_m) was documented (Terada et al. 2018; Stuthmann et al. 2020; Liang et al. 2021). Supra-optimal light irradiances of PAR induced additional stress on the physiology of sea grapes, resulting in higher F_v/F_m decreases and the trend of colour loss (Stuthmann et al. 2020). Hence, room irradiances (3 µmol photons m^{-2} s^{-1}) were suggested during sea grape storage (Stuthmann et al. 2020). Sea grapes are commonly stored for transport or retail in plastic containers, however, the plastic material differs and seemed to affect the physiological response of the seaweed (Terada et al. 2018; Stuthmann et al. 2020). Additionally, the initial constitution of the sea grapes, e.g. influenced by the harvesting season, had an effect on the physiological response during desiccation, with slower decomposition rates at better initial physiochemical constitutions (Sulaimana et al. 2021). Additionally, applying alternating current electric field (ACEF) on *C. lentillifera* to suppress reactive oxygen species (ROS) accumulation during storage resulted in reduced water loss, chlorophyll and phenol degradation, as well as MDA production and thus provides a post-harvest treatment method with potential that should be further investigated (Sulaimana et al. 2021).

Two studies investigated the ecophysiology of sea grapes which were not alive (Fig. 6D), but cured in a brine solution and oven-dried (Anantpinijwatna et al. 2018) during post-harvest to extend the shelf-life (Tolentino et al. 2021). Storage in brine solutions ≤ 5% exceeded the bacterial limit and was rated less acceptable in sensory testing, whereas storage in brine solutions of 10, and 15% for ten days had acceptable bacterial counts and better sensory evaluations, regarding e.g. colour, odour and texture, especially after re-hydration (Tolentino et al. 2021). However, total chlorophyll and carotenoid content decreased significantly more at higher salinity concentrations (Tolentino et al. 2021).

Table 1 Compilation of the different environmental cultivation parameters and their ecophysiological effects on sea grapes (*Caulerpa lentillifera*) during cultivation, post-harvest and in co-culture set-ups

Environmental parameter		Application	Effect	Studied interactions with…	Source
Light	Irradiances (PAR[a])	Cultivation	higher growth rate at 40 µmol photons m^{-2} s^{-1} (27.5 °C), than at 20 and 100 µmol photons m^{-2} s^{-1}, physiological stress at ≥ 100 µmol photons m^{-2} s^{-1}	temperature	(Guo et al. 2015b; Kang et al. 2020; Stuthmann et al. 2020; Fakhrulddin et al. 2021; Terada et al. 2021)
		Post-harvest	room irradiances (3 µmol photons m^{-2} s^{-1}) evoked best F_v/F_m values and least water losses, compared to high irradiances (70 µmol photons m^{-2} s^{-1}) and dark treatment	desiccation	(Stuthmann et al. 2020)
		Nutritional value	antioxidant activity was triggered on level of pomegranate by light stress (300 µmol photons m^{-2} s^{-1}, 14 days); antioxidant activity and total phenolic content more than doubled during irradiance exposure (50–600 µmol photons m^{-2} s^{-1}, 3–14 days), but targeted increase in antioxidant activity and total phenolic content negatively correlated to F_v/F_m, bleaching was caused with decrease in green colouration		(Sommer et al. 2022; Stuthmann et al. 2022)
	Photoperiod	Cultivation	12:12 light:dark had best weight gain percentage, compared to 8:16 and 16:8		(Kang et al. 2020)
	Spectrum	Cultivation	1:5 ratio of blue:red light (at 100 µmol photons m^{-2} s^{-1}, 12:12 h photoperiod) resulted in good growth and development		(Kang et al. 2020)
	Temperature	Cultivation	higher growth rates at ~ 27 °C, than at 20–25 and 30 °C, temperatures of 25–30 °C induced the formation of branches, enzymatic antioxidants (superoxide dismutase, catalase), chlorophyll *a* and carotenoid trend of being decreased at 27 °C temperatures, compared to 22 °C, photosynthetic parameters depended on nitrogen levels	nutrients	(Guo et al. 2015a; Cai et al. 2021b; Terada et al. 2021)
		Post-harvest	oven-drying temperatures (50–80 °C) affected colour of sea grapes and energy consumption of the process over different drying times		(Anantpinijwatna et al. 2018)
	Salinity	Cultivation	survival between 20 – 50 PSU, development at 30 – 40 PSU, maximum growth rate at 35 PSU, considering a range from 15 – 55 PSU, negative growth at salinities < 20 PSU, decrease of growth with salinities from 35 (5.62% day^{-1}), 30, 25 (2.54% day^{-1})		(Guo et al. 2015a; Tanaka et al. 2020; Fakhrulddin et al. 2021)
		Post-harvest	concentration of brine solutions of 10, 15% resulted in sensory evaluation and acceptable bacterial count, but total chlorophyll and carotenoid content decreased, compared to lower brine solution concentrations (0, 5%), where bacterial counts exceeded the acceptable limit		(Tolentino et al. 2021)
	Desiccation	Cultivation	continuous desiccation at humidity of 50% for ≥ 60 min. did not recover F_v/F_m after rehydration, F_v/F_m drop, when absolute water content was ≤ 90%	temperature	(Terada et al. 2021)

Table 1 (continued)

Environmental parameter	Application	Effect	Studied interactions with…	Source
	Post-harvest	progressing desiccation resulted in decreasing water content, F_v/F_m, and increasing content of oxidative stress biomarkers, re-hydration lead partly to recovery reactions	light	(Terada et al. 2018; Stuthmann et al. 2020; Liang et al. 2021; Sulaimana et al. 2021)
Nutrients	Cultivation	increased nitrate levels (48, 188, 750 µmol L^{-1}) caused increased soluble protein, chlorophyll *a*, carotenoid contents, photosynthetic parameters depended on temperature, interaction between phosphor and nitrogen contents in surrounding water	temperature	(Guo et al. 2015a; Cai et al. 2021b; Fakhrulddin et al. 2021)
Bottom sediment	Cultivation	presence increased ash, mineral elements, heavy metals		(Long et al. 2020b)

[a]Photosynthetically active radiations

Nutritional value

The nutritional value was the focus of two studies from the topic "Ecophysiology". The antioxidant activity was triggered by exposure of sea grapes to light-stress and resulted in higher antioxidant activity values of light-stressed algae (300 µmol photons m^{-2} s^{-1}, 14 days), compared to the dehydrated product and similar values to that of the renowned "super fruit" pomegranate (Sommer et al. 2022). However, the chlorophyll content decreased during light-stress exposure, causing a bleaching of the alga and potentially decreasing consumer acceptance (Stuthmann et al. 2022). Therefore, the duration and intensity of the light treatment should be applied to the intended usage of the biomass as a fresh (e.g. food product) or dry (e.g. cosmetic) product. Medium irradiances (200–600 µmol photons m^{-2} s^{-1}) and shorter exposure periods (3–7 days) resulted in significantly enriched antioxidants, but without strong bleaching of the sea grapes, whereas high irradiances and longer exposure periods (200–600 µmol photons m^{-2} s^{-1}, up to 14 days) increased antioxidants even more, but with significant loss of chlorophyll and colour (Stuthmann et al. 2022).

Biochemical composition

The topic "Biochemical composition" comprised the overall highest number of papers, compared to the other topics (Fig. 3A), with the applications of "Nutritional value" (n = 16), "Post-harvest" (n = 3) and "Cultivation" (n = 3) accounting for a total of 23 (Fig. 4). The authors focused on different biochemical compounds and hence conducted various analyses (Fig. 7, On-line Appendices IV). Considering all three applications, proximate analysis (n = 9) and antioxidant activity (n = 9) were analysed most frequently, followed by mineral (n = 8) and fatty acid analysis (n = 7) and the total phenolic content (n = 6, Fig. 7A). Most of the studies compared *C. lentillifera* (intra-species comparisons, n = 10) from different regions (Zhang et al. 2020), cultivation seasons (Wichachucherd et al. 2019) or set-ups (Syamsuddin et al. 2019), whereas nine and six studies compared *C. lentillifera* with species from a different (inter-species comparison) or the same genus (intra-genus comparison, Fig. 7B).

