Ecophysiology and community ecology studies of Philippine seaweeds: Insights, research opportunities, and possible implications for cultivation and management

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ABSTRACT

Seaweeds are vital to the marine ecosystem as primary producers and it serves as a widely consumed food source for humans. Some species of these marine resources are mainly mass cultivated due to the increased demand for raw materials and derived products. In the Philippines, studies on seaweed community ecology, reproductive biology, and growth began around the 1970s. Studies on seaweed photosynthesis are relatively new, beginning in the 1990s, and have since progressed through advancements in physiological and molecular analyses. This review paper examined a total of 123 studies, encompassing ecophysiology and community ecology in Philippine seaweeds, dating back to the 1970s and continuing up to 2025, from public and unrestricted access on scientific databases, including grey literature and the author's personal collection. This also analyzed and synthesized literature to determine the cumulative knowledge we have, the gaps that require attention, and the research opportunities to be prioritized. Generally, rocky substrates with wider intertidal zones have higher seaweed abundance and diversity than sandy substrates, which is attributed to local and regional hydrodynamics and meteorological phenomena, and is largely unaffected by physicochemical parameters due to minimal yearly variation. Seaweed communities exhibited a declining trend in composition, possibly due to anthropogenic pressure, and can serve as a biomonitoring tool. On the other hand, reproductive biology, growth, and photosynthetic studies have mainly focused on economically utilized eucheumatoid, agarophytes, and alginophyte species to improve production. Utilizing new cultivars/strains as planting materials in seaweed farming, especially those produced from tetrasporophytes, and applying organic fertilizer could enhance their growth rate and carrageenan content. Unfortunately, there are still limited photosynthetic studies, yet information can be significantly valuable for culturing and maintaining economically important seaweed in the laboratory and outdoor hatchery. This review paper recommends continuous monitoring to provide comprehensive insights into the variations in seaweed community ecology over time and to quantify the different ecological services offered by seaweed communities. Furthermore, continuous studies on photosynthesis, growth, and reproduction are necessary to provide

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baseline information for improving and developing seaweed farming techniques, ensuring effective and efficient farming practices.

INTRODUCTION

The Philippines, being an archipelagic country, has a vast number of seaweed species (Trono 1999, Ganzon-Fortes 2012, Ang et al. 2013, Lastimoso and Santiañez 2020). Ganzon-Fortes (2012) provides a comprehensive historical account of biodiversity studies on Philippine seaweeds, covering the period from 1800 to 1999. During the late 1950s, Gregorio T. Velasquez, known as the Father of Philippine Phycology, catalyzed studies on Philippine algae. Initially, most published studies focused on taxonomic accounts of both freshwater and marine algae. Later, they expanded to include analyses of spatial distribution and the utilization of edible seaweeds. Between 1970 and 1989, there was a surge in publications on the taxonomic, floristic, monographic, and morphological aspects of seaweeds, primarily due to the success of seaweed farming in the Philippines, which heightened interest in seaweeds. The publication topics primarily focus on floristic reports, systematics with detailed descriptions and illustrations, reports of new species or new records in the Philippines, and checklists and descriptive taxonomic treatments of marine algae from various parts of the country. Later on, a shift in applied research was observed in the last decade of the 20th century, primarily focusing on species being farmed, with an emphasis on their population biology, seasonality, phycocolloid yield and quality, and the use of molecular tools for taxonomic studies.

Seaweeds are marine macrobenthic algae, either multicellular or coenocytic. They are photoautotrophic organisms that manufacture carbohydrates by converting light energy into chemical energy through the process of photosynthesis. In addition, they absorb other macro- and micronutrients in the marine environment either through passive transport via facilitated diffusion and active uptake mechanisms. They inhabit marine environments ranging from different littoral zones (supratidal to intertidal and subtidal areas), areas with varying water velocities (from calm to strong wave areas), and various substrates (sandy, coral rubble, and rocky). Seaweeds are generally classified based on their most abundant pigments, wherein green seaweeds have *chl* a and b, brown seaweeds have fucoxanthin, and red seaweeds have phycoerythrin. In addition, seaweeds can be grouped according to their thallus morphology, namely sheet-like, filamentous-like, coarsely branched, thickly branched, and calcified, which are coined as functional-form groups (Littler 1980).

The body of seaweeds, conveniently called thallus, generally consists of root-, stem-, and leaf-like structures called holdfast, stipe, and blade, respectively. The holdfast is typically used for anchorage of seaweeds to the substrate. The stipe generally supports the distal portion of the thallus, but if the stipe is not present, the blade is directly attached to the holdfast. The blade is the photosynthetic part of the thallus, responsible for nutrient absorption. Seaweeds lack fruits and flowers. Seaweed can reproduce both asexually and sexually. Asexual reproduction occurs through the fragmentation of the thalli, where pieces break off and grow into new individuals. Additionally, it involves the formation of spores, either motile or non-motile, which are released from their thalli and produce a new individual thallus. In contrast, sexual reproduction involves the fusion of male and female gametes, which can be either isogamy (fusion of identical gametes) or heterogamy (fusion of two gametes with different sizes and forms). Heterogamy can be either anisogamy (fusion of large- and small-sized gametes) or oogamy (fusion of large, non-motile eggs and small, motile sperm). Sexual reproduction usually involves alternation of generations characterized by the alternation of gametophytes (n) and sporophytes (2n), including carposporophyte (2n, parasitic structure) observed among red seaweeds. Moreover, stages that are similar in morphology are called isomorphic, whereas those that differ in morphology are called heteromorphic.

Seaweeds provide significant ecological and economic services. Cotas et al. (2023) reviewed the different ecological services of seaweeds. Aside from providing food for other marine organisms, seaweeds offer a nursery, recruitment, and protection of other marine organisms due to their three-dimensional architecture. Seaweeds stabilize the sediment by means of holdfast anchorage, which traps and binds the sediment, thus preventing erosion, as observed with the numerous downward-growing rhizoids of *Caulerpa* spp. On the other hand, calcified seaweeds, such as *Halimeda* spp., are an important natural source of substrate in most sandy beaches. When the seaweed dies, its calcified segments break down and are pulverized by water action, producing fine sand. Seaweed beds also mitigate the wave effect by dissipating wave energy, thereby providing coastal protection and preventing coastal erosion. Lastly, seaweed beds have the potential to mitigate climate change by absorbing carbon dioxide from the environment. Jorrisen et al. (2021) showed that seaweed, specifically crustose coralline algae, is a substrate for coral larvae to settle on the reef.

On the other hand, Salido et al. (2024) reviewed different economic benefits from seaweeds. Aside from providing food for human consumption, seaweeds are valuable sources of food supplements, processed products, fertilizers, animal feed, and most especially, extracts from seaweed, i.e., carrageenan, alginate, agar, and others, are used for the food industry, pharma, nutraceutical, and industrial applications. Seaweed has the highest volume of production, amounting to ~385.69 thousand metric tons of wet weight, among other fisheries products (ranging from ~12.60 to 111.42 thousand metric tons) in the Philippines, primarily from farming (Philippine Statistics Authority, 2025).

Seaweed’s growth and development are highly dependent on its photosynthetic process of converting light to chemical energy. Thus, understanding the effect of both biotic and abiotic factors on seaweeds' photosynthesis and growth is necessary to determine their growth requirements, gain insight into productivity, and explain spatial and temporal distribution.

Among their ecophysiological responses, photosynthesis is one of the easily measured and routinely used parameters to assess the effects of environmental factors. Photosynthetic characteristics of a seaweed are commonly measured by its light absorption spectra, photosynthesis-irradiance (P-I) curve, and/or Pulse Amplitude Modulation (PAM) fluorometry. Light absorption spectra are usually measured to determine the pigment content using a spectrophotometer. The P-I curve measures either the production of the by-product of photosynthesis – oxygen, or the consumption of carbon dioxide with increasing irradiance levels (Geider and Osborne 1992, Henley 1993, Kirk 2011, Beer et al. 2014). Lastly, PAM fluorometry measures the re-emitted light by chlorophyll molecules after they have absorbed light energy, known as chlorophyll fluorescence, which originates close to the sites where photosynthesis occurs (Roháček and Barták 1999, Papageorgiou and Govindjee 2010). PAM fluorometry is a form of signal modulation technique where changes in the amplitude of a series of light signal pulses through time are directly linked to changes in the photosynthetic activity.

Moreover, community ecology studies using the traditional line transect-quadrat method provide a non-destructive way to determine the seaweed community structure, including abundance, dominant species, and diversity, as well as their possible relationships within and with the marine environment (Ganzon-Fortes 2011). These community ecology studies identify the responses of seaweed communities to environmental factors and disturbances, as well as the interactions between seaweeds and other species. In addition, studies of this kind provide insight into the processes and mechanisms that drive the ecological patterns of seaweeds in the marine environment. Moreover, these studies provide valuable information on the long-term changes in seaweed communities, which are essential for environmental monitoring. Additional ecophysiological responses include reproductive biology and phenology, which can be studied by directly observing the frequency of their life stages under a microscope or by measuring the abundance of their reproductive stage in their habitat. Information from this provides a basis for improvements in cultivars for mass cultivation, the development of culture technology, and data for a management plan for wild stock harvesting.

