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The Economics of Aquatic Plants: The Case of Algae and Duckweed

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Abstract

This review examines global microalgae, seaweeds, and duckweed (MSD) production status and trends. It focuses on cultivation, recognizing the sector's existing and potential contributions and benefits, highlighting a variety of constraints and barriers over the sector's sustainable development. It also discusses lessons learned and ways forward to unlock the sector's full potential. In contrast to conventional agriculture crops, MSD can rapidly generate large amounts of biomass and carbon sequestration yet does not compete for arable land and potable water, ensuring minimal environmental impacts. Moreover, MSD's applications are ubiquitous and reach almost every industrial sector, including ones essential to meeting the increasing needs of human society, such as foods, pharmaceuticals, and chemicals. To this end, the growing public awareness regarding climate change, sustainable food, and animal welfare yields a significant shift in consumer preference and propels the demand for MSD. In addition, once governments usher in durable and stable carbon policies, the markets for MSD are likely to increase severalfold.

1. INTRODUCTION

Aquatic plants grow in freshwater, coastal marine waters, or open oceans and are the starting point of many food webs. This survey focuses on three such plants: microalgae, seaweeds (or macroalgae), and duckweed (MSD). Although microalgae are a photosynthetic aquatic organism, seaweed and duckweed are aquatic plants. However, for simplicity, we refer to them as aquatic plants. These plants are mostly directly consumed as human food and animal feed; however, they are consumed in much smaller volumes in pharmaceuticals and cosmetics, textiles, biofertilizers/biostimulants, and biopackaging products and applications. MSD have considerable potential to become an essential player in the bioeconomy as a source for plant-based protein and other biochemicals, feedstock for bio-oils and biofuels, a variety of high-value bioproducts, and a viable source for carbon sequestration.

The comparative advantages of MSD are the much higher biomass productivity than that of terrestrial plants (Casoni et al. 2020) while not competing for land or freshwater (Palatnik & Zilberman 2017). Importantly, MSD have higher photosynthetic efficiencies than land-based biomass production and are more efficient in capturing carbon (Packer 2009, Duarte et al. 2017). Moreover, MSD can be cultivated efficiently without antibiotics, fertilizers, and pesticides (Golberg et al. 2020a), and the global MSD biomass cultivation potential can sustain the industry's rapid growth. For example, the offshore cultivation potential of seaweeds can provide up to a quarter of predicted plant protein demand by 2054 (Lehahn et al. 2016). Roughly 0.3% of the ocean surface would be enough to produce as much biomass as is produced annually in all of global agriculture (Bjerregaard et al. 2016).

Demand for meat, fish, and dairy is soaring, particularly among the rapidly growing middle classes in parts of the developing world (GFI 2021). Producing those products in traditional agriculture uses large amounts of land, water, and pesticides and produces gigatons of greenhouse gases. Commercial fishing may not be sustainable, and overfishing pushes fish populations to become endangered or threatened. Dairy production also creates a range of negative externalities. Thus, MSD cultivation is a double dividend and may significantly address humanity's primary challenges: food security and climate change.

In 2019 the market for MSD products and applications was worth approximately US$20 billion (FAO 2021). The growing demand for sustainable biobased products and applications can potentially significantly increase the market. Furthermore, carbon pricing might dramatically exacerbate the demand for MSD.

Reviewing global trends in MSD production highlights the sector's existing and potential contributions and benefits and the variety of constraints and challenges over the sector's sustainable development. To better understand these challenges and opportunities, we first probe the evolution of the existing aquatic plant-based supply chains and then discuss how new ones might develop. In addition, we discuss lessons learned and policy needs to unlock the full potential of this industry.

Although we note many similarities among the three aquatic plants, we also highlight several differences. For example, the macroalgae industry is more developed than the microalgae industry, as harvesting microscopic algae invisible to the naked eye is more challenging. Nevertheless, farming and cultivation are considerable barriers to all MSD.

This article is structured as follows. Section 2 discusses the richness of products produced from MSD and examines global MSD production status and trends. Section 3 stresses the importance of the educational-industrial complex as a critical facilitator in the transition to the cultivation of aquatic plants. Section 4 surveys two demand catalyzers, which contributed to the increased research and commercialization of alternative products. Section 5 explores alternative supply chains used to cultivate and process the feedstock. Section 6 discusses the opportunities and barriers as well as policy and uncertainties faced by the industry. Finally, we offer concluding remarks in Section 7.

2. CURRENT PRODUCTION AND PROCESSES OF ALGAE AND DUCKWEED

What products and processes can we develop from MSD? What is the status of these technologies, and did some get commercialized? When attempting to shed new light on these questions, we start with algae and proceed with duckweed. Finally, we discuss the regional segmentation and give examples of active applications and firms in the market.

2.1. Algae: From Microphytes to Macrophytes

Algae encompass a broad category of organisms classified into two main categories: microalgae (microscopic photosynthetic eukaryotic organisms and cyanobacteria) and macroalgae (seaweed). Whereas seaweeds are marine organisms, microalgae are phytoplankton found in both freshwater and marine systems. Different strains of algae vary for combinations of chlorophyll molecules. Algae comprise proteins, carbohydrates, fats, and nucleic acids, yet the proportions vary across the various types of algae. Algal biomass intended for commercial purposes is grown in open raceway ponds and closed systems such as photobioreactors and fermenters; it may also be harvested from seaweed farms or obtained from natural standing stocks and, potentially, with careful controls, from harmful algal blooms.

Algae have much higher solar energy conversion efficiency than most terrestrial crop species: with 3% versus 1%, respectively (Packer 2009), algae can provide the inputs for a range of low-carbon products that can help decarbonize the economy. Thus, algae can become a sustainable disruptive technology affecting many products and processes, from food to energy.

Algae, including seaweeds and microalgae, contributed nearly 30% of world aquaculture production measured in wet weight in 2019 (Cai et al. 2021). In addition, the sale of algal biomass for specialty products such as dietary supplements and food additives is well established (US DOE 2020). As a result, the global upstream algae economy in 2020 was US$592 to $691 million and projected to reach one billion US$ by 2027, growing at a compound annual growth rate of 6.3–6.6%.[1] In 2019 the global market for algal products accounted for 5.4% of world aquaculture production value, reaching about $15 billion (FAO 2021)—that is, the added value that algae generated throughout the entire supply chain is estimated at around $15 billion.