Cultivation Two intra-species comparisons quantified seasonal (Wichachucherd et al. 2019) and cultivation method (Syamsuddin et al. 2019) related effects on the biochemical composition of sea grapes in the frame of their "Cultivation" (Table 2, Fig. 4). Indoor and outdoor cultivation of *C. lentillifera* resulted in biochemical differences in sea grape tissue, possibly due to sediment type and light irradiances. *Caulerpa lentillifera* showed differences in mineral (indoor: 49.92—52.79% ash, outdoor: 32.04 – 36.60% ash), carotenoid (indoor: 1.32—2.11 ppm, outdoor: 1.71—2.29 ppm)

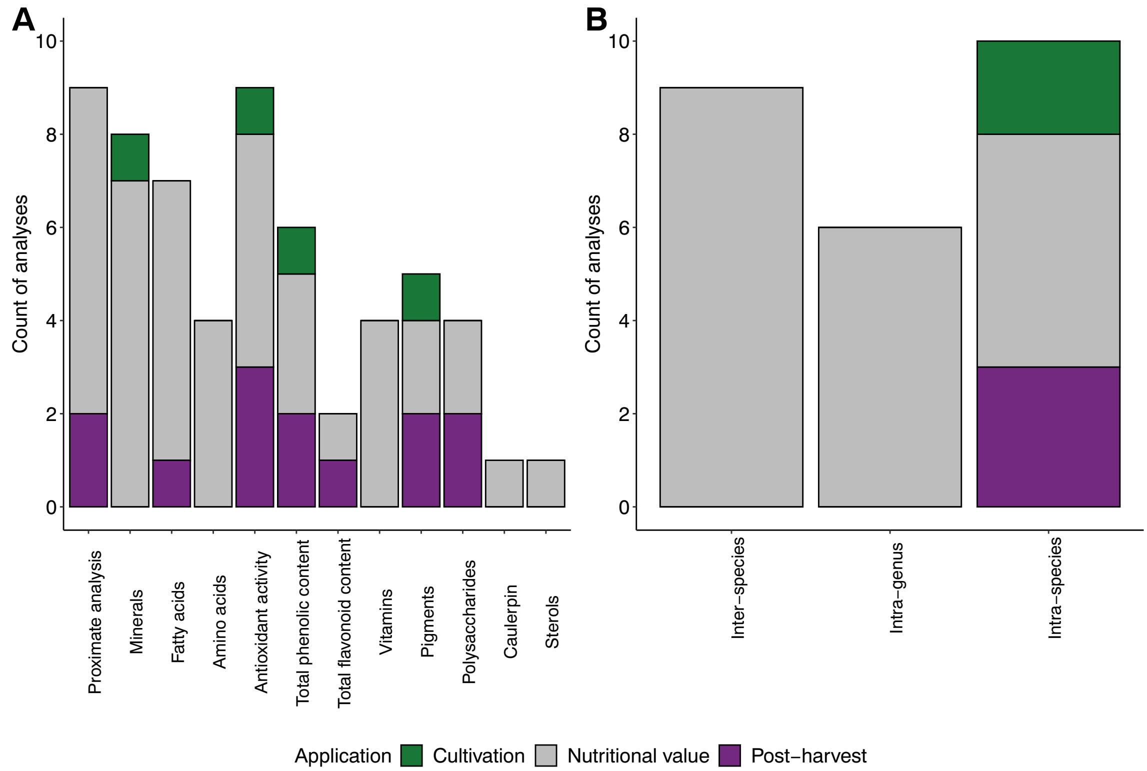

Fig. 7 Count of **A** analyses and **B** comparison with species of other genus (inter-species), other species from the genus *Caulerpa* (intra-genus) and comparisons of *Caulerpa lentillifera* (intra-species) performed in papers in the topic "Biochemical composition", grouped by the different applications (Count of papers: Cultivation (n=2), Nutritional value (n=16), Post-harvest (n=3))

and fibre (indoor: 5.03—5.56%, outdoors: 7.64—8.65%) content, as well as weight increase (indoor: 1.17 – 80.12 g, outdoor: 1.66 – 25.15 g; Syamsuddin et al. 2019). However, substrate mixture, culture depth (Syamsuddin et al. 2019) and temporal changes in salinity and nitrate content (Wichachucherd et al. 2019) also caused differences in specific target substances.

Nutritional value The edibility of sea grapes was the most common reason given for their research by scientists investigating the "Nutritional value" (Table 2). The components examined seemed to follow a pattern. Analysis of proximate composition was often conducted in combination with the fatty acid and amino acid content, vitamins and minerals (Ratana-arporn and Chirapart 2006; Salleh and Wakid 2008; Matanjun et al. 2009; Zhang et al. 2020). Researchers also focused on the antioxidant composition, namely the antioxidant activity, total phenolic content and/or total flavonoid content (Matanjun et al. 2008) in combination with minerals (Nufus et al. 2019; Ismail et al. 2020), pigments (Balasubramaniam et al. 2020), or the proximate composition (Nguyen et al. 2011;Table 2).

The authors quantified mean water contents ranging from 87.05 – 95.95% fresh weight (FW). Sea grapes were rather high in carbohydrates (27.19—72.90% dry weight/DW) and crude proteins (9.26—19.38% DW), but lower in crude lipids (0.70—2.87% DW) and fibre (1.91—12.98% DW). The mean ash content ranged widely (2.10—47.80% DW), which might have influenced the equally wide range of minerals (On-line Appendices V). Overall, highest concentrations of macro- and microminerals were found for sodium (Na, 1229.7—16,050 mg (100 g)$^{-1}$ DW) and iron (Fe, 9.3—1972.9 mg (100 g)$^{-1}$ DW), respectively (On-line Appendices VI). Regarding the fatty acid composition, *C. lentillifera* contained mostly saturated fatty acids (SFAs, 40.7—82.69% of total fatty acids) and approximately similar amounts of mono-unsaturated fatty acids (MUFAs, 8.43—36.83% of total fatty acids) and PUFAs (9.49—38.07% of total fatty acids). Palmitic acid (C16:0, 8.74 – 49.46% of total fatty acids), omega-6 PUFA Linoleic acid (C18:2N6C, 4.26—11.85% of total fatty acids) and omega-3 PUFA α-Linolenic (C18:3N3, 2.73—13.42% of total fatty acids) were most abundant (On-line Appendices VII). The total amino acids (101.63—147, with for human essential 44.02—57.01 and non-essential 54.08—89.99 mg g^{-1} DW) were mainly represented by the essential amino acids glutamic acid (Glu, 13.47 -17.8 mg g^{-1} DW), aspartic acid (Asp, 8.33—14.89 mg g^{-1} DW) and glycine (Gly, 5.14—19.23 mg g^{-1} DW) and the

Table 2 Overview of studies and absence or presence (+) of respective measurements (proximate analysis/PA, mineral content/M., fatty acid analysis/FA, amino acid analysis/AA, antioxidants/AO, total phenolic content/TPC, vitamin content/Vit, pigments/Pig, polysaccharides/Pol, caulerpin/Cau, sterols/St) for articles in the topic "Biochemical composition", as well as the purpose the study. The articles are grouped by the application