Over the past 50 years, research on Philippine seaweeds has expanded from taxonomy and biodiversity to reproductive biology and recent advancements in physiological and molecular analyses. Studies on seaweed community ecology encompass community structure, abundance, and distribution, while ecophysiology encompasses topics such as reproduction, growth, and photosynthesis. Published literature was sourced from public and unrestricted access on scientific databases such as Google Scholar and ResearchGate. While other published literature is from the author's personal collection since 2005, and some recent publications were personally communicated with the author. In the case of gray literature, such as theses/dissertations and technical reports, the author has limited access due to the limited availability of online databases from institutes and universities, and sometimes no online databases can be found. In this case, some of these grey literature sources were researched using online search engines, but they lacked online access. The proponent was personally contacted through email and/or social media platforms to obtain approval for a copy of the literature.

SEAWEED COMMUNITY ECOLOGY STUDIES

In the Philippines, most ecological studies focused on community structure, abundance, and distribution of seaweed species due to the ease of conducting assessments using the basic line transect-quadrat method. Table 1 summarizes the different studies on seaweed community ecology in the Philippines and their significant key findings. Research about the community structure in Philippine seaweeds has been conducted as early as 1970s, together with those studies on the effects of physicochemical parameters (Alcala et al. 1971, 1973, Saraya 1976, Saraya and Trono 1979, Ganzon-Fortes 1981, Castro 1986, Ang 1986, Ohno et al. 1987, Trono and Saraya 1987, Corrales-Domingo 1988, Trono and Bina 1987, Trono and BuchanAntalan 1987, Montes 1991, Trono and Ohno 1992). The seaweed community has been dramatically affected by both abiotic and biotic factors. The most common abiotic factors affecting seaweed communities mainly include light, temperature, substratum, water movement, and depth, apart from biotic factors such as grazing, competition, and microbial interaction.

On the other hand, the habitat of seaweeds varies from the lower intertidal to the shallow subtidal zones in the marine environment, wherein the differences in distribution are mainly accounted for by their adaptability to the ambient conditions in these habitats. As a result, some species are found only in sheltered bays and coves, while others can be found on rocky, exposed areas along the shores or margins of the habitats. Moreover, factors such as topography, substrate, wave actions, and others have a more significant effect on the seaweed community in the Philippines. In contrast, various physicochemical parameters, such as temperature and salinity, may have a minimal impact on the seaweed community, as measured values remain within a close range throughout the year (Cabrera et al. 2015, Saco et al. 2020). In particular, Saco et al. (2020) demonstrated that the different physicochemical parameters fluctuated within a narrow range at four sites in Verde Island, Batangas City, during the dry/hot season and the southwest and northeast monsoons. Seawater temperature ranged from 28 °C to 32 °C in Siirin Uno, 27 °C to 30 °C in San Agustin East and Liponpon, and 28 °C to 30 °C in San Antonio. While in all sites, salinity ranged from 32-33 psu, a pH of 8 (approximately), and dissolved oxygen ranged from 3 mg/L to 6 mg/L. Overall, the combined effects of various biotic and abiotic factors influence the distribution and existence of seaweed species in their habitat.

Studies on the effect of physical features on seaweed community ecology

Saco et al. (2020) determined the composition, distribution, and dominance of marine macrophytes, specifically seaweeds and seagrass, in four coastal areas in Verde Island, Batangas City, Batangas. They found that the differences across sites may be due to substratum type and topography, where a relatively wider intertidal zone with different substrata, such as rocky and sandy to muddy, provides a complex habitat that promotes higher macrophyte cover. Temporal differences in marine macrophyte composition were more pronounced in macroalgae-dominated sites, with species contribution generally peaking in summer. Similar observations by Elias et al. (2022) and Elias et al. (2024) support that the substrate significantly affects the community structure of seaweeds in Lemery, Batangas, and Mabini, Batangas, respectively. The former recorded a total of four (4) seaweed species, including *Ulva* spp., *Acetabularia,* and *Padina*, that inhabit muddy substrates. In comparison, the latter identified a total of 47 seaweed species that inhabit rocky substrates. In addition, Rula et al. (2022) conducted seaweed-seagrass assessment of selected sites in the Verde Island Passage, where they observed that the types of substratum, along with water depth and current (water motion), could be the driving factors behind the differences in macroalgal diversity. Rocky substratum in deeper waters and good water movement were suitable for the growth of canopy-forming seaweed - *Sargassum* sp. Similar trends were observed in other sites that promote higher macroalgal diversity. Moreover, Roleda et al. (2000) made a similar observation regarding the significant effect of substrate and topography on seaweed composition in Talim Bay, Lian, Batangas, which promotes higher diversity and abundance in the rocky substrate.

Clemente et al. (2017) conducted a comprehensive assessment in the Romblon Island Group, reporting a total of 129 macroalga taxa. The species' similarities among sites were attributed to similar substratum profiles, and differences among sites may be due to variations in oceanic current patterns. Similarly, Santiañez et al. (2015) showed that the floristic similarities in the macroalgae composition in the Balabac Marine Biodiversity Conservation Corridor between the Sulu and West Philippine Seas may be attributed to their prevailing ecological conditions, i.e., wave exposure, water movement, substrate, and among others resulting to a higher number of seaweed species in a relatively small area ~6,000 km^2. Moreover, Pascual et al. (2022) determined the diversity and distribution of the seaweed flora in some remote islands in Eastern Samar, i.e., in Homonhon, Sulu-an, and Manicani. They found that 41 out of 56 identified seaweed species were newly recorded in Eastern Samar, and the types of substrate and hydrodynamics significantly influenced the similarities and differences in their composition. Similar efforts have been made in the island towns of Northern Samar, Philippines, by Baldia et al. (2017) and Galenzoga (2023). Furthermore, Trapa et al. (2024) conducted a macroalgae survey on Mapun Island in Tawi-Tawi, one of the southernmost islands in the Philippines, for the first time. They recorded a total of 57 species across four selected sites, which were primarily influenced by the type of substrate in the intertidal area with tidepools.

Table 1: Summary of the significant key findings of studies in community ecology, reproductive biology, photosynthesis, and growth on Philippine Seaweeds from the 1970s to 2025.

<table>
<tr><th>YEAR</th><th>Seaweed Community Ecology Studies</th><th>Reproductive and Growth Studies in Seaweeds</th><th>Photosynthesis and Growth Studies in Seaweeds</th></tr>
<tr><td>1970s</td><td rowspan="3">• Pioneering studies on the seaweed community ecology in the Philippines, specifically in Bolinao, Pangasinan; Ilocos Sur; Calatagan, Batangas; Bacoor City, Cavite; Central Visayas; Southern Negros (Alcala et al. 1971, 1973, Saraya 1976, Saraya and Trono 1979, Ganzon-Fortes 1981, Castro 1986, Ang 1986, Ohno et al. 1987, Trono and Saraya 1987, Corrales-Domingo 1988, Trono and Bina 1987, Trono and Buchan-Antalan 1987, Montes 1991, Trono and Ohno 1992)</td><td>• Pioneering the development of eucheumatoid farming in the Philippines due to overharvesting (Doty and Alvarez 1973, 1975, Trono 1974)</td><td></td></tr>
<tr><td>1980s</td><td rowspan="2">• Studies on reproductive biology in eucheumatoid and agarophytes as an alternative seedling source for seaweed farming (Ganzon-Fortes 1982, Trono 1988, Azanza-Corrales 1990, Azanza-Corrales et al. 1992, 1996, Hurtado-Ponce 1994a, Azanza and Aliaza 1999, Roleda et al. 1997b)

• Management plan for wild-stock collection of agarophyte and alginophyte (Trono and Lluisma 1990, de Castro et al. 1991, Largo and Ohno 1992, Hurtado-Ponce 1994a, Roleda et al. 1997a, Calumpong 1999)</td><td></td></tr>
<tr><td>1990s</td><td>• Photosynthetic response in healthy and diseased thalli of Kappaphycus alvarezii (Ganzon-Fortes 1993)

• Extensive ecophysiological studies on the natural population of Gelidiella acerosa (Ganzon-Fortes 1997a, b, 1999)</td></tr>
<tr><td>2000s</td><td></td><td>• Detailed protocol and best practices on seaweed farming, including production technology (Hurtado and Agbayani 2000, Hurtado et al. 2015)

• Significant initiatives are underway to address the continuous decline in seaweed production, utilizing sporelings from carposporophyte and tetrasporophyte, as well as branch culture as seedling materials, in both laboratory and land-based facilities. (Araño et al. 2000, Rabanal 2000, Ganzon-Fortes 2014)</td><td></td></tr>
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<table>
<tr><th>YEAR</th><th>Seaweed Community Ecology Studies</th><th>Reproductive and Growth Studies in Seaweeds</th><th>Photosynthesis and Growth Studies in Seaweeds</th></tr>
<tr><td>2010s</td><td rowspan="2">• Rocky substrate with wider intertidal has higher seaweed abundance and diversity than sandy substrate, coupled with local and regional hydrodynamics.