The algae market is witnessing extensive growth opportunities, considering the increasing consumption across diverse areas, from food, plant-based proteins, fertilizers, and animal feed to cosmetics and pharmaceuticals (Fortune Bus. Insights 2020). Algae protein enriches the nutritional content of food, yields a positive effect on the immune system, promotes weight loss, and reduces fatigue and anxiety (Gómez-Zorita et al. 2020). Algae protein is also used to treat diabetes, attention-deficit hyperactivity disorder, and premenstrual heart diseases, among other health issues (Wells et al. 2017). Moreover, the plastic industry that searches for ways to produce biodegradable plastic contributes to the demand growth of MSD.

Climate, and especially carbon policy, can be a game changer for the MSD sector. Microalgae can fix carbon dioxide (CO_2) from three different sources: atmosphere, discharge gases, and soluble carbonates (Wang et al. 2008). Under natural growth conditions, microalgae assimilate

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[1] Reports available at **https://www.verifiedmarketresearch.com/product/algae-market/** and **https://www.grandviewresearch.com/industry-analysis/algae-protein-market**.

CO_2 from the air and can tolerate and utilize substantially higher levels of CO_2, up to 150,000 parts per million by volume (ppmv) (see Brown 1996). As a result, microalgae could sequester CO_2 emitted from power stations or other industrial sources, significantly reducing overall greenhouse gas emissions (Nigam & Singh 2011). Similarly, the use of seaweed aquaculture beds in potential CO_2 mitigation efforts has been already proposed with commercial seaweed production in China, India, Indonesia, Japan, Malaysia, Philippines, Republic of Korea (Chung et al. 2013), Thailand, and Vietnam, and more recently in Australia and New Zealand (Golberg et al. 2020b, Kelly et al. 2020). Algae can act as a novel form of carbon capture and storage (Economist 2021).

When comparing microalgae to macroalgae, we observe different technological paths likely driven by the algae's specific characteristics. Microalgae are single-cell microscopic organisms (microphytes) usually cultivated in freshwater tanks. In contrast, macroalgae are large multicellular macrophytes visible to the naked eye and found in ponds and coastal regions. The physical difference between microalgae and macroalgae (seaweed) yields differences in cultivation technologies that impact the sector's development.

2.1.1. Microalgae. Microalgae are phytoplankton found in both freshwater and marine systems. Microalgae are productive organisms that researchers strive to understand better and harness to create a spectrum of products used for various applications (Hochman & Zilberman 2014). They exhibit high photosynthetic efficiencies and yield up to ten times more (*Spirulina*) biomass per hectare than high-yielding corn hybrids (Dismukes et al. 2008). While research characterizes microalgae through the amount of protein, lipids, and carbohydrates they produce (Singh & Olsen 2011), the industry invests in microalgae-based products and expects high-margin applications.

As of 2021, most microalgae cultivated for commercial use are dried (e.g., *Spirulina* powder). The industry uses dried biomass for food and dietary supplements and the extraction of bioactive or biochemical compounds such as astaxanthin, β-carotene, omega-3, and fatty acids (Cai et al. 2021). The commercial production using microalgae includes nutraceuticals and other food additives with high nutritional value. Microalgae appeal to biofuel production because of their rapid growth rate, high lipid content, increased CO_2 absorption, and uptake rate. **Table 1** summarizes the potential of the products extracted from microalgal biomass.

Table 1 Products and applications of microalgae

Product	Applications	Reference(s)
Chlorophylls	Pharmaceuticals, cosmetics (e.g., deodorant)	Koller et al. (2014)
Astaxanthin	Food additive, antioxidant	Panis & Carreon (2016)
Canthaxanthin	Food additive, tanning pills	Matos (2017)
Fucoxanthin	Anti-adipositas	Loredo et al. (2016)
Lutein	Food additive, pharmaceuticals (antimacular degeneration), cosmetics	Nwachukwu et al. (2016), Gayathri et al. (2016)
Violaxanthin	Food additive	Koller et al. (2014)
Zeaxanthin	Food additive, animal feed, pharmaceuticals (e.g., anticolon cancer, eye health), pro-vitamin A, antioxidant food, cosmetics	Nwachukwu et al. (2016)
β-Carotene	Immunofluorescence techniques, antibody labels	Koller et al. (2014)
Bixin	Food additives, cosmetics	Koller et al. (2014)
Phycoerythrin	Immunofluorescence techniques, antibody labels	Pangestuti & Kim (2011)
Phycocyanin	Food colorant (e.g., beverages, ice cream, sweets), cosmetics, fluorescent markers in histochemistry, antibody labels, receptors	Henrikson (2009), BCC Research (2015)
α-Tocopherol	Food additive, antioxidant in cosmetics and foods	Pangestuti & Kim (2011)

To this end, a large body of literature shows the high potential of microalgal biorefinery to extract biogas, liquid and gaseous transportation fuel, kerosene, ethanol, aviation fuel, biohydrogen, biodiesel, bioethanol, and bio-oil (Gallagher 2011, Sharma et al. 2011, Levitan et al. 2014). Others have investigated various microalgae-produced gases such as biogas, biohydrogen, and syngas (Demirbas 2010, Nigam & Singh 2011). The US Department of Energy (US DOE 2016) identified microalgae to have the potential to synthesize 100 times more oil per acre of land than any other plant, which is better than soybeans. Several firms have been working to establish the economic feasibility of microalgae-based biofuels.

2.1.2. Macroalgae. Seaweeds or macroalgae refer to multicellular and marine algae, which grow in oceans, seas, lakes, rivers, and other water bodies (Ferdouse et al. 2018). When classifying the macroalgae market according to photosynthetic pigments, brown is ~47% of total world production, red is ~51%, and green colors are ~1% of total world biomass produced (FAO 2021). Most are grown either on the seabed or on ropes attached to it, but some are cultivated on small floating platforms (FAO 2018).

Seaweed's high biomass growth rates and its high content of organic compounds such as polyunsaturated fatty acids led to the increase in consumer demand for algae products and the commercial interest in algae production during the last several decades (Ullmann & Grimm 2021).