Reference	Purpose	Regions	Conducted analyses												Application
			PA	M	FA	AA	AO	TPC	TFC	Vit	Pig	Pol	Cau	St	
(Syamsuddin et al. 2019)	Intra-species comparison (indoors vs outdoors), including growth data	Sulawesi, Indonesia		+							+				Cultivation
(Wichachucherd et al. 2019)	Intra-species comparison (time-series over three month in pond culture)	Phetchaburi Province, Thailand					+	+							
(Balasubramaniam et al. 2020)	Inter-species comparison with *Eucheuma denticulatum, Sargassum polycystum* (edible algae)	Malaysia					+				+				Nutritional value
(Ismail et al. 2020)	Intra-genus comparison from two locations in Malaysia, Johor: *C. racemosa, C. manorensis;* Port Dickens: C. *sertularioides, C. racemosa* var *lamourouxii, C. lentillifera, C. racemosa* var *cylindracea* and *C. racemosa* (edible algae)	Port Dickens, Malaysia, Johor, Malaysia		+			+	+	+						
(Long et al. 2020a)	Assessment with one species	China										+			
(Matanjun et al. 2008)	Inter-species and Intra-genus comparison with *Eucheuma cottonii, E. spinosum, Halymenia durvillei, C. racemosa, Dictyota dichotoma, Sargassum polycystum, Padina sp.* (edible algae)	Borneo, Malaysia					+	+							
(Matanjun et al. 2009)	Inter-species nutritional comparison with *Eucheuma cottonii*, *Sargassum polycystrum* (edible algae)	North Borneo, Malaysia	+	+	+	+				+					
(Nagappan and Vairappan 2014)	Intra-genus comparison with *C. racemosa* var. *clavifera f. macrophysa, C. racemosa* var. *laetevirens* (edible algae)	Sabah, Malaysia	+		+								+		
(Nguyen et al. 2011)	Intra-species, Analytical assessment and antioxidants (freeze-drying vs thermal drying, oolong tea)	Penghu, Taiwan	+				+	+							
(Nufus et al. 2019)	Inter-species comparison with *Halimeda opuntia*	Pramuka island, Indonesia		+			+								

Table 2 (continued)

Reference	Purpose	Regions	Conducted analyses												Application
			PA	M	FA	AA	AO	TPC	TFC	Vit	Pig	Pol	Cau	St	
(Paul et al. 2014)	Intra-genus comparison with *C. racemosa* var. *laetevirens*@Including biomass production and properties (Frond/ stolon) (edible algae)	Townsville, Australia		+	+						+				
(Ratana-arporn and Chirapart 2006)	Inter-species comparison with *Ulva reticulata* (edible algae)	Phetchaburi, Thailand	+		+	+				+					
(Saito et al. 2010)	Intra-species comparison (cultured vs wild) and inter-species with *Cladosiphon okamuranus*	Okinawa, Japan			+										
(Salleh and Wakid 2008)	Inter-species and intra-genus nutritional comparison with brown and green seaweeds, *Padina gymnospora, Sargassum baccularia, Sargassum binderi, Turbinaria conoides, Caulerpa racemosa*	Port Dickson, Malaysia	+							+					
(Setthamongkol et al. 2015)	Inter-species and intra-genus comparison with red and green seaweeds *Chaetomorpha crassa, Chaetomorpha linum, Ulva rigida, Caulerpa racemosa, Caulerpa brachypus, Caulerpa taxifolia, Gracilaria tenuistipitata* and *Gracilaria fisheri*@Additional growth data of three weeks culture@Development of novel seaweed products	Thailand	+												
(Shevchenko et al. 2009)	Intra-specific comparison (laboratory vs mariculture grown)	Khanh Hoa Province, Vietnam										+		+	
(Terriente-palacios and Castellari 2022)	Inter-species comparison with various other commercial macro- and microalgae (products, including fresh and dried) and alga-enriched products	Commercial products bought at				+									

Table 2 (continued)

Reference	Purpose	Regions	Conducted analyses												Application
			PA	M	FA	AA	AO	TPC	TFC	Vit	Pig	Pol	Cau	St	
(Zhang et al. 2020)	Intra-species nutritional comparison between regions in China and lit. values	Hainan, China; Shandong, China	+		+	+				+					
(Chaiklahan et al. 2020)	Sea grape waste (different extraction methods), increase value by usage of waste	Phetchaburi Province, Thailand					+	+			+	+			Post-harvest
(Srinorasing et al. 2021)	Sea grape waste (different extraction methods), increase value by usage of waste	Phetchaburi Province, Thailand			+		+	+	+		+				
(Honwichit et al. 2022)	Sea grape waste (different extraction methods), increase value by usage of waste	Phetchaburi Province, Thailand	+				+					+			

non-essential valine (Val, 6.18—11.16 mg g^{-1} DW), leucine (Leu, 7.79—12.86 mg g^{-1} DW) and phenylalanine (Phe, 4.81—19.95 mg g^{-1} DW, A VIII). Lysine (1.22—8.2 mg g^{-1} DW) was reported to be the most limiting amino acid in *C. lentillifera* (Matanjun et al. 2009; Terriente-palacios and Castellari 2022).

The total phenolic content of *C. lentillifera* was quantified using the Folin-Ciocalteu (FC) assay and ranged from 1.30 to 57.97 mg gallic acid equivalents[GAE] g^{-1} DW (On-line Appendices IX, Matanjun et al. 2008; Nguyen et al. 2011; Ismail et al. 2020). The total flavonoid content was only determined once (1506.41 mg Quercetin equivalent $(100\ g)^{-1}$; Ismail et al. 2020). Different assays with individual sets of (dis)advantages (Karadag et al. 2009) were often used supplementary and correlations between the results were common (Matanjun et al. 2008).

Pigment composition was quantified by two studies, whereas one only focused on chlorophyll *a* and *b* (258 ± 25 and 147 ± 14 mg $(100\ g)^{-1}$ DW) and the other one on a variety of others, including canthaxanthin, and astaxanthin. Both studies also determined β-carotene (15 ± 1.0 and 19.5 ± 0.0 mg g $(100)^{-1}$ DW) content (On-line Appendices X). The vitamin contents of vitamins A, B1(thiamine), B2 (riboflavin), B3 (niacin), C (ascorbic acid), and E (alpha-tocopherol) were investigated in four studies. Vitamin C (1—50.33 mg $(100\ g)^{-1}$ WW) was the most prominent vitamin, followed by E (2.22—8.41 mg $(100\ g)^{-1}$ WW). However, B vitamins 1, 2, 3 were present in concentrations < 1.1 mg $(100\ g)^{-1}$ WW (On-line Appendices XI). Vitamin D content has not yet been quantified, even though the vitamin was found in other (green) seaweeds (Debbarma et al. 2016). The majority (n = 9) of studies conducted an inter-species comparison of *C. lentillifera* with seaweeds from genera outside of *Caulerpa*, followed by six studies comparing the alga with other *Caulerpa* species and five studies investigating only *C. lentillifera* (Fig. 7B).