• Most seaweed communities are unaffected by physicochemical parameters due to minimal yearly variation.
(Cabrera et al. 2015, Santiañez et al. 2015, Baldia et al. 2017, Clemente et al. 2017, Roleda et al. 2020, Saco et al. 2020, Elias et al. 2022, Pascual et al. 2022, Rula et al. 2022, Galenzoga 2023, Elias et al. 2024, Trapa et al. 2024)

• Higher seaweed species in the southwest than northeast monsoon
(Mendoza and Soliman 2013, Evangelista et al. 2015)

• Declining trend in seaweed species possibly due to anthropogenic pressures
(VinceCruz-Abeledo et al. 2019, Bataan et al. 2022, Camaya et al. 2024)

• Seaweeds as a biomonitoring tool in the marine environment
(Carayo et al. 2005, Cabatay et al. 2022, Saco et al. 2022, Elias et al. 2024, Mance et al. 2024, Gamez et al. 2024)</td><td rowspan="2">• Subsequent studies focus on the phenotypic diversity, growth, physiology, and reproductive biology of both the natural population and laboratory-grown eucheumatoid and agarophyte species, as well as site suitability for identifying new farming sites.
(Dumilang et al. 2016, 2022, Persia et al. 2020, Luhan et al. 2021, Hinaloc and Roleda 2021, Narvarte et al. 2022, Dangan-Galon et al. 2024, Endomo et al. 2024, Roleda et al. 2024, Narvarte and Roleda 2025, Gonzaga et al. 2025)

• Nutrient uptake and assimilation of eucheumatoid species
(Narvarte and Roleda 2025, Narvarte et al. 2025)

• Eucheumatoid farming near an area with freshwater input, but with high nutrient levels and rainwater exposure during post-harvest
(Gacura et al. 2025, Tahiluddin et al. 2025)

• Prevalence of 'ice-ice' disease in eucheumatoid farming
(Tahiluddin et al. 2021, Tahiluddin and Damsik 2023, Tahiluddin and Terzi 2024)

• Controversial use of inorganic fertilizer in eucheumatoid farming
(Sarri et al. 2021, Tahiluddin et al. 2021, Muyong and Tahiluddin 2024, Tahiluddin and Roleda 2025, Roleda et al. 2025)

• Use of organic fertilizer from various seaweed species
(Borlongan et al. 2011, 2024, Tahiluddin et al. 2022, Toroy et al. 2024)

• Reproductive, growth, and culture studies in Halymenia, Asparagopsis, Ulva, Phycocalidia, Sargassum, and Caulerpa
(Ame et al. 2010, Monotilla and Notoya 2010, Santiañez et al. 2016, Peralta 2019, Largo et al 2020, Aaron-Amper et al. 2020, Estrade and Dionisio-Sese 2020, Estrada et al. 2021, Rula et. 2021, Monotilla 2024, Saco et al. 2024a, Saco 2025)</td><td>• Photosynthetic response of laboratory-maintained eucheumatoid cultivars
(Manulon-Diansuy 2014)

• Photosynthetic response of Padina spp.
(Barrow et al. 2015, Aaron and Dy 2016)

• Photosynthetic response of 'Neosiphonia sp. epiphyte-infected' and healthy K. alvarezii
(Borlongan et al. 2016)</td></tr>
<tr><td>2020s</td><td>• Photosynthetic response of green and red morphotypes of eucheumatoid
(Aguirre-von-Wobeser et al. 2021)

• Photosynthetic response of seaweeds with varying thallus morphology
(Dangan-Galon et al. 2013, Saco and GanzonFortes 2022)

• Fluorescence-photosynthesis of Ulva and Asparagopsis
(Saco 2024a, b)</td></tr>
</table>

Studies on the effect of monsoons on seaweed community ecology

Mendoza and Soliman (2013) demonstrated that monsoons in Lagonoy Gulf, Bicol Region might have a significant impact on variations in seaweed composition, with a higher number of seaweed species observed during the southwest monsoon than the northeast monsoon, particularly in areas with rocky substrates compared to sandy ones. In addition, strong winds and heavy rain brought by these monsoons can dislodge macroalgae that have fragile and broad thalli. Heavy rain causes siltation and lower salinity, which can smother seaweed species, reducing their ability to photosynthesize and eventually leading to the disappearance of smaller and more fragile species. Furthermore, strong currents promote a higher number of species than areas with weak currents and waves. Similarly, Evangelista et al. (2015) documented that the changes in the monsoon and Kuroshio current could be the driving force on the composition and distribution of marine benthic algae in Catanduanes Island, Bicol Region, consisting of a majority of green seaweeds and several economically important species, i.e., *Asparagopsis taxiformis*, *Caulerpa* spp., *Gelideilla acerosa*, *Sargassum* spp.

Studies on the effect of anthropogenic pressures on seaweed community ecology

Recent studies on seaweed community structure have focused on changes over time and the potential effects of climate change and other anthropogenic pressures. VinceCruz-Abeledo et al. (2019) reported that changes in seaweed composition in Calatagan Bay, Batangas, from 1985 to 2019 might be due to the possible effect of the warming of coastal waters, wherein they observed that some seaweed genera, such as *Ceramium, Gayliella,* and *Gelidiella* were not observed during the 2019 sampling compared to previous reports in the area in 1985, coinciding with significant warming events from June 1998 to 2019, with peak sea surface temperature at 31.9°C. However, this could also be due to the differences in the sampling period in 2019 from that previously reported in 1985 in the area.

On the other hand, Bataan et al. (2022) examined historical accounts of seaweed composition in Siloy Bay, Cebu, by comparing historical (1969–1970) and contemporary (2013–2014) collections that covered both the southwest and northeast monsoons. Historical collections are from the study by Zarzuelo (1975), and the contemporary collections are ground truth data. The comparison analysis revealed that half of the 30 seaweed species from the historical collections were not accounted for in the contemporary collections, resulting in a higher percent reduction (64%) specifically among red seaweeds. This relative decline in the marine benthic algal composition may be attributed to sedimentation indirectly caused by urbanization and human population increase.

Furthermore, Camaya et al. (2024) made an update on the seaweed status in Lagonoy Gulf, Bicol Region, after more than a decade. They also observed a similar higher species composition during the southwest monsoon compared to the northeast monsoon, and in areas with strong wave movement, consistent with the findings of Mendoza and Soliman (2013) in the exact location. However, the present study of Camaya et al. found a much fewer number of species recorded in both monsoons. The lower number of species recorded may imply a declining seaweed population, possibly due to increased anthropogenic factors in the area, such as siltation, navigation and anchorage, establishment of fish corrals, and other fishingrelated damages.

Seaweed community ecology could also be utilized to extract information about the health, status, and condition of the marine environment. For example, Saco et al. (2022) showed that the majority of the identified and dominant seaweed species (ca. 80%) in Verde Island, Batangas City, were characterized by coarsely branched, thick and leathery, and jointed calcareous thalli. The high percentage of species exhibiting these functional forms may be indicative of intermediate and mature communities, which are typically found in relatively stable, non-stressful marine environments (Littler and Littler 1980, Littler et al. 1983). Similarly, observations of Elias et al. (2024) reveal that the dominant seaweed species have coarsely branched and jointed calcareous thalli in Mabini, Batangas.

On the other hand, Cabatay et al. (2022) conducted an assessment of green tide-blooming seaweed species in an industrialized area in Batangas City. They showed the presence and abundant cover of different *Ulva* spp, both during the southwest and northeast monsoon. There was a declining trend of nitrate from southwest (2.13 mg/L) to northeast (<0.075 mg/L) monsoons, and coinciding with an increase in *Ulva* biomass during the northeast monsoon, which might be due to the accumulation of nitrate in *Ulva* spp. Moreover, Mance et al. (2024) showed a positive relationship between the nitrate and phosphate levels in the tissues of *Ulva* spp. and their percent cover in selected sites in Batangas with different degrees of industrialization and human activities. However, no correlation was established between the nitrate and phosphate levels of the seawater and the percent cover of *Ulva* spp. Results suggest that as the total nitrogen and phosphate levels in the tissue increase, the *Ulva* spp. percent cover also increases, showing the species' bioaccumulation potential. Carayo et al. (2005) observed that the relatively high nutrient concentration in March may have contributed to the increase in green tide algal biomass in the eastern part of Mactan Island, central Philippines. In addition, Gamez et al. (2024) inferred that the high intrate level in Talaga Port, Mabini, Batangas could explain the higher percent cover of *Ulva* spp. and suggested using the species for biomonitoring.

Moreover, Saco et al. (2020) discussed the distribution of *Padina* sp. in different monsoons. It was revealed that in Verde Island, Batangas City, the area showed dominance during the summer, with a lesser cover in the succeeding monsoons. Furthermore, this species especially exhibited high cover in sites near populated areas and backyard pig pens. Additionally, *Ulva* spp. and *Caulerpa verticillata* were also identified as potential bioindicator species in the area. Similarly, Baleta and Nalleb (2016) found high species density of *P. sanctae-crucis* in Nangaramoan, San Vicente, Sta. Ana, Cagayan. In addition, Bayer et al. (2024) discussed the potential of brown seaweeds, specifically *Dictyota* and *Padina* spp., as a bioindicator in Ilijan, Batangas City, due to their high percent cover, especially near runoffs, power plants, and resorts. These seaweed species could be good candidates for biosurveillance of marine ecosystems due to their bioaccumulation properties, in parallel with their higher abundance.