Seaweeds, particularly kelp, are popular in Asian cuisines. Moreover, seaweed farms bring benefits beyond the immediate value of their crop. Advancements in science and technologies led to the diversification of macroalgae applications to food and beverages (Torres et al. 2019), pharmaceuticals (Golberg et al. 2020b), wastewater treatment (Wang et al. 2020), biorefining (Prabhu et al. 2020, Seghetta et al. 2016), dietary supplements (Peñalver et al. 2020), cosmetics (Pereira 2018), animal feed (de Morais & Costa 2007), and other intermediate factors of production (Janarthanan & Kumar 2018).

One leading example is the use of seaweed-based hydrocolloids (agar, carrageenan, and alginate) as natural binders and emulsifiers employed in foods, cosmetics, and drugs (Duarte et al. 2020). The annual global growth rate of carrageenan was 2% between 2009 and 2015, valued at more than half a billion US dollars in 2015 (Ferdouse et al. 2018).

Seaweeds used as human foods tend to be more valuable (higher priced) than those used for industrial applications (Cai et al. 2021). Roughly 47% of the produced seaweed is for food, and more than 50% is for hydrocolloids (Buschmann et al. 2017). **Table 2** provides a brief list of compounds and applications for a glimpse of the breadth of macroalgae products that are already in place or have a high potential for implementation.

Advances in increasing the nutritional value of animal feed have increased significantly (de Morais & Costa 2007). For instance, Roque et al. (2019) investigated how seaweed can enhance the sustainability and health of cattle farming. Their study has further discovered that adding specific seaweed varieties can help livestock to gain weight and also decrease greenhouse gas (methane) emissions by up to 67%.

The utilization of macroalgae for bioethanol and biomethanol was widely investigated (Alvarado-Morales et al. 2013, Jiang et al. 2016). However, to the best of our knowledge, none of the efforts has materialized into a commercial application so far. Nevertheless, the research continues toward the commercialization of biochar (Cai et al. 2021), biogas (Marquez et al. 2014), and other energy applications (Nazemi et al. 2021).

2.2. Duckweed

Aquatic monocots in the Lemnaceae family, commonly called duckweeds, are plants endemic to most parts of the world (Landolt 1986). Duckweed, like algae, is a highly productive and nutritious

Table 2 Examples of seaweed-derived products and their applications

	Applications	References
Dried seaweed		
	Direct consumption for food, food additives after being milled	Wells et al. (2017), Leandro et al. (2020)
	Cosmetics (after being milled)	Pereira (2018)
	Feed, fertilizers	Hernández-Herrera et al. (2014), Rajauria (2015), Roque et al. (2019)
Polysaccharides		
Carrageenan	Food additives, pharmaceuticals	Bleakley & Hayes (2017)
	Cosmetics	Pereira (2018)
Agar	Food additives	Bleakley & Hayes (2017)
	Pharmaceuticals (culture media)	None
Algin or alginates	Food additives	McHugh (2003)
	Pharmaceuticals	Ullmann & Grimm (2021)
	Cosmetics	Pereira (2018)
	Various industrial products (e.g., paints, fiber, explosives, pesticides, fire retardants)	Lim et al. (2008), Janarthanan & Kumar (2018)
Micronutrients	Food	Bleakley & Hayes (2017)
Bio-oils (methane, butanol, ethanol, acetone)	Energy	Wargacki et al. (2012), Jiang et al. (2016), Kumar et al. (2020)
Polymers	Industrial products and construction materials using isohexides	Rose & Palkovits (2012), Pacheco-Torgal et al. (2016)

aquatic plant that can be scalable for urban and rural deployment. It requires low water input and does not compete for arable land. Duckweed is the fastest dividing flowering plant globally, with a doubling time as short as 20 hours for some species. It can rapidly remove nitrogen and phosphorous from anthropogenic wastewater streams through biomass accumulation. Thus, scholars for the past three decades showed that duckweed is a candidate for low-cost wastewater treatment platforms and can be deployed for environmental monitoring (Korner et al. 2003). At the same time, its abbreviated structure and tendency to float allow for rapid, low-energy input collection with minimal carryover water. The low lignin levels [<5% (Blazey & McClure 1968)], together with a high protein content (up to 40% dry weight) in some strains and a large surface area to body mass ratio, make duckweed easy to collect and use.

Overall, duckweed is not used as feedstock to extract various products. Instead, the industry uses duckweed for what it contains, including starch, protein, fat, minerals, vitamins, and phytosterol content, as well as a spectrum of amino acids and fatty acids (Hillman 1976; Appenroth et al. 2017, 2018). Currently, end users consume duckweed because of its nutritional value (Bhanthumnavin & McGarry 1971) or as spices, food additives, feed, and bioplastics (Zeller et al. 2013).

In addition, studies show that duckweed can be used in fuel production (Sun et al. 2007) and possesses therapeutic monoclonal antibodies against interferons (Cox et al. 2006). Thus, duckweed may provide an efficient and safe system for vaccine production to supplement rising vaccine demand, including the development of protective antigens against the porcine epidemic diarrhea virus (Ko et al. 2011) and tuberculosis (Peterson et al. 2015). Moreover, several studies have shown the potential of using duckweed to express antigens against the avian influenza virus H5N1 (Bertran et al. 2015, Firsov et al. 2015, Thu et al. 2015). Firsov et al. (2018) have also successfully expressed a part of the M2e surface protein to develop an edible vaccine.

Another area that has witnessed the commercialization of duckweed products is animal feed for cows, chickens, pigs, sheep, and horses. Moreover, a broad spectrum of fishes was reported to feed on duckweeds (Landolt & Kandeler 1987, Sarubbi 2017, Sonta et al. 2019, Lawrence et al. 2021). In addition, comparing duckweed with corn revealed that duckweed, with its protein-rich content, is a better raw material for making protein-rich animal feed than corn kernels (Lee et al. 2016).

The renewed interest in bioenergy during the twenty-first century did not skip duckweed. Duckweed, like algae, is viewed as a potential feedstock for bioenergy production (Cheng & Stomp 2009). Although the plant is not rich in starch, it is possible to enhance the duckweed starch accumulation (Cui & Cheng 2015, Liu et al. 2018, Guo et al. 2020, Shao et al. 2020, Xu et al. 2018). Duckweed biomass can also produce biogas via anaerobic digestion (Ren et al. 2018), significantly enhancing duckweed's total energy output (Calicioglu & Brennan 2018, Kaur et al. 2019).