Authors stated that they chose the seaweeds based on their presence at the study location, and often also due to their role in human nutrition. Hence, *Sargassum* and *Eucheuma* were most prominent, besides *C. lentillifera* (Table 2; Matanjun et al. 2008, 2009; Salleh and Wakid 2008; Balasubramaniam et al. 2020). In the direct comparison with these seaweeds, *C. lentillifera* showed significantly enriched carbohydrate, sodium, magnesium, and total amino acid contents, but was significantly depleted e.g. in ash, crude fibre, and iodine (Matanjun et al. 2009). On the other hand, *C. lentillifera* had by far the highest ash content when compared to *Chaetomorpha*, *Gracilaria* and *Ulva* (Setthamongkol et al. 2015). The vitamin contents were in a similar range with *Sargassum* and *Eucheuma* species (Salleh and Wakid 2008; Matanjun et al. 2009), but seemed to be higher compared to *Ulva reticulata* (Ratana-arporn and Chirapart 2006). Besides, the PUFA content of *C. lentillifera* was significantly lower compared to *E. cottonii* and *S. polycystum* (Matanjun et al. 2009). Homotaurine and hypotaurine contents of *C. lentillifera* (0.60 ± 0.05, 0.14 ± 0.02 mg (100 g)$^{-1}$ DW), as well as the essential to non-essential amino acid ratio (0.51 ± 0.02) were compared to a variety of other commercial seaweed products (Terriente-palacios and Castellari 2022). The total phenolic content and antioxidant activities (ABTS, FRAP) were enriched compared to *E. cottonii* and *E. spinosum* (22.50 ± 2.78, 15.82 ± 1.24 mg phloroglucinol equivalents[PGE] g^{-1} DW) and other red and brown seaweeds of the genera *Dictyota*, *Padina* and *Halymenia* (Matanjun et al. 2008). On the other hand, radical scavenging activity (DPPH assay) and antioxidant activity (ORAC) of sea grapes were lower than in *Eucheuma denticulatum* (Balasubramaniam et al. 2020).

In the intra-genera comparison, *C. lentillifera* was mostly investigated alongside *C. racemosa* (Table 3; Matanjun et al. 2008; Salleh and Wakid 2008; Nagappan and Vairappan 2014; Paul et al. 2014; Setthamongkol et al. 2015; Ismail et al. 2020), but the results did not show a clear trend and seem to be highly influenced by local factors. Thus, *C. lentillifera* was reported to have overall lower nutritional values than *C. racemosa* regarding the PUFA and pigment content (Paul et al. 2014), but also with higher PUFA content (Nagappan and Vairappan 2014). The total phenolic content values of both *Caulerpa* species were similar (*C. lentillifera* 42.85 ± 1.22 vs *C. racemosa* 40.36 ± 1.05 mg PGE g^{-1} DW; Matanjun et al. 2009), however, the growth rates were unanimously reported significantly higher for *C. lentillifera* (Paul et al. 2014; Setthamongkol et al. 2015). Intra-species comparisons were conducted in order to test for the effect of growth region (Zhang et al. 2020), cultivation set-up (laboratory, the wild, or mariculture; Shevchenko et al. 2009; Saito et al. 2010) or different extraction and analytical methodologies (Nguyen et al. 2011; Long et al. 2020a). Zhang et al. (2020) found among others significant differences in the proximate composition, and vitamin C content in *C. lentillifera* from China´s Hainan and Shandong province. However, the cultivation set-up (Shevchenko et al. 2009; Saito et al. 2010), and the analytical methodology also had an effect on the nutritional composition. Thermal drying yielded significantly lower phenolic contents, compared to freeze drying (1.30 ± 0.02 vs 2.04 ± 0.03 mg GAE g^{-1} DW; Nguyen et al. 2011).

Post-harvest Three studies investigated the “Biochemical composition” of sea grapes within the application of “Post-harvest” (Fig. 4), all aiming to contribute to a circular economy approach by valorising waste biomass of *C. lentillifera* generated during the aquaculture. The nutritional value was reported to be not different from that of food-grade products (Chaiklahan et al. 2020). The studies focused on the polysaccharide (Chaiklahan et al. 2020; Honwichit et al. 2022), as well as the lipid (Srinorasing et al. 2021) fraction. In intra-species comparisons (Table 2) different extraction methods, namely varying algae-to-ethanol ratios, extraction times, stages and purifications were tested to obtain the highest yield of the respective target metabolites (Chaiklahan et al. 2020; Srinorasing et al. 2021). Regarding polysaccharide extraction, two-stage extraction with 60 min/stage, a solid-to-liquid ratio of 1:15 (w/v), extraction temperature of 90 °C, and two time precipitation by a concentration of 75% ethanol was reported to obtain highest polysaccharide yields of around 25% of DW (Chaiklahan et al. 2020) and the hot water extraction (pH 6, 90 °C for 20 min) was the most cost-effective (Honwichit et al. 2022). For lipid extracts, optimum extraction conditions were three-stage extraction with 15 min/stage, solid-to-liquid ratio of 1:10 (w/v) at room temperature for 30 min. At these conditions, crude lipids yields of around 28% DW were obtained (Srinorasing et al. 2021). One study conducted an economic evaluation for the production of polysaccharide in Thailand (Chaiklahan et al. 2020). Based on their estimation the polysaccharide extract could be profitable for the farmers.

Water treatment

Within the topic of "Water treatment”, papers were grouped into the applications “Industrial effluents” (n = 10), “Cultivation” (n = 11), and “Nutritional value” (n = 2), of which only the latter two were evaluated here.

Snails, fish, and shrimp were most often co-cultivated with *C. lentillifera*, followed by other seaweeds (Fig. 8A). The most prominent treatment and response variable quantified were the mono- vs co-culture applied by seven studies (Fig. 8B) and the nutrient removal/uptake rate (n = 9, Fig. 8C).

Cultivation A total of eleven studies focused on the application of “Cultivation” within the topic of “Water treatment”. The majority were conducted in pilot aquaculture systems (n = 8), including e.g. experimental recirculating aquaculture systems (RAS), open water integrated multitrophic aquaculture (IMTA), or larger scale same tank cultures, whereas three studies were conducted at laboratory scale (Table 3). The experiments conducted in larger-scale systems had considerably longer experimental runs (19 – 120 days, mean: 58 days), compared to the laboratory-based studies (10 h, 24 h and 15 days, Table 3, On-line Appendices XII).

The majority of studies focused on *C. lentillifera* as a bioremediator of nutrients in aquaculture effluents from different organisms (Table 3), whereas one study investigated the ability to remove sterol hormones (Lu et al. 2021). *Caulerpa lentillifera* was mostly integrated with one other

Table 3 *Caulerpa lentillifera* in integrated aquaculture, compilation of basic data, as well as success stories and pitfalls. In the column "Success ?" the sign + indicates that authors refer to the integration of *C. lentillifera* in the respective integrated system as an overall success, whereas the sign – indicates that authors report of profound problems

Source	Location	Co-cultured organism	Culture system	Success?	Lesson learned	Treatment	Result parameter	Experimental run	Application
(Anh et al. 2021)	Vietnam	Whiteleg shrimp (*Litopenaeus vannamei)*	Experimental, 120 L tanks	+	Pilot, significant reduction of nitrogen and phosphorous and improvement of shrimp post larvae growth, survival, yield, compared to mono-culture; RGR [a] of *C. lentillifera* increased with feeding rate of shrimp; *C. lentillifera* as complementary food source for shrimp	Mono vs co-culture, feeding rate/ratio formulation, stocking density of fed species	Biomass production, water quality, nutrient removal capacity	45 days	Cultivation
(Bambaranda et al. 2019b)	Thailand	Saline molly (*Poecilia latipinna*)	Experimental RAS[b]	+	Significant reduction of inorganic nutrients of aquaculture effluents by *C. lentillifera*	Proof of concept: *C. lentillifera* as bioremediatory species	Biomass production, water quality, nutrient removal capacity	60 days	
(Chaitanawisuti et al. 2011)	Thailand	Juvenile spotted babylon snail (*Babylonia areolata*)	Hatchery scale low-technology RAS[b]	+	Pilot, highest growth rate at algal density of 280 g m^{-3}, increased survival rate of snails with *C. lentillifera*	Mono vs co-culture, stocking density *C. lentillifera*	Biomass production, water quality, nutrient removal capacity	120 days	
(Dobson et al. 2020)	Vietnam	Spotted babylon snail (*B. areolata*), sea cucumber (*Holothuria scabra*)	Experimental, 500 L tanks	+	Pilot, underestimation of *C. lentillifera* biomass, total ammonia reduced with *C. lentillifera,* growth unaffected by co-culture, sea cucumber weight gain decreased when *C. lentillifera* present	Mono vs co-culture	Biomass production, survival and production of fed species, water and sediment quality, nutrient removal capacity, economic evaluation	84 days	
(Largo et al. 2016)	Philippines	Abalone (*H. asinina*)	Open water IMTA[c] system, cage culture	-	Fragile nature of the seaweed thalli did not allow culture in strong currents	Proof of concept	-	-	