REPRODUCTIVE AND GROWTH STUDIES IN SEAWEEDS

Commercially cultivated seaweed species have gained significant interest, likely due to their substantial economic value, which includes carrageenan, agar, alginate, and ulvan extracts, as well as pigments used in the food, nutraceutical, and pharmaceutical industries.

Carrageenan is primarily extracted from eucheumatoid species such as *Kappaphycus alvarezii* and *K. striatum* ('cottonii' of commerce) and *Eucheuma denticulatum* ('spinosum' of commerce), which are common red seaweed species commercially cultivated in the Philippines through seaweed farming. These species, specifically *K. alvarezii*, account for 80% of the total Philippine production for export purposes (SEAFDEC Aquaculture Department 2017). Dumilag et al. (2016) presented molecular evidence that the Philippines has a total of 6 *Kappaphycus* species, suggesting that the country could be the center of *Kappaphycus* biodiversity in the world. Moreover, Dumilag et al. (2022) documented a total of 66 cultivars being farmed across 58 provinces in the Philippines. Farmers mostly favored *Kappaphycus* due to its fast-growing nature, ease of farming, and ability to tolerate wide fluctuations of environmental factors such as temperature, irradiance (Trono 1974). Recent efforts have been made to select high-quality cultivars as new planting materials for seaweed farming (Luhan et al. 2021, Hinaloc and Roleda 2021, Roleda et al. 2024, Dangan-Galon et al. 2024). On the other hand, agar is primarily extracted from *Gracilaria* spp., *Gracilariopsis* spp., and *Gelidiella acerosa* (Hurtado-Ponce et al. 1992, Ganzon-Fortes 1994). In contrast, phycoerythrin pigment, used as a colorant, is extracted from *Halymenia* spp. (Trono 2010). Other red seaweeds, such as *Phycocalidia* spp. and *Asparagopsis taxiformis*, are gaining increasing interest due to local demand for food and their climate mitigation properties by reducing methane emission from cows, respectively (Ame et al. 2010, Santiañez et al. 2022). Hurtado et al. (2020) reviewed the biology and distribution of various red seaweeds, including *H. durvillei*, *A. taxiformis*, *Phycocallidia* spp., with emerging potential applications focusing on their bioactive compounds (proteins, lipids) and biological activities (anticoagulant, anti-viral properties). *H. durvillei* is generally distributed across the country and present year-round. *A. taxiformis* has a limited distribution but is represented in all main islands in the Philippines with pronounced seasonality from October to November and April to May. *Phycocallidia* spp. is limited in Northern Luzon, specifically in Ilocos Sur and Cagayan, with pronounced seasonality from October to March. Table 1 summarizes the various reproductive and growth studies on Philippine seaweeds, highlighting their significant key findings.

Reproductive and growth studies in eucheumatoid species

To date, Doty (1969) documented the practice of harvesting natural beds of eucheumatoid species as 'cottonii' and 'spinosum' in the Philippines as an export product to the United States and the United Kingdom. This led to a high demand for raw materials, which in turn drove the exploitation of natural stocks, resulting in a decline in production and the availability of source materials. Addressing the shortage of supplies, Dr. Gavino C. Trono and Dr. Maxwell S. Doty of the University of Hawaii, along with Mr. Vicente B. Alvarez, pioneered the formulation of euchuematoid farming technology through the vegetative propagation of seedstock using bottom and floating methods (Doty and Alvarez 1973, 1975, Trono 1974).

Reproductive studies on carrageenan-producing species—specifically *Kappaphycus* and *Eucheuma* spp.- began in the early 1980s in response to the need for alternative sources of seedlings beyond traditional vegetative cuttings in seaweed farming. Azanza-Corrales (1990) and Azanza-Corrales et al. (1992) identified three distinguished reproductive structures (observed with most red seaweeds), namely tetrasporic form (tetrasporophyte), sexual male (spermatia), and female forms (carposporophyte) in both the natural population of *Kappaphycus alvarezii* and *Eucheuma denticulatum* at farming sites in Danajon Reef, Northern Bohol, during 1987 and 1988. Most of the *K. alvarezii* samples exhibited both male and female reproductive structures but lacked the tetrasporic form, whereas in *E. denticulatum* samples, only the male and tetrasporic structures were observed. In addition, Azanza-Corrales et al. (1996) conducted recruitment experiments at a farming site in TawiTawi, Philippines, using artificial substrates, and found that successful recruitment was significantly associated with current speed, the number of days with minus tides, and salinity. Moreover, Azanza and Aliaza (1999) conducted laboratory-based experiments on the release and germination of carpospores (female form) of *K. alvarezii*, which was farmed in TawiTawi, Philippines. Their findings indicated that higher irradiance (~200 μmol photons m^{-2} s^{-1}) and salinity levels at 30 and 35 PSU promote the highest carpospore release and germling growth in a more enriched medium.

Hurtado and Agbayani (2000) provided a detailed manual on the farming of *Kappaphycus* that includes criteria for farming, culture methods, harvesting, post-harvest management, and marketing strategies. Subsequently, Hurtado et al. (2015) summarized the various breakthroughs in *Kappaphycus* production technology in the Philippines, encompassing molecular taxonomy, factors affecting sporulation, tissue culture and mutagenesis, protoplast isolation, strain selection, and mitigation of 'ice-ice' disease. Persia et al. (2020) explored the potential of Olo-olo, Lobo, Batangas as a new *Kappaphycus* farming site with a higher growth rate (3.63% d^{-1}) under 30ºC, 32 PSU, and 1.8 m depth.

Due to the continuous decline in the production of eucheumatoid species in the Philippines, Ganzon-Fortes (2014) led a national program on "Culture Technology Enhancement to Improve Production Capacities of Philippine Seaweed Farms," funded by the Department of Science and Technology - Philippine Council for Agriculture, Aquatic, and Natural Resources Research and Development. These initiatives led to significant milestones in addressing the decline in production by utilizing sporelings from carposporophyte and tetrasporophyte, as well as branch culture reared in the laboratory as seedling materials. Additionally, the establishment of a seaweed culture facility, including both laboratory and land-based facilities, will maintain different farming strains. This will be readily available to farmers in times of major natural calamities, such as typhoons that could wipe out entire seaweed farms. Lastly, there is a need to identify a new site for seaweed farming, as the present sites have already exceeded their carrying capacity.

Luhan et al. (2021), Hinaloc and Roleda (2021), Narvarte et al. (2022), Roleda et al. (2024), and Narvarte and Roleda (2025) synthesized various efforts to study the phenotypic diversity, growth, physiology, and reproductive biology of the natural population and laboratory-grown *Kappaphycus* spp. and *Eucheuma* spp. These studies provided the baseline information for efforts to produce new cultivars from natural populations, where these cultivars—with their unique genetic makeup and desirable traits—could provide alternative seed stocks to supplement the currently cultivated strains, which are primarily derived from vegetative cuttings.

Luhan et al. (2021) further advanced the development in *Kappaphycus* farming by determining the growth and carrageenan quality of cultivars from the gametophyte and tetrasporophyte phases, with the latter showing superior potential as a source of seed stock for mariculture. Tetraporophytes have significantly higher responses compared to gametophytes in terms of their growth rates (2.57 vs 1.84 % day^{-1}), carrageenan yield (45.29 vs 39.30 %), viscosity (83.83 vs 45.33 cPs), and gel strength (550.54 vs. 460.99 g cm^{-2}). Hinaloc and Roleda (2021) showed that the growth rates of diploid tetrasporophytes and their haploid gametophyte progenies did not differ significantly and could be a good source of strain for future farming. In addition, they observed that tetrasporophytes grown from carpospores exhibited color variation inherited from their parents, ranging from green to brown and/or bicolor individuals. In contrast, those gametophytes grown from tetraspores produced multicolored individuals. Narvarte et al. (2022) showed that the 'SamW-014' strain from wild *K. alvarezii* collected from Guian, Eastern Samar has a remarkably higher growth rate compared with other strains under hatchery conditions. However, biochemical properties among strains did not differ significantly. Thus, we recommend further analysis of the growth capacity of the 'SamW-014' strain in open-ocean cultivation and its carrageenan yield.

Roleda et al. (2024) conducted a comprehensive review on the reproductive biology and new strain development of *K. alvarezii*. They mentioned that the continuous decline in production can be attributed to the low genetic variability of the seedlings being farmed, as the same strains have been used through vegetative propagation for more than 50 years. Thus, advancements in the development of new strains for farming were achieved using wild individuals for culturing, releasing spores, and cultivation. They reviewed several studies on the reproductive biology of wild *K. alvarezii*, which showed a higher percentage of the tetrasporophyte stage, followed by the carposporophyte stage (female population), and a much lower percentage of the male population. The higher percentage of tetrasporophytes implies successful fertilization, even with a low percentage of the male population. Moreover, the tetrasporophyte is considered more robust and genetically sound due to the genetic exchanges from its parental genes. Thus, cultivars sourced from tetrasporophytes would have better survival. Recently, Gonzaga et al. (2025) published their significant initiatives on the establishment of Seaweed Culture Laboratory and Gene Bank (SCL & GB) alongside an Outdoor Land-based Nursery (OLBN) culturing a total of 577 strains across different commercially important eucheumatoid aiming to preserve the species' genetic diversity, enable the selection of superior strains, and continuing reproductive biology, ecophysiology, and phenotyping studies.