2.3. Commercial Applications of Microalgae, Seaweeds, and Duckweed

Table 3 briefly describes randomly selected firms to represent the diversity of the MSD industry and its uses and applications.

Table 3 Examples of companies and activities in the microalgae, seaweeds, and duckweed (MSD) industry

Company	URL	Products and applications
Microalgae		
Algenuity	**https://www.algenuity.com**	Palatable green algae that maintains antioxidants, vitamins, minerals, and essential fatty acids
Checkerspot	**https://checkerspot.com**	Polyurethane and aspen used in products such as surfboards and skis that are light and stiff
AlgiKnit	**https://www.algiknit.com**	Algae-based yarn and textile that is nontoxic and biodegradable
Macroalgae		
Acadian Seaplants	**https://www.acadianseaplants.com/**	Crop biostimulants, feed supplements, food, and cosmetics
Irish Seaweeds	**https://irishseaweeds.com/**	Drying and cultivation techniques for sea vegetable seaweeds
Leili Marine Bioindustry, Inc.	**http://en.leili.com/**	Seaweed-based fertilizers and crop biostimulants
Mara Seaweed	**https://maraseaweed.com/**	Scottish seaweed seasonings that are wild harvested, sourced, and processed
Seakura	**https://seakura.co.il/en/**	*Gracilaria* and *Ulva* grown in the ponds are either sold directly as human foods or processed into a series of *Ulva*-based iodine and multivitamin supplements
Sealaria	**https://www.sealaria.co.il/**	Gelatinized products for health care and pharmaceuticals
Duckweed		
GreenOnyx	**https://www.greenonyx.ag/**	Direct-to-consumer offering of fresh khainam as a vegetable supplement to an array of dishes or as a raw nutrient and dietary supplement
Hinoman	**https://www.hinoman.com/**	A specific variety of *Wolffia globosa*, which provides significant benefits for human health
Lemnature	**https://www.lemnatureusa.com**	Superfood drinks, protein powders, and nutrition bars
Plantible	**https://www.plantiblefoods.com/**	Nutritional food additives and water lentils to extract RuBisCo, a protein-rich, plant-based alternative food

Table 4 Top ten algae-producing and -exporting countries, 2019

Rank	Microalgae cultivators		Seaweed producers by region[a]			Exporters of seaweed and seaweed-based hydrocolloids[b]		
	Producer	Total production (metric tons wet)	Producer	Total production (metric tons wet)	Share of world total	Exporter	Million USD	Share of world total
1	China	54,850	China	20,296,592	56.75%	China	578	21.79%
2	Chile	903	Indonesia	9,962,900	27.86%	Indonesia	329	12.41%
3	France	207	South Korea	1,821,475	5.09%	South Korea	320	12.07%
4	Greece	142	Philippines	1,500,326	4.20%	Philippines	252	9.50%
5	Tunisia	140	North Korea	603,000	1.69%	Chile	209	7.88%
6	Burkina Faso	140	Chile	426,605	1.19%	Spain	145	5.47%
7	Central African Republic	50	Japan	412,300	1.15%	France	124	4.68%
8	Chad	20	Malaysia	188,110	0.53%	United States	102	3.85%
9	Bulgaria	2.65	Norway	163,197	0.46%	Germany	82	3.09%
10	Spain	1.52	Tanzania	106,069	0.30%	United Kingdom	78	2.94%
	NA	NA	Rest of the world	231,712	0.65%	Rest of the world	432	16.29%
	World	56,456		35,762,504	100.00%		2,652	100.00%

[a] Data from FAO (2021).

[b] Data from the UN Comtrade Database (**https://comtrade.un.org/**).

Abbreviation: NA, not applicable.

2.4. Regional Segmentation

Geographically, production of both micro- and macroalgae is concentrated in Asia (**Table 4**). China currently dominates the algae nonfeed market (Cai et al. 2021). Commercial microalgae production is significantly smaller than that of macroalgae. Global microalgae production in 2019 equaled 56.5 thousand metric tons, with *Spirulina* and *Arthrospira* summing to 54.7 thousand metric tons (99.5% of the global cultivation of microalgae). In contrast, global wild seaweed collection equals 1.1 million tons, and cultivation increased to 34.7 million tons in 2019 in all seaweed groups: brown, red, and green (FAO 2021). However, microalgae cultivation might be underestimated in the UN Food and Agriculture Organization (FAO) statistics, as microalgae are regulated separately from aquaculture in a few key countries (Cai et al. 2021).

Commercial microalgae production is a mostly land-based operation, with three landlocked countries in Africa reporting the production and cultivation of *Spirulina* and *Arthrospira* (Burkina Faso, Central African Republic, and Chad). In contrast, 49 countries and territories contributed to world seaweed production in 2019 (Cai et al. 2021). And, unlike microalgae, seaweed cultivation is mostly done in marine areas. Notably, seven out of the top ten seaweed-producing countries in 2019 were in Asia (**Table 4**). However, when accounting for seaweed export, including seaweed-based hydrocolloids, four European countries and the United States enter the top ten exporters.

Cultivation technologies dominate macroalgae (seaweed) production in Asia, Africa, and Oceania. In contrast, wild collection dominates production in the Americas and Europe (Cai et al. 2021). The world's wild seaweed collection declined by about 20% from 1990 to 2019, while world seaweed cultivation increased sevenfold from 4.2 million metric tons in 1990 to 35.8 million metric tons in 2019, with red and brown seaweeds leading the growth of cultivation. The cultivation of green seaweeds declined by half.

3. FROM RESEARCH TO APPLICATION

Research and development yielded technological breakthroughs in the MSD industry, with far-reaching implications. For example, scientific publication metrics suggest that bioprospecting research between 1965 and 2012 resulted in 3,129 products or bioactive molecules from seaweeds (Cai et al. 2021). And decades of research culminated in microalgae cultivation to produce β-carotene (see **Supplemental Materials**).