Table 3 (continued)

Source	Location	Co-cultured organism	Culture system	Success?	Lesson learned	Treatment	Result parameter	Experimental run	Application
(Ly et al. 2021)	Vietnam	Whiteleg shrimp (*L. vannamei*)	Experimental, 500 L tanks	+	Pilot, significant reduction of inorganic nutrients and improvement of shrimp growth, survival, and production. Algal density of 1 kg m^{-3} shows best trend, but 0.5 – 2 kg m^{-3} possible	Mono vs co-culture, stocking density *C. lentillifera*	Biomass production, water quality, nutrient removal capacity, survival, production, and feed conversion ratio of fed species	56 days	
(Paul and de Nys 2008)	Australia	Barramundi (*Lates calcarifer*)	Settlement pond	-	Growth restricted due to uninitiated growth of green filamentous tide alga	Culture method, seedling size, culture depth	Biomass production, water quality, nutrient removal capacity, culture parameter	6 weeks (pond)/19 days (RAS[b])	
(Paul et al. 2014)	Australia	Focus on *C. racemosa* co-culture, but wastewater from abalone and sea urchin	Experimental RAS[b]	+	Co-culture with *C. racemosa* in the same tray possible, but *C. lentillifera* has higher biomass production	Mono vs co-culture	Biomass production, biomass properties, biochemical properties	6 weeks	
(Bambaranda et al. 2019a)	Laboratory	Sailfin molly (*Poecilia latipinna*)	Plastic containers filled with 300 mL filtered aquaculture effluents from *P. latipinna* culture	+	Pilot, best uptake rates modelled at Salinities between 29.1–30.7 ppt. and algal densities of 20, ~ 30,50 g L^{-1}	Stocking density of *C. lentillifera*, culture parameters (Salinity, Aeration)	Nutrient uptake rates	24 h	
(Liu et al. 2016)	Laboratory	Comparative study with *Gracilaria lichenoides*	1 L Erlenmeyer flasks		*C. lentillifera* selectively takes up nitrate prior to ammonia and the nitrate uptake rate was 7.43–50.43 µmol g^{-1} (dw) h^{-1}	Artificial changes (nutrient concentrations/ratios)	Biomass production, nutrient uptake rates, biochemical properties	15 days (growth experiment) 10 h (nutrient uptake experiment)	
(Lu et al. 2021)	Laboratory	Grouper	500 mL beaker, 50 L tanks containing effluents of grouper culture		Efficient removal of steroid hormones 17β-estradiol and 17α-ethinylestradiol (90% of 10 g L^{-1} within 12 h) from mariculture effluets	Mono vs co-culture, artificial changes (nutrients, sterols), culture parameter	Biochemistry, steroid removal	14 days (tank experiment)/24 h (beaker experiment)	

Table 3 (continued)

Source	Location	Co-cultured organism	Culture system	Success?	Lesson learned	Treatment	Result parameter	Experimental run	Application
(Anh et al. 2022)	Vietnam	Whiteleg shrimp (*L. vannamei*)	Experimental 500 L tanks	+	Co-culture with shrimp lead to higher contents of protein, lipids, and ash (compared to initial) of *C. lentillifera*, maintenance of appropriate water quality even at high shrimp densities, improvement of production efficiency with shrimp densities of up to 400 ind. m^{-3} with 1 kg m^{-3} sea grapes	Stocking density of *L. vannamei*	Biomass production, water quality, biochemical composition of cultured organisms, survival, and feed conversion ratio of fed species	56 days	Nutritional value

[a] Relative growth rate

[b] Recirculating aquaculture system

[c] Integrated multi-trophic aquaculture

species. Snails (*Babylonia areolata*, abalone) and fish (*Poecilia latipinna*, *Lates calcarifer* and grouper) were the most prominent organisms co-cultured with sea grapes, followed by shrimp (*Litopenaeus vannamei*), sea cucumber (*Holothuria scabra*) and sea urchin (Table 3, Fig. 8A). However, even though abalone were investigated in two studies (*Haliotis asinine:* Largo et al. 2016*;* species unknown: Paul et al. 2014), reports on its compatibility for co-culture with *C. lentillifera* are still missing. On the one hand, *C. lentillifera* was reported to be too fragile for the culture in baskets as part of an open water IMTA system with abalone, and therefore had to be replaced with a more robust species (Largo et al. 2016). On the other hand, although Paul et al. (2014) used abalone and sea urchins as cultivation medium, the authors focused on the co-cultivation of two *Caulerpa* species and did not further report on the fed-species.

The biomass production, usually expressed as growth rate, ranged from 0.46 – 4% day^{-1} (On-line Appendices XII). On the one hand, *C. lentillifera* showed higher growth rates when compared to *C. racemosa* (Paul et al. 2014) and *Gracilaria salicornia* (Chaitanawisuti et al. 2011). On the other hand, similar and lower values were obtained when compared to *G. lichenoides* (Liu et al. 2016) and other *Caulerpa* species (Paul and de Nys 2008). Besides biomass production, the texture of sea grapes is a unique selling point (de Gaillande et al. 2017) and therefore, biomass properties, including the respective frond to stolon ratio, the harvestable biomass, as well as the ramuli density are important parameters to consider, so far reported by two studies (Paul et al. 2014; Dobson et al. 2020). Most studies experimentally compared the mono-culture of fed-species with the integration of *C. lentillifera* (mono- vs. co-culture, Fig. 8B), reporting positive effects on the water quality and the fed-species (Table 3).

The nutrient removal/uptake was the most prominent response variable ($n = 8$, Fig. 8C), highlighting the function of the seaweed in the co-culture set-ups as a bioremediator. Various studies reported that *C. lentillifera* efficiently removed nutrients from aquaculture effluents, leading to decreased N (total ammonia, nitrite, nitrate; Dobson et al. 2020) and P levels (Chaitanawisuti et al. 2011; Bambaranda et al. 2019a, b; Anh et al. 2021; Ly et al. 2021), also recognizable by negatively correlated nutrient loads with sea grape densities (Anh et al. 2021; Ly et al. 2021; Margono et al. 2021) and N-enrichment in sea grape tissue (Paul and de Nys 2008; Liu et al. 2016; Bambaranda et al. 2019b). Sea grape tissue-N was one of the quantified response parameters summarized as biochemical composition, along with tissue-C content (Paul and de Nys 2008; Liu et al. 2016), chlorophyll (Lu et al. 2021), and heavy metal content (Bambaranda et al. 2019b). The growth of *C. lentillifera* was higher in a low N environment (0.017 mg L^{-1}, ~ 3% day^{-1}), compared to a high N environment (1.4 mg L^{-1}, ~ 4.2% day^{-1}; Paul