In addition, recent studies on eucheumatoid seaweed farming have focused on nutrient uptake, which is critical for the species' growth and productivity. Narvarte and Roleda (2025) showed different nutrient uptake strategies of land-based cultures of different eucheumatoid species, wherein the highest growth was observed in *K. alvarezii* and *K. striatus* under 40 µM NH_4^+ : 0 µM NO_3^- and 40 µM NH_4^+ : 0 µM NO_3^-, respectively, while the highest growth was observed in *E. denticulatum* in all treatments. Overall, the authors revealed that the different eucheumatoid species generally increase their NH_4^+ and NO_3^- uptake with increasing substrate concentration, showing their efficient utilization of various nitrogen sources. Moreover, the different nutrient uptake strategies did not affect their biochemical indicators, such as pigments, carbohydrates, protein, and polyphenols. Given the optimal response of the different eucheumatoid species to various nitrogen sources, these species could be practically incorporated into Integrated Multi-Trophic Aquaculture as extractive species. In addition, Narvarte et al. (2025) demonstrated that the nutrient uptake and strategies of previous euchuematoid species in a controlled setting were higher during the nighttime period and were independent of light and photosynthesis.

Another interesting study by Gacura et al. (2025) demonstrated the potential of farming eucheumatoid species in sites with freshwater input and high nutrient levels. Traditionally, site selection for eucheumatoid farming has been recommended to occur in an area with seawater salinity greater than 30 PSU. Thus, this study explored experimental treatments that lowered salinity, resulting in a consequent increase in nutrient concentrations, to examine the effects on the nutrient uptake, growth, and biochemical responses of *K. alvarezii, K. striatus,* and *E. denticulatum*. Results showed that the growth rate of eucheumatoid species was higher at lower salinity (24-27 PSU) with higher nutrient concentration (Total Inorganic Nitrogen = 2-14.56 µM and Phosphate = 0.6-1.89 µM), suggesting that the eucheumatoid species can be farmed in areas with fluctuating salinities, given that the freshwater input has high nutrient levels. Furthermore, biochemical indicators such as total polyphenol content, total soluble carbohydrate, and total protein did not differ significantly among treatments in both *K. alvarezii* and *K. striatus*, except for *E. denticulatum*. Additionally, Tahiluddin et al. (2025) observed that the common post-harvest practice on eucheumatoid farming is drying the seaweeds using the hanging method, and they are often exposed to rain. The authors revealed that rainwater significantly lowered the dry yield biomass and reduced moisture content in both fresh and dried forms, but had improved carrageenan yield and had no effect on viscosity. In addition, the gelling temperature was affected by rainwater in the fresh form but not in the dried form, which is the opposite of its effect on the gelling temperature.

Another problem that hinders eucheumatoid production is the 'ice-ice' disease (IID), characterized by the visible bleaching of the thalli, which leads to the disintegration of the affected thalli and subsequently results in biomass loss and reduced carrageenan yield (Ward et al. 2021). Tahiluddin and Terzi (2024) demonstrated that the IID is one of the major threats to the seaweed farms in Tawi-Tawi, Southern Mindanao, exhibiting significant seasonal variations, with higher incident rates during the dry season compared to the wet season, and this effect is more pronounced when plants are grown in deepwater rather than shallow water. In addition, they observed that there was no interactive effect on the incidence of IID among physicochemical and meteorological parameters (temperature, salinity, pH, water current velocity, and wind speed) or nutrient concentrations (phosphate, nitrate, and nitrite), but there was an inverse relationship with ammonium. In contrast, Tahiluddin and Damsik (2023) demonstrated that *K. striatus* are less susceptible to IID when farmed in deep water in Sibutu, Tawi-Tawi. The authors further observed that, regardless of the cultivated species (either shallow or deepwater) and cultivation time, there was no significant effect on the prevalence of IID. Moreover, temperature and salinity do not correlate with the prevalence of IDD among the farmed species, but a remarkably higher temperature of ~33°C was recorded in the area. One factor contributing to the prevalence of IID is the presence of pathogenic bacteria, as documented by Tahiluddin et al. (2021). They observed a significant number of bacterial counts attached to one of the macro-epiphytes, *Ulva lactuca,* which entangle the seaweed farms, implying that the macro-epiphyte could be a vector of pathogenic bacteria that cause IDD.

Traditionally, seaweed farmers have used inorganic or chemical fertilizers as a means of nutrient enrichment, which may have a negative impact on the environment. In Tawi-Tawi, Southern Mindanao, seaweed farmers utilize inorganic nutrients such as ammonium phosphate (8.82 g L^{-1}, practice dosage in farms) to boost growth and reduce the incidence of IID, which is caused by extensive farming practices in the area, leading to nutrient depletion in the seawater. Sarri et al. (2021) investigated the effect of urea and phosphate in promoting growth, carrageenan yield, and the occurrence of IDD in *K. striatus*. It showed that the specific growth rate is higher when treated with urea (8.82 g L^{-1}, standard dosage practiced in farms) than when treated with phosphate. Neither nutrient differed significantly in the occurrence of IDD, nor did it affect the carrageen yield.

Additionally, Muyong and Tahiluddin (2024) investigated that nutrient enrichment using ammonium phosphate (3.5 g L^{-1}) significantly improved the growth rate, carrageenan yield, and occurrence of IDD in *K. alvarezii*, regardless of farming method. Moreover, Tahiluddin et al. (2021) determined that 6 or 9 g L^{-1} is the standard concentration of ammonium phosphate as an enrichment for *K. striatus* to achieve high nitrogen assimilation. Tahiluddin and Roleda (2025) and Roleda et al. (2025) reviewed various studies on the use of inorganic nutrients in seaweed farms, concluding that there is a consistent positive effect on the growth rate and a lesser occurrence of IDD, but with inconsistent results regarding carrageenan yield and quality. However, this practice raises concerns because carrageenan is labelled as 'organic' in the food industry and could pose an adverse effect on the marine environment.

This practice is highly controversial due to its impact on ethical and social considerations; therefore, it warrants a thorough review to ensure sustainable practices for the environment and the global market.

The following studies investigate the beneficial effects of using organic fertilizers derived from various seaweed species. Borlongan et al. (2011) investigated the use of seaweed-based fertilizer on the growth rate and epiphytism occurrence in the two varieties of *K. alvarezii* cultivated at different depths. Results showed that cultivars treated with seaweed-based fertilizers, such as Acadian Marine Plant Extract Powder (AMPEP), before planting exhibited higher growth rates (1-fold higher) and a lower incidence of epiphytic infestation by the red alga *Neosiphonia* sp. (~50% reduction in infestation). In addition, the authors recommended planting cultivars at 50-100 cm to reduce epiphytic infestation by up to ~60%. Moreover, Borlongan et al. (2024) explored the efficacy of two European, commercial liquid extracts from the brown seaweeds, i.e., *Ascophyllum nodosum* and *Laminaria digitata*, as biostimulants on the survival, direct axes formation, and axes length of *E. denticulatum* and *K. alvarezii*, subjected to a tissue culture experiment. The authors revealed significantly higher survival rates, higher percentages of direct axes formation, and longer axes in euchuematoid species when grown under a lower concentration (0.005 mL L^{-1}) of the liquid extract, with a decreasing trend observed at increasing concentrations up to 2.5 mL L^{-1}. In addition, Tahiluddin et al. (2022) used the extracts from brown seaweeds *Sargassum cristaefolium* and *Turbinaria conoides* as organic fertilizers and tested them on the growth rate, carrageenan yield, and ice-ice disease occurrence of *K. striatus*. Results showed that cultivars treated with biofertilizer had a 1-fold higher growth rate. At the same time, the ice-ice occurrence significantly decreased by 45 days, and there were no differences in carrageenan yield compared with the control. Furthermore, Toroy et al. (2024) investigated the use of *Ulva* spp. liquid extract to enhance the growth of commercially important eucheumatoids, wherein high concentration (1-3 mL L^{-1}) of seaweed liquid extract from *Ulva* spp. significantly improved the growth rate, specifically the direct axes formation (99.8–100%), and the longest shoot measurements (3.6–3.8 mm), and the chlorophyll-*a* content of commercially farmed *Eucheuma denticulatum* in tissue culture.

Reproductive and growth studies in agarophyte species

Traditionally, coastal communities in the Philippines have used *Gelidiella acerosa* and *Gracilaria* spp. as primary ingredients in desserts such as 'gulaman', a jelly-like dessert. Roleda et al. (1997a) explored the natural population of *G. acerosa,* providing a management plan for wild-stock collection. The best period for harvesting is during the dry month of April, when biomass is optimal, and the extracted agar is at an average quantity, with high gel qualities. Furthermore, Roleda et al. (1997b) demonstrated the concurrent occurrence of both vegetative and tetrasporic life stages in a natural population of *G. acerosa*, suggesting that a regulated harvest should be conducted with vegetative thalli to allow tetrasporic thalli to shed spores for recruitment.