Supplemental Material >

The evolution of the MSD industry mimics that of agriculture, whereby early human hunter-gatherers mainly obtained their resources and food through fishing and harvesting of wild MSDs. However, production systems became more efficient by learning and accumulating scientific knowledge (Zilberman 2014). Similarly, the MSD industry is now transitioning from harvesting to cultivation, mainly producing low-value products (FAO 2021). However, based on insights from industry stakeholders, we presume the industry will start transitioning to high-value MSD products and applications in the future through research and development of biorefinery processes.

The development of the MSD industry, which is in its infancy, hinges on multidisciplinary research. While biology identifies strains of the different plants/organisms and their specific characteristics, chemistry and biotechnology strive to understand the use of alternative chemical compounds for pharmaceuticals, cosmetics, or food. Some basic research leads to new concepts, whereas others are more applied, translating an idea into a product (Kortum 1997, Zilberman et al. 2022). Basic research leads to the understanding of the products and processes. Close cross-disciplinary research that includes the natural and social sciences and the MSD industry is needed to transform the vast potential of MSD into acceptable, available, and affordable food or nonfood products and applications. However, continued success is an elusive process. In addition, budget constraints limit resources channeled to research, with a return to research guiding the allocation of funds (Pardey & Alston 2021).

The characterization of alternative strains, evaluation of carbon fixation potential, and identification of alternate processes yield supply chains with considerable benefits to society and suggest others that might emerge in the future.

4. THE DEMAND FOR ALTERNATIVES

Two fundamental changes in producer and consumer preferences increase the demand for MSD-based products. The first is the rising demand for sustainable food and plant-based alternatives to meat, fish, and dairy products, and the second is the need to decarbonize the economy.

4.1. The Consumers

The increasing demand for MSD production is associated with the rising awareness of climate change and the popularity of veganism and plant-based products. In addition, the consumers' perception that plant-based products are sustainable, safer, and healthier than animal-based products fuels growth in the MSD-based food, pharmaceutical, and cosmetic markets.

Within Eastern Asia, consumers frequently consume MSD as human foods. However, outside of Eastern Asia, MSD are largely niche or novel products used for various purposes. Currently, a strand of literature that aims to characterize Western consumers pertinent to the aquatic market and its segments focuses primarily on seaweed because the seaweed food market is significantly larger than other MSD markets. These analyses address the considerations across different customer touchpoints. For example, a consumer survey conducted in Australia revealed that most respondents had eaten seaweed, and they are aware of its health and nutritional benefits (Birch et al. 2019b). Surveys of French and Swedish seaweed consumers confirmed these results (Lucas et al. 2019, Wendin & Undeland 2020). However, Lucas et al. (2019) stressed the importance of labeling in promoting seaweed consumption. Other studies indicated that the barriers to seaweed consumption are the lack of knowledge of and familiarity with seaweed and the perception that it is expensive (Birch et al. 2019a,b). Notwithstanding, in a study that added seaweed to whole wheat bread, the consumers accepted only small amounts of seaweed that did not affect the taste of the bread (Lamont & McSweeney 2021).

4.2. Environmental Aspects

Climate change and the depletion of many of Earth's resources, including the availability of freshwater and arable land, are other drivers that increase the demand for the utilization of MSD. Currently, global agriculture is the largest user of freshwater and consumes about 70% of the water withdrawn. At the same time, agriculture is also responsible for most of the alterations in nitrogen and phosphorous cycling through the widely adopted use of synthetic fertilizers. Therefore, further expansion of current agricultural practices by simply scaling up will likely exacerbate the critical environmental boundaries and hasten the destruction of ecosystems globally. Thus, the limit in terrestrial resources (land area and freshwater) increases the global demand for fast-growing MSD resources (Pereira 2018, Leandro et al. 2020).

Significant potential environmental benefits can come from MSD: carbon sequestration, eutrophication mitigation, reduction of ocean acidification, and habitat generation for many marine creatures, including fish. Other examples include bicarbonate-based integrated carbon capture and MSD production, systems-integrated MSD bioenergy carbon capture and storage, and macroalgal ocean afforestation (Leong et al. 2021). Moreover, large-scale seaweed farming is considered a geoengineering remedy for climate mitigation; dumping the algae grown on the ocean floor is used to stop the carbon from returning to the atmosphere. In addition, MSD can use nutrients from various wastewater sources (e.g., agricultural runoff, concentrated animal feed operations, industrial and municipal wastewater). The use of these feedstocks can result in sustainable bioremediation with environmental and economic benefits (Shilton et al. 2008). However, the realization of those benefits hinges on policy.

Nonetheless, MSD production can lead to negative externalities. For example, shading may result in adverse effects on bottom fauna, causing harmful seaweed blooms. Demel et al. (2020) studied the willingness to accept disamenity caused by seaweed farms and the production of green energy. In a choice experiment conducted in the United Kingdom, the researchers found that people are willing to make this trade-off.

Various scholars assessed the sustainability of cultivation and biorefineries using life cycle assessment (e.g., Alvarado-Morales et al. 2013, Seghetta et al. 2016, Czyrnek-Delêtre et al. 2017). Philis et al. (2018) demonstrated that seaweed protein has environmental advantages owing to the low usage of mineral phosphorus and marginal use of land to produce it. Furthermore, protein production based on seaweed can be a sustainable alternative to soy protein because no agricultural area is needed to grow this type of biomass (Koesling et al. 2021). Overall, the literature agrees that the cultivation of MSD contributes to ecological restoration and climate mitigation (Golberg et al. 2020b, Acosta et al. 2021).

The demand for alternatives to the incumbent industries has resulted in the need for multidisciplinary research and the commercialization of MSD-based products to significantly increase. As a result, current supply chains aside, new supply chains are developed.