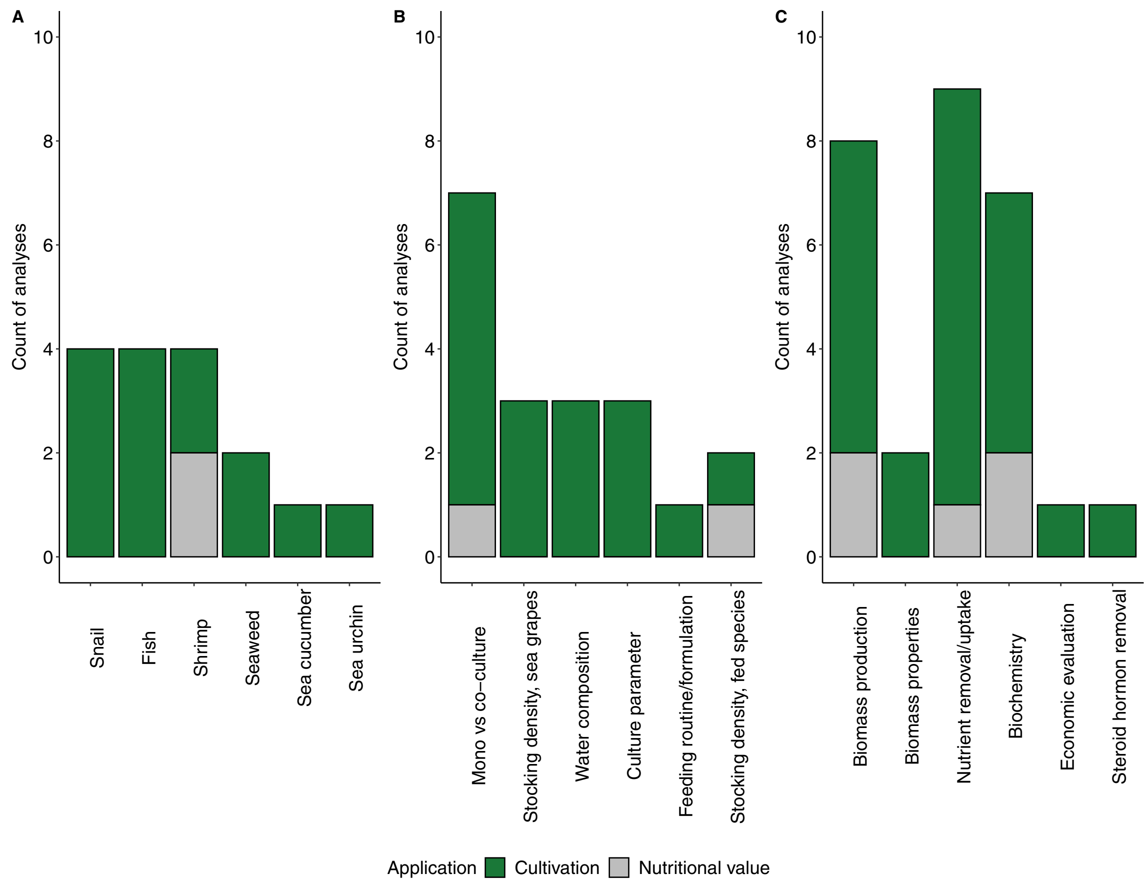

Fig. 8 Count of analyses of **A** organisms, **B** treatment during the study and **C** response parameter quantified in a co-culture set-up with *Caulerpa lentillifera* in the topic of "Water treatment", grouped by the different applications (Count of papers: Cultivation (n=11), Nutritional value (n=2))

and de Nys 2008) and at ammonia:nitrate ratios of around 1:5, as the species seemed to prefer nitrate over ammonia as a N source, in the presence of both (Liu et al. 2016). As the nutrient load entering an aquaculture system mainly depends on the fed-species, it is not surprising that the growth rate of sea grapes was also affected by the feeding rate and density of *L. vannamei* in the same tank (Fig. 8B; Anh et al. 2021). The growth rates increased from 0.46 to 1.05% day^{-1} with increasing feeding rates, but decreased (0.45 – 0.82% day^{-1}) with increasing shrimp densities (1000—3000 ind. m^{-3}), possibly influenced by shrimp grazing on *C. lentillifera* (Anh et al. 2021).

However, in other cases, the growth performance and biomass properties of sea grapes were independent of the presence of the co-cultured species, such as for snails and sea cucumbers (growth rate: 1.86 ± 0.12% day^{-1}; Dobson et al. 2020). These results indicated that the relation between nutrient input (feeding, stocking densities), water volume and algal biomass is essential, which can also be altered by adapting the initial seaweed stocking density in the system, as reported in three studies (Fig. 8B; Chaitanawisuti et al. 2011; Bambaranda et al. 2019a; Ly et al. 2021). Interestingly, the positive effect of the presence of *C. lentillifera* on growth rate, survival, and production of *L. vannamei* shrimp (Ly et al. 2021), as well as slight improvement of the yield and survival rate of snail *B. areolata* did not or only minimally depend on the initial *C. lentillifera* stocking densities (investigated ranges of 0.5 – 2 kg m^{-3}; Ly et al. 2021 and 0.280 – 0.840 kg m^{-3}; Chaitanawisuti et al. 2011). However, *C. lentillifera* growth rates significantly decreased with increasing initial biomass (Chaitanawisuti et al. 2011; Ly et al. 2021), e.g. from 2.58 ± 0.09% day^{-1} at a density of 390 g m^{-2}, to 1.92—1.70% day^{-1} at higher initial densities (790 g m^{-2}, 1170 g m^{-2}; Chaitanawisuti et al. 2011). Additionally, the growth tended to be highest in the first 14 – 20 days of the longer experimental runs, compared to the subsequent periods (Bambaranda et al. 2019b; Ly et al. 2021). This is most likely caused by changes in the light environment, due to increasing mutual shading of the algae (Bambaranda et al. 2019b) or loss of water transparency (Ly et al. 2021). Besides, feeding on *C. lentillifera* by *L. vannamei* may have led to improved food conversion ratios

(FCR) of the shrimp, but also to decreases in sea grape biomass (Anh et al. 2021).

Same tray co-culture with *C. racemosa* resulted in lower biomass productivities regardless of the initial stocking densities, potentially due to a delayed establishment, suggesting rather a mono-culture of the species (Paul et al. 2014). On the other hand, the presence of sea grape trays was assumed to result in a nearly 50% decreased yield of sea cucumber *Holothuria scabra*, compared to the set-up without the seaweed. Arguably because the shading provided by the trays inhibited the growth of microalgae in the sediment, which are an essential food source of sea cucumbers (Dobson et al. 2020). Only one study conducted an economic assessment (Dobson et al. 2020), reporting that the integration of *C. lentillifera* could increase the gross yield value substantially (US\$ 44.27 m^{-2}), compared to a sandfish mono-culture (US\$ 3.80 per m^{-2}) and a sea cucumber – *Babylonia* (US\$ 21.53 per m^{-2}) system. The monetary yields were only based on the farm-gate prices and neglect the initial investment, as well as work-force (Dobson et al. 2020).

Apart from nutrients, *C. lentillifera* can also be used to effectively remove steroid hormones from grouper aquaculture effluents (Lu et al. 2021), which was investigated by changing the sterol content in the water and quantify the sterol uptake rates (Fig. 8B, C). Of the four investigated seaweeds (*Ulva pertusa, G. lemaneiformis,* and *Codium fragile*), *C. lentillifera* was most efficient in removing steroid hormones 17β-estradiol and 17α-ethinylestradiol (EE2) within 12 h (4 g L^{-1} seaweed, more than 90% removal). The sterol removal rates were also affected by temperature and salinity (Lu et al. 2021). Salinity and aeration affected nutrient uptake rates of *C. lentillifera* from effluents of a saline molly (*Poeicilia latipinna*) in a 24 h laboratory study, and the authors identified optimal salinity levels (29—30 PSU) and aeration regime (to be present) using (non)linear regression (Bambaranda et al. 2019a), before testing the set-up (30 g L^{-1}, 30 PSU, aeration) in a scaled-up system (Bambaranda et al. 2019b). Due to substantial losses in an *in-situ* settlement pond experiment of a commercial barramundi (*Lates calcarifer*) aquaculture, possibly induced by epiphytic filamentous algae, the influence of fragment size and culture depth was tested. Depth did not affect *C. lentillifera* growth, but larger fragments (60.3 ± 10.6 g) seemed to induce higher losses compared to fragments one decimal smaller (6.4 ± 1.3 g; Paul and de Nys 2008).