Other red seaweeds with potential for agar extract include *Gracilaria* spp. and *Gracilariopsis heteroclada*. Trono (1988) and Hurtado-Ponce (1994a) reviewed various studies on the biology, ecology, and farming systems of *Gracilaria* spp. and *G. heteroclada,* showing that the occurrence of reproductive stages was not significantly correlated with temperature, salinity, or turbidity, while farming systems range from cage to pond and bottom-line cultivation. On the other hand, de Castro et al. (1991) and Hurtado-Ponce (1994a) showed a marked seasonality in the natural population of *Gracilaria* spp. biomass varies across locations, possibly due to an inverse relationship with rainfall. Observations revealed a major *Gracilaria* spp. biomass peak around January to February (~170 g dry wt m^2), a minor peak around September to October (~90 g dry wt m^2), and low biomass in June. The low biomass of *Gracilaria* spp. could be attributed to the shift from dry to wet season, characterized by intense rain, typhoons, and strong wave actions, which cause damage to the thalli and eventually lead to uprooting or tearing. Moreover, Hurtado-Ponce (1994a) suggested that when harvesting *Gracilaria* spp. from their natural population, 75% would be an appropriate amount of 'seeds' for the next cropping season. In addition, Hurtado-Ponce (1994b) showed the interactive effect of salinity and NaOH treatment wherein the strongest gel was achieved when laboratory-grown *G. heteroclada* was grown at 24 and 32 PSU treated with 3% NaOH.

On the other hand, Luhan (1992) found a negative correlation between agar yield and gel strength in a farm setting, where gel strength was high during the early dry season and low during the wet season. Furthermore, Araño et al. (2000) tested three agarophyte species grown under controlled outdoor flow-through culture conditions. *Gracilaria firma* showed superior growth and agar quality, and was highly resistant to epiphytes under 900 µmol photons m-2 s-1 and 150 µM NH4Cl, compared to *Gracilaria* sp. and *Gracilariopsis bailinae*. Moreover, Rabanal (2000) evaluated the agar quality of laboratory-grown carposporelings of *G. bailinae,* achieving good quality agar when grown in the field at a depth of 1.0 m. Endomo et al. (2024) showed higher agar yield and viscosity in *G. heteroclada* under short-term tank culture and exposure in hypersaline conditions (~50 PSU) with high cohesiveness, gel breaking strength, and gel strength at ~40 PSU.

Ganzon-Fortes and Trono (1982) documented the different reproductive occurrences of the natural populations of *Laurencia* sp., another agar-producing species. They found no significant correlation between the different reproductive occurrences and various physicochemical parameters, including water movement, pH, temperature, and salinity, in Calatagan, Batangas. In addition, Ganzon-Fortes and Trono (1982) found that tetrasporophytes dominate over other reproductive stages, which might indicate that the environment is suitable for spore production throughout the year.

Reproductive and growth studies in some emerging seaweed species

Due to the highly valued pigments from *Halymenia durvillei,* such as phycoerythrin, Saco (2025) conducted pilot testing on the vegetative stage of the species for farming, examining their growth response and pigment concentration across three sampling periods: dry/hot (April), southwest (October), and northeast (January) monsoons. The pilot testing concluded that during the northeast monsoon, the highest growth rate and pigment concentration were observed, likely due to colder temperatures and the use of lower wet weights as planting materials. During the southwest monsoon, lower growth rates and pigment concentration were observed due to higher turbidity from several typhoons. Lastly, during summer coinciding with El Niño, a negative growth rate and an increase in allophycocyanin were observed, which could be their defense mechanisms under stress. On the other hand, Rula et al. (2021) found that the growth rate and pigment content of the vegetative *H. durvillei* grown under land-based conditions were best under a combination of full light (100% = 203 ± 76 µmol photons m^{-2} s^{-1}), moderate water motion (in terms of mean loss of the calcium sulfate blocks = 18.34 ± 5.48 g in 24 h), and 50-g stocking density. The relatively low irradiance during the experimentation coincides with the cold, dry season, characterized by days with overcast skies, which may have influenced *H. durvillei* to maximize the use of available resources, such as light, and possibly increased nutrient availability from water motion, to promote growth and phycobiliprotein synthesis. However, white rot disease and epiphytism were reported on the land-based culture of this species, which contributed to the decrease in production (Santiañez et al. 2016). Further studies should be conducted on the reproductive biology of the species to establish the occurrence of reproductive stages, which could provide baseline information for selecting the best-fitted cultivar/strain for mass cultivation.

Moreover, another carrageenan-producing species, especially "lambda," is *Acanthophora specifera*. Although this species has not been commercially cultivated yet, it is traditionally utilized as food for human consumption. Information about their reproductive phenology could be a basis for their culture development and resource management plan. BuchanAntalan and Trono (1983) studied the reproductive occurrence of the natural population *A. specifera,* showing dominance of tetrasporophytes, followed by carposporophytes and the male population. Results suggest that the environment is suitable for spore production throughout the year, making it a potential source of new seedlings for mass cultivation of the species.

Due to the climate change mitigation property of reducing methane emissions from cows of another red seaweed, *Asparagopsis taxiformis*, there is an increased interest in the species for possible mass cultivation. Saco (2024a) studied the reproductive occurrences of *A. taxoformis,* showing that the carposporophyte stage appears to exhibit seasonality, which is observed only during the cold, dry season. In contrast, the tetrasporophyte stage was observed throughout the year. Therefore, the *A. taxiformis* tetrasporophyte is proposed to be a candidate stage for mass cultivation. On the other hand, *Phycocalidia* sp., also known as "gamet," is only distributed in the northern part of Luzon Island in the Philippines, specifically in Ilocos Norte and Cagayan Provinces. Ame et al. (2010) provided insights into the industry of this species in the country, wherein the gatherers of the species are mainly fisherfolk who primarily benefited from the wild harvesting of the species, which coincides with the lean months for fishing operations in the area. Observations revealed that the species thrived at 22-24°C, 29-30 PSU, 85-87% humidity, and with wave splashing occurring 5-8 times per minute. Moreover, Monotilla and Notoya (2010) first reported the growth and development of this species (as *P. macrosii*) under laboratory conditions, which exhibited a typical biphasic life history with alternating sporophytic conchocelis (spore settlement in shells) and gametophytic blades.

One of the commercially important brown seaweeds, due to its alginate, is extracted from *Sargassum* spp. Member of this genus typically undergoes four (4) phases in their life history: regeneration and slow growth, fast growth, reproductive, and senescence (Largo and Ohno 1992, Calumpong et al. 1999). Calumpong et al. (1999) showed that the major biomass peaks of *Sargassum* spp. in Negros Island, Central Philippines, occur before they become reproductive. On the other hand, Ortiz and Trono (2000) documented temporal variations in the thallus length and reproductive patterns between intertidal and subtidal populations of *Sargassum* in Bolinao, Pangasinan wherein the intertidal *Sargassum* population reached maturity in November with a shorter thallus length (20.5-25.0 cm) than the subtidal population (26.0-31.6 cm) that matured in December, while peak fertility occurred in December for both intertidal and subtidal populations. Furthermore, Trono and Lluisma (1990) observed inter-annual variations in the standing crop of the natural population *Sargassum* spp. in Bolinao, Pangasinan, wherein the standing crop was generally lowest (~250 g wet wt m^{-2}) in February to April or May and highest (~1,500 g wet wt m^{-2}) in November to January, and poorly correlated with the environmental factors such as temperature, salinity, water movement, and daytime minus tide.
However, due to the increasing demand for the raw materials of *Sargassum* spp. from uncontrollable wild-stock harvesting, the Department of Agriculture, through the Bureau of Fisheries and Aquatic Resources, issued Fisheries Administrative Order (FAO) No. 250-2 Series of 2018 regarding the "Regulations on the Collection, Harvesting, Gathering, Selling, and Exporting of *Sargassum* spp." FAO No. 250-2 prohibits the collection or gathering of naturally growing species, as well as those still floating/drifting, but allows the collection of those washed ashore. Given the demand for the species, Largo et al. (2020) were able to produce a mass production technique on the seedlings of *Sargassum* spp. by collecting large amounts of fertilized eggs from their receptacles (found throughout the branches) and transferring them onto different artificial substrates such as clay panel, limestone panel, and nylon string wherein the clay panel was proved to be more efficient based on the density of recruits. In addition, Largo et al. (2020) showed that a 100-200 egg-bearing receptacle excised from fertile *Sargassum* spp. could produce up to 2000–3000 seedlings, which can supply at least a hectare of farm.

Furthermore, Aaron-Amper et al. (2020) showed that young juveniles of *Sargassum* sp. on clay substrate out-planted in the sea grew from 64.6 ± 16.0 mm to 95.6 ± 37.9 mm after 84 days, but some thalli had evidence of grazing. Thus, the authors suggested that transplanted juveniles should be placed in sites with fewer grazers and epiphytic organisms, less sedimentation, and suitable water currents for effective mass cultivation. Moreover, site selection should be carefully planned to ensure efficient production, and the optimal months for cultivation should be identified.