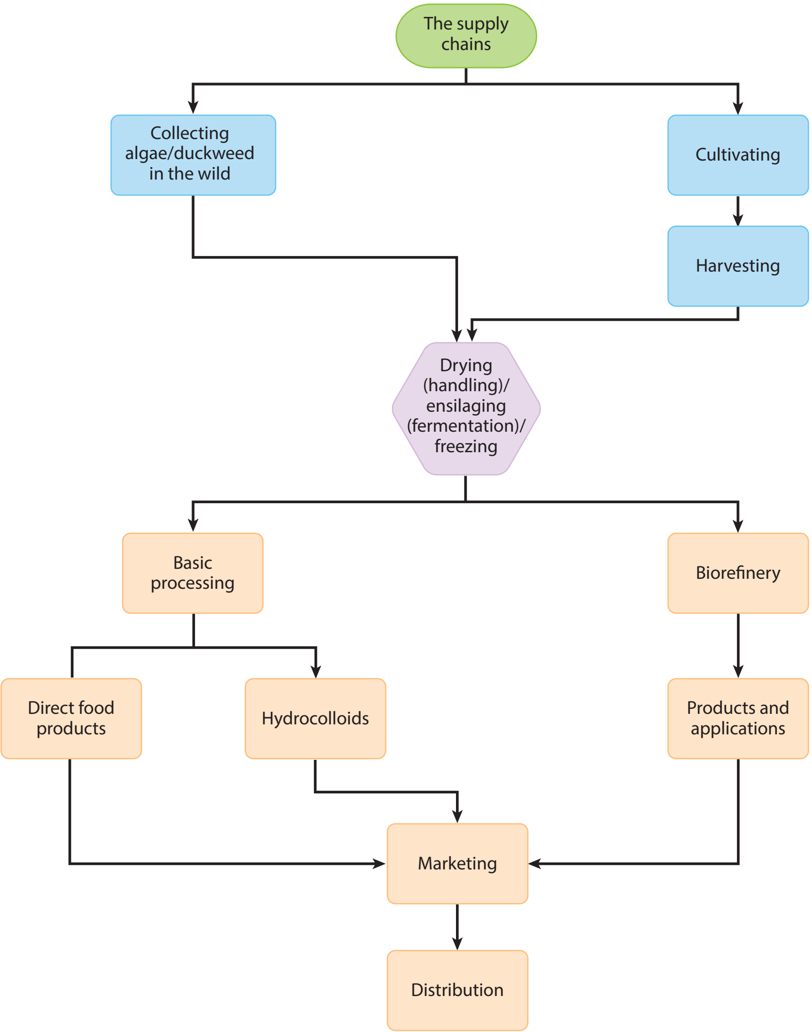

Figure 1

Supply chains of microalgae, seaweeds, and duckweed (MSD) products.

5. MICROALGAE, SEAWEEDS, AND DUCKWEED SUPPLY CHAINS

The general design of MSD supply chains includes producing or procuring MSD as feedstock, processing (with/without biorefinery), distribution, and marketing (**Figure 1**). The supply chains utilize MSD through three primary forms.

1. Using the fresh feedstock as a source of seedlings, or propagules, or direct consumption as food;
2. Using the dried feedstock as raw materials in basic processing (e.g., carrageenan extraction or feed); and
3. Using the feedstock in the biorefinery to extract chemicals and other coproducts.

In Asia, traditional supply chains of macroalgae start with offshore cultivation, followed by drying for direct consumption as food or by basic processing into hydrocolloids (Valderrama et al. 2013). However, the value of outputs rises from $0.69 per kilogram of dried seaweed harvested in Malaysia to $30 per kilogram of refined carrageenan (Nor et al. 2020), an edible red seaweed used for traditional cooking or by the food industry as a thickener and gelling agent.

To unlock MSD's potential, researchers and entrepreneurs strive to produce high-value products using biorefineries (Sonnenberg et al. 2007) and by employing anaerobic digestion, fermentation, transesterification, liquefaction, or pyrolysis technologies (**Figure 1**). These technologies convert MSD biomass into proteins and sugars, resulting in food, chemicals, and biofuels (Torres et al. 2019). To this end, several initiatives involving research and commercial actors (e.g., Seabioplas, BioMara, MAB4, EnAlgae, Seafarm, Seagrant, ARPA-E MARINER) develop cultivation and biorefinery processes for various applications (Stévant & Rebours 2021).

The producers must decide how much to produce, what segments of the supply chain to undertake in-house versus sourcing externally, and what institutions to coordinate with (Zilberman et al. 2017). At each stage of the production process, researchers and entrepreneurs decide between various options, which ultimately affect the irreversible (sunk) and variable costs, productivity, output, and thus total profitability. In addition, the choice of the MSD farm's location impacts the direct costs of production. Although offshore locations are usually abundant with nutrients and escape issues related to area use along the coastline and stakeholder conflicts related to multiuses of the same place (Emblemsvåg et al. 2020), coastal farms better control the cultivation. Moreover, the choice of MSD species is crucial for the profitability of the system, as it defines not only the protein content but also the harvesting season and its length (Koesling et al. 2021).

Numerous studies focus on the effort to evaluate costs from scaling up (e.g., Seghetta et al. 2016, Emblemsvåg et al. 2020). However, many of these studies lack (or do not report) a structured production function that supports a cost function. Instead, a linear approximation is usually assumed (Palatnik & Zilberman 2017). This approximation should be treated cautiously and verified against actual data when production is scaled up. One exception is Diatin et al. (2020), who estimated a Cobb–Douglas production function of seaweed cultivation combined with milkfish and shrimp polyculture. Another is Palatnik et al. (2018), who evaluated the profitability of seaweed cultivation and processing, assuming learning over time.

The notion of learning is especially relevant in novel processes of natural resource utilization, such as MSD. Learning improves input-use efficiency and reduces cost by combining various mechanisms such as learning-by-doing, economies of scale, technological innovation, and factor substitution in manufacturing (Weiss et al. 2010). Palatnik et al. (2018) found that increasing the learning rate at the stage of MSD cultivation has a higher impact on profit than the learning rate at the biorefinery, indicating the primary focus of MSD research.

Other initiatives to maximize the profit and the environmental benefits of MSD cultivation include integrated multi-trophic aquaculture (IMTA) systems. Under the IMTA systems, growers cultivate species of different trophic levels within a complementary ecosystem—one species' waste/output becomes another's input. In IMTA systems, MSD production is combined with other processes, e.g., raising fish or invertebrates combined with seaweed production (Diatin et al. 2020, Lawrence et al. 2021). These systems help capture fertilizer runoff from intensive agricultural areas and thus prevent damage to aquatic ecosystems (Alexander et al. 2016). In addition, the economic potential of offshore farms of seaweed cocultured with fish, which results in a higher yield of seaweed biomass, is also investigated (Korzen et al. 2015, Emblemsvåg et al. 2020).