Nutritional value Two studies in the topic of "Water treatment" focused on the nutritional value of *C. lentillifera*. Both studies evaluated the co-cultivation of sea grapes and *L. vannamei* in the same culture unit with capacities of 50 L (Omont et al. 2022) and 500 L (Anh et al. 2022), respectively (Fig. 8A). The studies tested the effect of a shrimp and/or sea grapes mono- vs. co-culture (eight shrimp and 15.23 ± 0.02 g sea grapes, respectively; Omont et al. 2022) and different *L. vannamei* densities (100—500 ind. m^{-3} and 1 kg m^{-3} sea grapes; Anh et al. 2022) on sea grape biomass production, biochemical composition, including proximate composition (Anh et al. 2022; Omont et al. 2022) and mineral content (Omont et al. 2022), as well as nutrient removal efficiency (Fig. 8C; Omont et al. 2022). The presence of shrimp significantly increased the percentage (DW) content of protein, lipids and ash, while decreasing the carbohydrates, compared to the initial biomass retrieved from pond cultivation. However, increasing shrimp densities significantly increased the protein content and decreased the ash content of sea grapes, with fibre, moisture, carbohydrates and lipids being similar among the density treatments (Anh et al. 2022). On the other hand, Omont et al. (2022) also reported an increased percentage (DW) of protein for sea grape tissue in co-cultivation, but relatively lower ash contents. However, the total content of trace elements increased significantly (Na by 12.5%, molybdenum by 78.0%, boron by 50.8%), whereas the content of cobalt decreased (Omont et al. 2022). The growth of sea grapes was highly negatively affected by the presence of shrimp (40.6 ± 9.8 vs 2.6 ± 0.4% day^{-1}; Omont et al. 2022) and tended to decrease with increasing shrimp densities, with significant depletion at the highest density treatment (500 ind. m^{-3}, 1.30 ± 0.11% day^{-1}; Anh et al. 2022). Grazing might have been a reason for this pattern, but it resulted in increased levels of iron (Fe) and zinc (Zn), total body cholesterol and muscle lipid content in the shrimp (Omont et al. 2022).

Discussion

Main research topics, applications, and author affiliation

Sea grape aquaculture has its roots in The Philippines and Japan (Okinawa) in the 1980s (Trono and Toma 1993; Estrada et al. 2021). Reliable, global production statistics for *Caulerpa* seaweeds are missing and local data are scarce, as they are not listed in national aquaculture statics (Moreira et al. 2021). However, it is generally accepted that the production and demand for this species is rising since approximately a decade ago. This might explain the elevated number of articles since 2018 revealed in the scientometric analysis, with > 60% of all publications (Scientometric analysis: Number of publications, research topics and applications). First authors were mainly from Asian countries (Scientometric analysis: Research networks) where the majority of sea grape cultivation takes place (Chen et al. 2019). The dominance of the research topic "Biochemical composition" and the application in "Pharmaceutics" highlights the interest in *C. lentillifera* for its bioactive compounds (Scientometric analysis: Number of publications, research topics and applications). Considering that marine natural products isolated from Chlorophyta are still underrepresented in the database *MarineLit* with 8% (1965–2012) compared to red (53%) and brown (39%) algae (Leal et al. 2013; Moreira et al. 2021), a further growth of interest in this topic and application is to be expected. This trend is possibly also driven by the comparatively higher values of these bioactive compounds in pharmaceuticals or cosmetics, compared to biomass e.g. for animal feed and biopolymers of feedstock (Chopin and Tacon 2021).

Sea grapes and their (a)biotic environment

Several environmental parameters are important for the cultivation of *C. lentillifera*. They can be adjusted precisely to the seaweeds´ needs during indoor cultivation, which is, however, associated with higher effort compared to outdoor cultivation. For the outdoor cultivation, crossed and interactive effects of different environmental factors are particularly important, considering daily, seasonal, or long-term changes and shifts. In the Northwestern Pacific, temperature and irradiance were major factors limiting *C. lentillifera* cultivation to certain seasons (Terada et al. 2021), whereas in The Philippines and other South-East Asian regions, temperature and salinity, caused by precipitation during the rainy season, restrict the cultivation to the dry season (Estrada et al. 2021). The cross-effects of many of these factors on the seaweeds' physiology and biochemical composition, like salinity and temperature, have not yet been tested in experimental set-ups, leaving room for further studies. Chemical diversity within a single seaweed species is not uncommon and spatial as well as temporal variability of environmental parameters are often cited as causes (Stengel et al. 2011). Different compounds are generally the result of specific responses to environmental parameters (Stengel et al. 2011). However, many of the studies evaluated in Nutritional value conducted inter-species or intra-genus comparisons of sea grapes´ nutritional value with other, often edible or economically interesting, seaweeds from the same location. In contrast, only a few studies intra-specifically compared biochemical composition of *C. lentillifera* across spatial regions, temporal scales, and culture methods (Cultivation, Nutritional value). However, the reported intra-specific variability enforced the importance of understanding the effects of single and crossed (a)biotic culture factors on the physiology (Cultivation), microbial community (Topic: "Microbiome", Application: "Cultivation"; Pang et al. 2022), and biochemical composition (Nutritional value; Wichachucherd et al. 2019) of the sea grapes observed in the pond environment. Besides, chemical variability between thallus parts is common within seaweeds (Stengel et al. 2011), and should be investigated for *C. lentillifera*, especially since differential gene expression in the thallus parts have been reported (Arimoto et al. 2019b).

The special role of light

Light has been identified as a major stressor for sea grapes, due to their unusually low irradiance saturations, also compared to other green seaweeds (e.g. *Codium* spp*.*, *Ulva* spp.; Nakamura et al. 2020; Marques et al. 2021). Hence, supra-optimal irradiances induced oxidative stress during cultivation (Cultivation) and post-harvest (Nutritional value), but they were also reported as an opportunity to increase the nutritional quality of *C. lentillifera*, by triggering its antioxidant production (Nutritional value). Sub-optimal irradiances, on the other hand, might have caused decreases in growth rates after a certain cultivation period, as reported from pilot co-culture systems (Cultivation). Consequently, management of initial biomass or harvest periods could ensure continuously optimal light conditions or purposefully increase sea grapes' quality already in the culture set-up (Magnusson et al. 2015). Most studies focused on the continuous exposure to PAR with consistent photoperiods (Water treatment) and only individual studies included changes in absorption spectra for photosynthesis, photoperiod, and short or extended exposure times (Kang et al. 2020; Terada et al. 2021). This leaves various knowledge gaps for further studies, such as considering variations on the temporal continuums, from high frequencies (e.g. evoked by high turbidity, movement of the cultivation covers, passing of co-cultured species), medium frequencies (daily solar cycle) to low frequencies (seasons; Comerford et al. 2021). Additionally, even though *C. lentillifera* seemed to contain only minor quantities of UV-absorbing compounds (Tanaka et al. 2020), the exposure to this stressor could impact the physiology of the alga and alter the secondary metabolite composition, as observed for other seaweeds (Polo and Chow 2022).