Green seaweed gaining popularity for utilization is the green tide-blooming species, *Ulva* spp., and other related genera. The green-tide bloom event is becoming one of the significant environmental challenges in the coastal environment due to the overproliferation of *Ulva* spp. caused by high light conditions and high-temperature levels, and is significantly associated with eutrophication, i.e., increased nutrients (Liu et al. 2012, Wan et al. 2017). In the Philippines, the green tide blooms along the beaches of Boracay became controversial and gained widespread publicity in 2017, which led to the suspension of tourism activities and the temporary closure of the whole island for rehabilitation (Rodriguez 2017). This phenomenon has also been documented in certain parts of the country, such as Mactan Island, Cebu, Central Visayas (Largo et al. 2004), and El Salvador, Misamis Oriental, Northern Mindanao (Villaluz et al. 2016). The incident in Cebu consisted mostly of *Ulva* spp. (i.e., *U. lactuca* and *U. reticulata*), while those in Misamis Oriental were co-dominated by *Cladophora vagabunda, U. clathrata, U. intestinalis*, and *U. reticulata*. Peralta (2019) explored the processing of *Ulva* spp. as fertilizer and feeds during the Boracay island green-tide bloom event in 2017, wherein at least four *Ulva* species were preliminarily identified morphoanatomically as *U. clathrata, U. intestinalis, U. lactuca,* and *U. reticulata.*

On the other hand, Monotilla (2024) highlighted the potential of cultured *Ulva* spp. for biomass production and commercial use in the Philippines, citing their high nutrients in the proximate analysis and potential source of food and feed, thus possibly an alternative livelihood for fishermen and seaweed farmers. In addition, the use of tanks would be the practical method for biomass production under controlled light, temperature, and stocking density while mitigating blooming events in the area. Commercially farmed green seaweed *Caulerpa* spp. (commonly known as 'lato' locally in Cebu, but also true in other parts of the Philippines) is traditionally utilized as food for human consumption. Trono (1998) mentioned that *Caulerpa* farming in the Philippines began in the early 1950s in Central Visayas, where Trono (1987) observed seasonality in growth rates, with higher rates obtained during the summer/dry months and minimal to zero growth rates during the rainy/cold months. Although the species has been widely cultivated and harvested in the Philippines for years, its production has not been well-documented, and limited information is available on its current status.

Estrada and Dionisio-Sese (2020) documented for the first time the current status of *Caulerpa* harvesting in Coron, Palawan, where a total of two species, *C. lentillifera* and *C. racemosa,* and two varieties, *C. racemosa* var. *turbinata* and *C. racemosa* var. *laetevirens,* have been identified. The peak production of *Caulerpa* spp. was observed during the dry season from January to April, with an estimated total of 101 kg (fresh weight) of *Caulerpa* spp. per month. In addition, Estrada et al. (2021) showed an estimated 42,222 kg (fresh weight) of *Caulerpa* spp. per month, at peak production in different areas in the Philippines, with Mactan, Cebu, as the top producer. Given their potential as a major source of livelihood, recommendations for improving farming techniques should be explored to enhance their sustainability.

PHOTOSYNTHETIC AND GROWTH STUDIES OF SEAWEEDS

Photosynthesis is the major ecophysiological mechanism among seaweed species; however, limited studies have been conducted in the Philippines, and most focus on economically important species, such as eucheumatoids and agarophyte. Table 1 summarizes the various photosynthetic and growth studies on Philippine seaweeds, highlighting their significant key findings.

Photosynthetic and growth studies in eucheumatoid species

One of the earliest studies utilizing their photosynthetic responses was by Ganzon-Fortes et al. (1993) on *K. alvarezii,* which showed higher photosynthetic capacity with healthy thalli compared to diseased thalli, wherein the former showed 50% higher photosynthetic rate in all light levels up to 800 µmol photons m^{-2} s^{-1} than the latter, which showed photoinhibition at 600 µmol photons m^{-2} s^{-1}. The healthy thalli have a steeper slope (α = 0.04) with a corresponding lower compensation point (Ic = 11.99 µmol photons m^{-2} s^{-1}) than the diseased thalli (α = 0.02, Ic = 52.71 µmol photons m^{-2} s^{-1}). The diseased thalli have a higher respiration rate than the healthy thalli, coinciding with a decrease in chlorophyll *a* and both accessory pigments, r-phycocyanin and r-phycocrythrin, which might imply their metabolic response to stress. Furthermore, Borlongan et al. (2016) studied the photosynthetic capacity of '*Neosiphonia* sp. epiphyte-infected' and healthy *K. alvarezii,* showing lower Pmax (0.7–2.0 mg O_2 g^{-1} FW h^{-1}) and high initial saturation irradiances (Ek = 90–519 µmol photons m^{-2} s^{-1}) on the former than the latter (Pmax = 0.9-2.1 mg O_2 g^{-1} FW h^{-1}; Ek = 103-290 µmol photons m^{-2} s^{-1}), resulting in their low photosynthetic efficiency (α = 0.002–0.010). The responses might imply light requirement competition between the host plant and the epiphyte, but neither thallus showed photoinhibition up to 850 µmol photons m^{-2} s^{-1}.

Moreover, Aguirre-von-Wobeser et al. (2021) compared the photosynthetic responses of green and red morphotypes of *K. alvarezii* collected in the Philippines, along with their corresponding pigment analysis. The results showed that both morphotypes had similar productivity and efficiency in utilizing low light levels for photosynthesis, as well as a similar phycoerythrin composition; however, there was a 2-fold higher concentration of phycocyanin and allophycocyanin in the green morphotype, indicating the phenotypic appearance of the green morphotype. Furthermore, Manulon-Diansuy (2014) investigated the photosynthetic responses of laboratory-maintained cultivars of different eucheumatoid species collected from different seaweed farms in the Philippines. These cultivars have been maintained for several months to years. The results showed varied responses, wherein *K. alvarezii* cultivars exhibited ecotypic differentiation, retaining their photosynthetic capacity as observed when they were originally collected. In contrast, *K. striatus* cultivar showed phenotypic plasticity wherein their photosynthetic capacity was different and considered 'sun' adapted plant responses (i.e., high Ik, Ic, Pmax, and low α) when compared to the freshly collected sample as 'shade' adapted plant responses (i.e., low Ik and Ic, high α).

Photosynthetic and growth studies in agarophyte species

Ganzon-Fortes (1997a, b, 1999) conducted extensive ecophysiological studies on the natural population of *G. acerosa* to explore potential culture technologies in response to increasing demand for raw materials. Ganzon-Fortes (1997b) demostrated that the photosynthetic responses of *G. acerosa* collected from intertidal, tidepools, and subtidal did not differ significantly in terms of photosynthetic rate (Pmax =10.6 to 17.8 mg O_2 g d wt^{-1} h^{-1}), and light requirements (Ik = 52–112 µmol photons m^{-2} s^{-1}; Ic = 3–14 µmol photons m^{-2} s^{-1} and α = 0.15–0.35). Thus, any of the populations collected from different locations could be used as culture materials, as observed from relatively similar photosynthetic responses and light requirements. Moreover, Ganzon-Fortes (1999) showed that *G. acerosa* from intertidal areas is more tolerant to wide temperature ranges (22, 28, 34°C) and low salinity levels, while those collected from tidepool and subtidal were least affected by salinity variations (22, 28, 34, 40 PSU) but quite sensitive to different temperatures. This information can serve as a baseline for developing culture technology for this species.

Photosynthetic and growth studies in some seaweed species with emerging commercial potential

Saco (2024b) showed possible ecophysiological cues influencing the bloom-forming mechanisms in *Ulva* spp. utilizing profiles from their fluorescence-photosynthesis characteristics and growth rate analysis. The maximum quantum yield has shown that the natural populations of *U. lactuca* and *U. reticulata* can tolerate a wide range of temperatures (20-35°C) and nitrate levels (5,000, 10,000, and 20,000 µM of KNO_3). Meanwhile, the effective quantum yield of both species showed temperature and nitrate tolerance consistently but exhibited lower and positive responses at higher irradiance (1,500 µmol photon m^{-2} s^{-1}). Additionally, both species exhibited interactive effects among the various abiotic factors. To mitigate the lower and positive effective quantum yield at higher irradiance, the photoprotective response of *Ulva* spp. was increased at higher irradiance to protect their photosynthetic apparatus. On the other hand, the growth analysis of unialgal *U. lactuca* indicated a significant preference for irradiance levels of 26 and 83 µmol photons m^{-2} s^{-1} rather than 217 µmol photons m^{-2} s^{-1}. Furthermore, irradiance level had no significant effect on all *Ulva* thalli across all temperatures. Moreover, no interactive effect was observed between the growth rates of *U. lactuca* in varying temperatures and irradiance levels. Bao et al. (2024) explained that the relative electron transport rate and growth rate of green tide blooming *U. linza* from the Yellow Sea, China, were significantly higher in high light conditions (~300 µmol photons m^{-2} s-1). *U. linza* increases its pigment concentration to optimize its response under low light conditions, while at high light conditions, it reduces its pigment concentration to compensate for its metabolic processes. This observation implies their mechanisms for producing green tide bloom events. In addition, Gu et al. (2022) observed the production of a large amount of digalactosyldiacylglycerol, synthesized in the photosynthetic membrane, as a possible photoprotective and repair mechanism in *U. prolifera* collected from the Yellow Sea, China.