Current industrial IMTA systems process the organic waste via conversion to usable mass, return water to the environment without the added nitrogen and phosphorus, decrease the cost of filters because MSD serve as a biofilter for the water, and reduce waste output. MSD can play a significant role in the development of IMTA systems, yielding a reduction in feed costs while reducing pollution and offering support to the filtration system.

Accordingly, the circular bioeconomy principles (i.e., which strive to eliminate waste via composting biodegradable waste or reusing and recycling materials) guide the development of MSD supply chains. These are used to make products with the highest possible added value sustainably, on a cascaded use of materials (and upcycling whenever possible), minimizing resource input from and output to the natural environment. This generates both environmental and economic benefits (Mohan et al. 2018), where the recovery of biobased wastes or by-products prevents pollution and promotes potential valorization, turning waste into marketable products with added value (Kwan et al. 2018) and allowing economic growth (Reim et al. 2019).

Zilberman et al. (2022) distinguish between research supply chains and the industry's supply chain. The research supply chain starts from basic science, while profit-minded entrepreneurs base their actions on the demand expectations. In this context, the MSD research supply chain considers climate change. Given the potential, environmental benefits, and constraints, researchers are interested in understanding whether and under what conditions the MSD-based bioeconomy will flourish while benefiting the environment. Yet, the industry's supply chain considers the current policy in place. To this end, the lack of carbon pricing narrows commercial applications of MSD to food, fertilizers, and cosmetics (**Table 3**). Next, we discuss barriers and policy needs for further MSD sector development.

6. THE FUTURE OF THE INDUSTRY

MSD cultivation and biomass fractionation technologies provide a broad spectrum of products and exhibit high growth rates, yet they face technical constraints in cultivation, harvesting, and conversion (Abdelaziz et al. 2013).

From cultivation and processing to prices and demand, uncertainty challenges the development of a mature and impactful MSD sector. In addition, the challenging environment and unusual biomass composition (de Jong et al. 2012, Golden et al. 2015, Acosta et al. 2021) result in high levels of uncertainty of these projects' technological and economic feasibility. Furthermore, these production technologies are more expensive than those for terrestrial crops due to increased initial investment, cultivation, and harvesting costs (Ullmann & Grimm 2021).

The uncertainty in cultivation stems from the dependency of the feedstock on saturation kinetics by light intensity, ambient dissolved inorganic nutrient concentration, temperatures, and airborne pathogens (Buschmann et al. 2004, Sutherland et al. 2015). Furthermore, stochastic weather and seasonal variability between regions, within years, and between years exacerbate cultivation uncertainty (Qarri & Israel 2020). In addition, farm location significantly impacts yield (Koesling et al. 2021). The type of cultivation system (Golberg et al. 2020b) and wild harvesting technologies (Mac Monagail et al. 2017) also significantly impact yields. Another challenge is dewatering and concentrating the harvested biomass to be suitable for processing and utilization in the biorefinery. Finally, disease outbreaks are a critical concern for a consistent supply of feedstock.

Asymmetric information regarding feedstock quality negatively impacts the industry and introduces barriers to its wide deployment. First, there is low trust in relationships between processors, intermediaries, and farmers on seaweed quality, resulting in penalties for the farmers (Nor et al. 2020). Next, low labor and capital costs are vital to reducing the cost of cultivation (Cai et al. 2021). Moreover, challenges arise from identifying and improving the traits to understanding the biomass's characteristics and developing cost-efficient cultivation systems that minimize resource use and costs while maximizing productivity (Richardson et al. 2012, 2014; Acosta et al. 2021).

More specific concerns regarding seaweed include grazing by fish or other organisms and rising sea temperatures that slow macroalgae growth (Hurtado 2013). In coastal and open sea farms, a genuinely industrial scale will consequently only become possible if the technical challenges of offshore production conditions, such as waves, currents, storms, and mooring, can be solved cost-effectively (Koesling et al. 2021). Furthermore, with a general trend of deteriorating farming environments and declined seedling quality, global seaweed cultivation is subject to increased risks of disease outbreaks (Hurtado 2013). The economic profit potential for seaweeds is currently one of several hurdles for developing a European seaweed industry (van den Burg et al. 2016). However, recent studies indicate that seaweed cultivation can become a highly profitable industry in the developed world and that the externalities' monetary values are relatively small compared to the revenues generated (Camus et al. 2019, Hasselström et al. 2020).

Cultivation costs are high. Recoverable bioproducts are highly dependent on biomass composition, which is dynamic and dependent on the species strain, nutrient inputs, and the cultivation environment (US DOE 2020). The potential to produce bioenergy triggered the demand for kelp cultivation in the United States and Europe, which began around 2005 in Norway at an experimental scale, and in France, Germany, Ireland, and Scotland (Stévant & Rebours 2021). Yet, biofuel production from MSD is economically, energetically, and technically challenging at scale (Nazemi et al. 2021). Thus, crucial barriers to the commercialization scale are the production costs and competition with the existing alternatives such as oil and cheap chemicals.

In addition to production costs, the value of biorefinery products when reaching end users may also reflect the expenses of research and development, formulation, and marketing (Valderrama et al. 2013). However, specific information on these aspects is generally lacking. In addition, the biorefinery yields are highly uncertain, signaling the immaturity of the technology. The upper value can be ten times larger than the lower one, significantly affecting the potential profitability of the process (Prabhu et al. 2020). In addition, the development, design, and construction of a new biorefinery require substantial investments (Stichnothe et al. 2016). Like many new and emerging industries, demand is uncertain, and the willingness to adopt and pay is not apparent to the grower, further contributing to price variability and uncertainty.

Different impetuses may jump-start MSD cultivation and processing, yet these need strong value chains to become sustainable. Healthy, strong, and sustainable value chains need to be characterized by inclusiveness, low transaction costs, less asymmetric information, and effective risk-sharing mechanisms (Cai et al. 2021).

There is a general lack of detailed information and knowledge on MSD food market potential, which is essential to informed decision making in policy and planning to develop MSD cultivation. Therefore, more in-depth, comprehensive assessments of MSD markets and value chains are needed at the global, regional, national, and subnational levels.