Sea grapes (not only) as bioremediators in co-culture approaches

The nutrient acquisition of seaweeds is complex and depends on various parameters (Roleda and Hurd 2019). The N and P loads in the application of cultivation water were reported to affect biomass production and composition of sea grapes in both mono-, and co-culture (Cultivation and Cultivation). Sea grapes bioremediated nutrients from the water, as indicated by reduced water nutrient levels (Cultivation). However, the actual nutrient acquisition rate was only examined once in the context of preferred N-sources (Liu et al. 2016). The comparison between studies focusing on the nutrient uptake was difficult, as different thallus parts of *C. lentillifera* were used. Fronds and the below ground parts (stolon with rhizoids) are expected to have different N and

P acquisition rates, as reported for *C. prolifera* (Alexandre and Santos 2020). This might explain the differences in composition, caused by the presence of bottom sediments and potentially higher nutrient loads in the pore water, compared to the water column (Long et al. 2020b). These information have important implications for the choice of cultivation method (trays, sowing method or the open water cage cultivation; Syamsuddin et al. 2019), especially when sea grapes are exposed to unusually high (e.g. for nutrient bioremediation in aquaculture; Cultivation, or eutrophication; Cai et al. 2021b) or rather low (oligotrophic waters) nutrient loads. Besides, salinity (Bambaranda et al. 2019a), N-sources (Liu et al. 2016) and potentially various other parameters (Roleda and Hurd 2019) affected the nutrient uptake rates. Higher growth rates than other *Caulerpa* species and the preference of nitrate over ammonia makes *C. lentillifera* a promising candidate for co-cultures (Cultivation). Regarding the application of sea grapes as a bioremediator in aquaculture systems with fed-species, it might be beneficial to implement polyculture of different seaweeds in order to remove different nitrogen compounds more efficiently. Commonly used species for biofiltration include *Ulva lactuca* and *Undaria pinnatifida* (Cahill et al. 2010), *Gracilaria birdiae* and *Gracilaria vermiculophylla* (Marinho-Soriano et al. 2009; Abreu et al. 2011), and *Porphyra leucosticta* which take up mainly ammonia (Chung et al. 2002). Since aquaculture effluents are usually higher in nitrate than ammonia content, implementing *C. lentillifera* together with commonly used species can enhance the bioremediation of the effluents (Neori et al. 2004). This has only been studied once (Paul et al. 2014). In general, *C. lentillifera* is a promising candidate for the use as a biofilter in integrated tank-based aquaculture systems, rather than in open water systems, at least when exposed to high water movements (Water treatment). However, when sea grapes were integrated in the same unit with *L. vannamei*, grazing of the shrimp on the seaweed was reported (Water treatment), leading on one hand to a loss of biomass, but on the other hand to reduced FCRs and a beneficial change in nutritional composition of the shrimp (Ly et al. 2021; Omont et al. 2022). Similarly, the integration of *C. lentillifera* powder in the feed (30 g kg^{-1}) of the black tiger shrimp (*Penaeus monodon*) significantly increased growth rate and FCR of the post larvae (Topic: "Biochemical composition", Application: "Animal feed"; Putra et al. 2019). However, a spatial segregation of the species could allow for a targeted feeding with sea grape biomass, e.g. the lower quality waste, integrated in the feed or provided fresh, and still allow for the seaweeds to bioremediate nutrients. On the other hand, this would require more space which could negatively impact the costs for the farmers (Dobson et al. 2020), reinforcing the importance of an economical assessment as basis for farmers decision making.

Economic assessment

Sea grape farming has been described as a lucrative business in The Philippines, among others, with the potential for global upscaling, but limited awareness has been identified as a hurdle (Dumilag 2019; Estrada et al. 2021). Ethnophycological studies are least represented in this literature review (Scientometric analysis: Number of publications, research topics and applications), even though the sea grape farmers are an essential part of the value chain of *C. lentillifera,* their knowledge, needs and access to scientific findings are of great interest. An essential part of such applied research could be the integration of an economic analysis of new co-culture approaches or cultivation and post-harvest methods, which has only been done scarcely (Chaiklahan et al. 2020; Dobson et al. 2020). The farm-gate price, likely for the use in human nutrition, of sea grapes reported from Vietnam (US$ 4.35 kg^{-1}; Dobson et al. 2020) lies clearly above the rather low average value of brown, red and green seaweed biomass (US$ 0.47, 0.39, 0.79 kg^{-1} WW, respectively; Cai et al. 2021a). Hence, sea grape farming could provide a good source of income, especially as initial investments, e.g. in the tidal pond cultivation, are rather low. Considering that parts of the harvest do not meet the required quality standards (Chaiklahan et al. 2020), the waste valorisation should be brought into focus (Post-harvest).

Sea grapes as human food

Red and brown algae dominate the commercial seaweed production and the share of green macroalgae is vanishingly low (FAO 2020; Moreira et al. 2021). *Caulerpa lentillifera* can compete with commercial seaweeds regarding their nutritional value, exhibiting similar or even higher amounts of for example minerals, vitamins, and antioxidative properties (Cultivation). The biochemical composition, including protein, lipid and carbohydrate content and quality, as well as bioactive compounds over vitamins and pigments varied considerably between studies (Biochemical composition, On-line Appendices V—XII), supported by a recent review on health benefits and nutrients of *C. lentillifera* (Syakilla et al. 2022).

Since the amounts of different biochemical compounds showed a large variability, it is important to understand the factors leading to these differences in order to improve their concentrations in the framework of *C. lentillifera* as functional food ingredient. The cultivation conditions or set-ups could even be managed to increase certain target compounds, like antioxidants (Nutritional value) or proteins through co-cultivation (Nutritional value). One delicate part in the life-cycle of *C. lentillifera* is post-harvest handling, as the product is still alive and photosynthetically active.

The shelf-life is therefore considerably short and quick transportation and retail are required. The packaging and storage materials differ locally, as well as the form of retail (de Gaillande et al. 2017), ranging from natural materials up to plastic (Terada et al. 2018; Stuthmann et al. 2020). The packaging materials (Terada et al. 2018; Stuthmann et al. 2020), in addition to the environmental conditions during previous cultivation (Minh et al. 2019) and during storage, influenced the quality of the sea grapes (Nutritional value; Stuthmann et al. 2020). However, considering studies on *C. lentillifera* during cultivation, it is expected that temperature (Terada et al. 2018), as well as the microbiome (Topic: "Microbiome", Application: "Cultivation; Liang et al. 2019; Kopprio et al. 2021) also have a major impact on the quality of the sea grapes during storage. The main costumer base for *C. lentillifera* is currently in Asia. However, the interest in this food product might be growing in Europe as well, especially since the demand for vegetarian/vegan food products (Lusk 2017) and the awareness of health and environmental issues related to food choices (de Boer et al. 2007; Wendin and Undeland 2020) is increasing. Sea grapes, with their unique texture and nutritional components, are an interesting candidate to contribute to human nutrition outside the current market in Asia. However, this requires advances in the land-based cultivation of this tropical species or in the improvement of the shelf-life. Furthermore, *C. lentillifera* is not yet considered by the European Novel food law (Barbier et al. 2019; Mouritsen et al. 2019). While single brown and red seaweeds (e.g. representatives of the orders Laminariales, Fucales and of the genera *Porphyra/Neopyropia*) are included in the Novel Food Catalogue, edible green macroalgae were rather neglected (Lähteenmäki-Uutela et al. 2021).

Conclusions

Caulerpa lentillifera is a promising candidate for aquaculture in general and for co-cultivation, especially since the value of the product is higher compared to other seaweeds, among others due to its striking texture ("green caviar"). The present review highlighted the interest in the alga's "Biochemical composition" with the application for "Pharmaceutical" and "Nutritional value", likely due to the various bioactive compounds of the sea grapes and the nutritional benefits for the human nutrition. However, more research is needed to understand the complex interactions between environmental parameters, which vary over regional and temporal scales, and the biochemical composition of the species, in order to potentially increase the production of target-compounds. Additionally, the comparable short shelf-life of the fresh product and the main restriction to the Asian market were identified as bottlenecks for global retail.

In the future, sea grapes could contribute to strengthen the role of green algae in the global seaweed aquaculture sector.

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