Moreover, Saco (2024a) investigated the photosynthetic characteristics of the different life stages of *A. taxiformis* collected from their natural population, which could provide baseline information for selecting a strain for mass cultivation. The tetrasporophyte and carposporophyte stages of *A. taxiformis* have significantly higher photosynthetic fluorescence under saturating irradiance (190 µmol photon m^{-2} s^{-1}) compared with the gametophyte, with the latter showing decreasing photosynthetic fluorescence as temperature increases. Although both are similar in their responses at tetrasporophyte and carposporophyte stages, the former exhibits a sturdier morphology than the latter.

Photosynthetic and growth responses in seaweed species affected by intrinsic and extrinsic variations

Barrow et al. (2015) studied the ecophysiological responses of *Padina* spp. collected from contrasting sites such as *P. antillarum* from turbid, high-nutrient waters and *P. minor* from clear, low-nutrient waters, showing both "shade-adapted plants" based on their high α values, low compensation irradiances, and low saturation irradiances, and similar growth rates, but differ in their nutrient uptakes. The differences in nutrient uptake rates of Padina spp. from contrasting sites revealed that both species exhibit enhanced initial uptake rates within the first time interval (0–30 min). However, this effect was more pronounced in *P. minor* than in *P. antillarum*, with the former displaying a higher and longer-lasting surge uptake capacity. These physiological mechanisms may be the species' strategies for survival in their respective habitats. Furthermore, Aaron and Dy (2016) showed that the photosynthetic efficiency and growth of *Padina sanctae-crusis* decrease with increasing total copper concentration in the specimens collected from Mactan Island, Central Philippines, indicating the severe impact of copper on the overall ecophysiological response of the species. The photosynthetic efficiency of *P. sanctae-crusis* decreases from ~4.0 mgO_2 g^{-1} dw h^{-1} at 0 µg total Cu L^{-1} to ~0.5 mgO_2 g^1 dw h^{-1} at 500 µg total Cu L^{-1}, coinciding with their daily growth rate from 0.6 g ww day^{-1} at 0 µg total Cu L^{-1} to ~-0.3 g ww day^{-1} at 500 µg total Cu L^{-1}.

Saco and Ganzon-Fortes (2022) conducted extensive studies on the effect of thallus morphology among fifty (50) seaweed species collected in the intertidal area in Bolinao, Pangasinan, utilizing different parameters of the Photosynthesis-Irradiance (P-I) curve. They showed that the photosynthesis and efficiency of utilizing low light for photosynthesis [α (slope)] are shown to be correlated with thallus morphology wherein very thin tubes/sheets/strips have the highest photosynthesis and steepest slope (Pmax = 58.70 ± 9.67 mg O2 gdw^{-1} h^{-1}; α = 0.60 ± 0.22), while, those heavily calcified thalli have the lowest photosynthesis (Pmax = 3.13 ± 0.92 mg O_2 gdw^{-1} h^{-1}. On the other hand, the light compensation and saturation values did not differ significantly among the different thallus morphology groupings, which may be due to the same shallow intertidal zone where samples are collected. In addition, Dangan-Galon et al. (2013) had the same observation among four (4) collected seaweed species, wherein the sheet form *Ulva lactuca* had the highest photosynthetic rate, while the slightly calcified *Ganonema farinosum* had the lowest photosynthetic rate. However, they did not utilize other P-I curve parameters to elucidate possible relationships. The functional-form grouping can be used as a tool for furthering our understanding of the dynamic interaction between these seaweed species and their surrounding environment. At the same time, it could be used as a proxy for determining the health and status of the marine environment. In addition, Saco (2014) showed that the diel and diurnal patterns of the photosynthetic rates among 34 intertidal seaweed species in Bolinao, Pangasinan, were also affected by their thallus morphology, wherein those calcified thalli do not have an apparent pattern, which might be due to their allocation of resources for structural integrity.

SUMMARY AND RECOMMENDATION

In summary, the 1970s marked the beginning of a significant surge in interest in studying the seaweed community ecology across the country, as evidenced by studies on major islands in Luzon, Visayas, and Mindanao, which continued until the 1990s, facilitated by the ease of conducting assessments using the line transect-quadrat method. The 1990s saw pioneering reproductive biology and growth studies in eucheumatoid, agarophyte, and alginophyte species, driven by the need for an alternative source of seedlings in seaweed farming. From the 2000s to the present, there have been continuous efforts to understand the phenotypic diversity, growth, physiology, and reproductive biology of both natural populations and laboratory-grown eucheumatoid, agarophyte, and alginophyte species, as well as some emerging seaweed species. At the same time, further studies on eucheumatoid species are needed to identify new farming sites, enhance understanding of ‘ice-ice’ disease, and explore the use of biostimulants to promote faster growth rates and improve carrageenan quality. During the 2010s to the present, studies have advanced our understanding of the interactions of seaweed communities with and within their marine environment, as well as changes in seaweed communities over time. Lastly, photosynthetic studies on Philippine seaweeds began around the 1990s, focusing on echuematiod and agarophytes species; however, there have been few studies on the photosynthetic capacity and adaptation of seaweeds.

Studies on community ecology have given us insights into the adaptation of seaweed species in their natural environment, specifically their preference for rocky substrates and monsoondriven variations. However, there are still a lot of gaps that need to be addressed on the quantification of the different ecological services of seaweed communities, such as quantification of seaweed beds i.e., *Sargassum* bed on protecting coastal communities, quantification of support value of seaweed bed among different marine organisms habiting the bed, and possible valuation of seaweed beds as part of the marine protected areas. In the future, studies on the changes of seaweed communities over time should be increased, as we have already gathered several baseline data from the past all over the country. By conducting a comparative analysis of previous and current seaweed community data, we can gain valuable insights into the potential effects of various pressures on the marine environment. In addition, a comparative analysis of seaweed community ecology between pristine and eutrophic areas, considering various degrees of stressors, should be explored to gain insight into the potential of seaweed species as a biomonitoring tool due to their high bioaccumulation potential for nutrients. Lastly, there is still a significant amount of unpublished literature, particularly gray literature, submitted by undergraduate and some graduate students on the seaweed community ecology that needs to be explored. Publication of this kind warrants a thorough review, considering the limited access to the onsite library and the lack of access to their databases or the absence of a database altogether. Furthermore, efforts of this kind position State Universities and Colleges well to make their science more accessible to the public.

There are already numerous studies on the reproductive biology and growth patterns of eucheumatoid species that can be used to mitigate the declining production. It is recommended to use new cultivars/strains as planting materials in seaweed farming, especially those produced from tetrasporophytes, and to apply organic fertilizer to improve their growth and carrageenan content. In addition, continuous studies are recommended on the prevalence of ice disease and epiphytism to provide ways to mitigate the incidence. Furthermore, the lessons from the eucheumatoid farming should be applied to some emerging seaweed species to give sustainable technology for mass cultivation and prevent farm-related problems and consequences. Moreover, reproductive, growth, and biomass analyses provided science-based information for the management of some economically harvested wild-stock seaweeds, specifically regarding the regulated harvest of vegetative thalli to allow other reproductively matured seaweeds to shed spores. For example, the controlled harvesting of vegetative thalli of agarophyte species enables tetrasporic thalli to shed spores, thereby recruiting as former and latter stages, which coincides with natural populations. In addition, these studies provided us with a basis for understanding their response to the improvement of farming techniques and methods. For example, the use of cultivars/seedlings generated from tetrasporophytes is considered robust and genetically sound due to genetic exchanges from their parental genes. Another example is the establishment of seaweed farms on sites with freshwater influx but with high nutrient levels and the use of biostimulants to promote high growth rates and improve carrageenan yield and quality. With the recent advancements in eucheumatoid farming, we can better understand their responses in a changing environment. Thus, this review paper recommends applying this knowledge, such as cultivars/seedlings generated from tetrasporophyte, the use of biostimulants, and others mentioned above, to improve and increase eucheumatoid production in the country. On the other hand, emerging seaweed species with commercial farming potential should undergo further research on their reproduction and growth to refine and define effective farming methods for mass cultivation and production.

As reviewed in this paper, there are still limited studies on photosynthesis in the Philippines; yet, photosynthesis is a primary physiological mechanism of seaweed. The information gained from photosynthesis and growth experiments provides a better understanding of the seaweeds' responses under different physicochemical parameters, with reference to the combined external and internal factors of the species that enable them to achieve optimal responses. For example, information on the saturating light level provides insight into the maximum light level the species can utilize for photosynthesis; thus, species can be cultured up to this light level, especially those species such as *Ulva* and *Asparagopsis* that can be cultured both in the laboratory and outdoor hatchery. Observed photoinhibition at specific light levels could be a basis for adverse light conditions that hinder species growth and development. In addition, information on the slope/alpha provides insights into the efficiency of utilizing low light for photosynthesis; thus, maintaining species in the laboratory under low light conditions would be appropriate. This information would contribute to the continued improvement of the culture technology of some economically important seaweeds, as well as some emerging species.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

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