Maximum use of input is the central insight of the circular bioeconomy. Prabhu et al. (2020) showed the potential for almost 100% utilization of macroalgae feedstock in a biorefinery. However, in existing traditional supply chains, the feedstock is underutilized. The underutilization creates waste and inefficiency (Khanna & Zilberman 1997). Increased utilization will raise revenue and diminish waste and related externalities such as diseases, water pollution, and rotting.

A crucial barrier to using waste-to-input technologies is the required diverse set of tools and expertise needed to support and maintain these systems, which necessitate the development and training of human capital. Maximizing the efficiency of MSD feedstock utilization and externalities caused by technologies requires understanding fish- and plant-based biological systems (Hochman et al. 2018). Relevant human capital is scarce, preventing the adoption of these technologies because the farmer does not include the social benefits of learning and education in their benefit-cost calculations. Market intervention and institutional change (e.g., extension services) are needed to significantly reduce the barriers to adopting technologies for recycling and reusing. Policies and incentives that correct market failure due to waste-based pollution yield sustainable development of the MSD industry through the strengthening of conservation, recycling, and reuse and the development of the circular economy (Zilberman et al. 2013, Wesseler & von Braun 2017).

The utilization of MSD as human foods, particularly for local consumption, tends to be the most stable market force that can stabilize the sector's development. Forming or changing dietary habits tends to be a long-term process that entails joint efforts of stakeholders and experts in policy, business, and scientific communities.

The European Commission highlights seaweed aquaculture as having the strategic potential to contribute to blue growth by providing low-carbon and renewable products for the European bioeconomy. However, concerns and uncertainties over the safety of MSD products pose a significant challenge to promoting their consumption in new markets where food safety guidelines or regulations tend to be stringent for precautionary purposes (Lähteenmäki-Uutela et al. 2021). Therefore, science- and evidence-based laws, rules, and guidelines (e.g., environmental regulations, spatial planning, food safety standards, occupational health requirements, technical procedures, and good aquaculture practices, among others) on MSD are essential to laying a solid foundation for the sector's sustainable development.

To benefit from the potential of MSD for carbon sequestration, development of corresponding supply chains is needed. First, basic research is required to identify carbon flux in the sea in the short term versus long term. Next, it is still unclear who owns the sea where the algae will be grown, who will invest in those technologies, and who will regulate them.

The potential of the MSD circular bioeconomy is in market development, where a mature market would lead to significant ancillary benefits in terms of providing a renewable resource while sequestering carbon and mitigating marine eutrophication. Research needs to make a fundamental part of the MSD supply chain much cheaper. This drawback has not stopped investors from entering the sector. They are doing so on the basis that biotechnologists are both resourceful and armed with ever more subtle tools. The firms operating in the industry are not big enough to serve a national or even a significant regional market, but they are big enough to provide a proof-of-concept that could justify the capital investment needed for future growth. The MSD industry has been growing and has the potential to support a transition to a sustainable future. But correcting market failures in terms of policy instruments such as carbon pricing and subsidies for nutrient uptake based on the economic value of nutrient sequestration can become the tipping point for MSD market development.

7. CONCLUDING REMARKS

Global food security faces two significant challenges: a population increase to an estimated 9.5 billion by 2050 and an accelerating rise in annual temperatures in most world regions, which will likely drastically alter global weather patterns (IPCC 2021). In addition, estimates suggest that the increase in demand for food will require 60% more output in crop production by 2050, along with 20% more freshwater for agricultural and domestic use (Zilberman et al. 2022). Over the past 50 years, crop productivity significantly increased through improved practices. However, the advancing effects of climate change are likely to increase abiotic stresses on field crops and lower their productivity. Therefore, the rising food demand and expected pressure on productivity by worsening climatic conditions will likely increase food prices as we approach 2050 (IPCC 2021). The coronavirus disease 2019 (COVID-19) outbreak only exacerbated these forces and led to a global crisis that disrupted people's lives, especially those living in remote areas (Davis 2021).

The world needs deep decarbonization (IPCC 2021), with technologies and processes leading to significantly shrinking food and energy production emissions while increasing productivity. We believe the MSD sector can be part of the solution. Although MSD applications have been present in human history for decades, the push to develop MSD organisms as industrial resources is a very recent objective. Future research should help develop a deeper and broader understanding of the potential of blue carbon sequestration. To this end, understanding how to develop viable supply chains that sequester carbon while generating economic value-added is a promising path.

Nutritious, eco-friendly, and versatile MSD have excellent potential in a variety of food and nonfood applications (Ullmann & Grimm 2021). Yet, realization is not immediate for various reasons, such as low consumer exposure or preference, high cultivation and production costs, immature biorefining technology, market competition, and stringent regulations. One example is the lack of commercial success in algae-based biofuel production (primarily because of high production costs and low fossil fuel prices) despite much interest and substantial investments in the sector. Future research on the viability of the food, feed, and nutrition of aquatic plant-based supply chains presents much potential and is needed to support the growth of this industry in the coming decades.

The industry is in its infancy and depends heavily on multidisciplinary basic and applied research where agronomy, engineering, and biology meet economics to create a sustainable and profitable MSD industry based on the circular bioeconomy. Interdisciplinary research is also crucial for supply chain design. It is essential to identify a profitable value chain.

Another critical element is to increase input use efficiency of MSD feedstock with limited unutilized materials that also depend on incentive and continuous learning and research. Given the existing incentives, the industry supply chain is driven mainly by the demand for plant-based alternatives for food, feed, and chemicals. On top of that, the research supply chain incorporates the advantages of MSD in carbon sequestration and the sustainable use of renewable resources.

Most of the value generated by the current global MSD industry is in direct food consumption. However, advancements in research and development can potentially bring in the foreseeable future higher-value products produced at a significant scale, such as MSD-based proteins, biomaterials, bioenergy, and fertilizers. More importantly, and if governments usher in durable and stable carbon policies, the impact of the MSD industry will be much more significant (Filbee-Dexter & Wernberg 2020, Van Dam et al. 2021). The potential of carbon sequestration is enormous, and the capacity of MSD to produce fine chemicals looks promising. However, we need durable and stable financial incentives to internalize the MSD feedstocks' positive externalities.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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