Aquaculture Reports 45 (2025) 103224

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Mono-trophic seaweed polyculture of sea grapes (*Caulerpa lentillifera*) and *Kappaphycus alvarezii*: A case study from Van Phong Bay, Viet Nam

Lara Elisabeth Stuthmann [a,*], Beatrice Brix da Costa [a,b], Aaron Johannes Cordes [c,d], Hoang Trung Du [e], Andreas Kunzmann [a,1], Karin Springer [b,1]

[a] *Leibniz Centre for Tropical Marine Research, Fahrenheitstraße 6, Bremen 28359, Germany*
[b] *Marine Botany, Faculty Biology/Chemistry, University of Bremen, BIOM, James-Watt-Straße 1, Bremen 28359, Germany*
[c] *Hochschule Bremerhaven, University of Applied Sciences, An der Karlstadt 8, Bremerhaven 27568, Germany*
[d] *University of the Algarve, Estr. da Penha, Faro 8005-139, Portugal*
[e] *Institute of Oceanography, Vietnam Academy of Science and Technology, 01 Cau Da, Nha Trang, Khánh Hòa, Viet Nam*

ARTICLE INFO

Keywords:
Phycoculture
Sustainable Food Production
Green caviar
Co-culture
Economic

ABSTRACT

Kappaphycus alvarezii and *Caulerpa lentillifera* are economical important seaweeds cultivated in Van Phong Bay, Viet Nam, respectively. The complementary light and nitrogen requirements of the seaweeds introduce the opportunity for a mono-trophic seaweed polyculture. Three different set-ups were tested, namely the integration of *K. alvarezii* in sea grape ponds, the integration of sea grape plastic cages on longlines and the polyculture of both species in net cages. The relative growth rates (RGRs) of *K. alvarezii* were highest on longlines, compared to net cages in mono- and polyculture (4.4 ± 0.8 % day^{-1} *vs* 2.1 ± 0.6, 0.6 ± 0.5 % day^{-1}), whereas fragments died off due to warm temperatures and absence of water movement in ponds. Strong recurring water movements at the experimental site caused high losses of *K. alvarezii* fragments (39 % of initial) and impaired growth of delicate *C. lentillifera* causing negative RGRs in all treatments (plastic cages without gauze: -9.8 ± 0.6 % day^{-1}, net cages: -6.4 ± 0.9 % day^{-1}), but with least loss in plastic cages with gauze wrapping (-1.3 ± 0.8 % day^{-1}). $F_v{}'/F_m{}'$ values of both species showed typical midday depression and *C. lentilliferas*´ F_v/F_m were influenced especially by gauze wrapping. Here, we show that the *K. alvarezii* cultivation on longlines with *C. lentillifera* integrated below in inexpensive, self-made, customizable plastic cages with additional gauze protection is the most promising set-up from a physiological and economic point of view for Van Phong Bay and beyond. However, further research is needed before implementation of the system.

1. Introduction

In the last decades, sustainability has become a key concept for aquaculture (Boyd et al., 2020; FAO, 2024; Frankic and Hershner, 2003). Polyculture systems, as well as the cultivation of autotrophic seaweeds, offer an opportunity to move towards a more sustainable aquaculture industry (Duarte et al., 2022; Thomas et al., 2021). Even though, seaweeds contribute already > 50 % of the biomass to the current marine aquaculture sector (FAO, 2024), species are often farmed in mono-cultivation (Neori et al., 2004). Polyculture approaches require the species to thrive in the same production system (species compatibility) and the potential advantage of poly-, over mono-culture is achieved by exploiting the species complementarity (Thomas et al., 2021). Hence, mono-trophic polyculture of seaweeds with complementary properties offers an opportunity to enhance the yield area^{-1}, the bioremediation capacities and/or the security for farmers by product diversification (Kang et al., 2021; Stekoll et al., 2024). In sight of a growing interest in marine macrophytes, e.g. in the context of sustainable blue foods or for climate change mitigation (Duarte et al., 2022; Morales-Nin et al., 2024), there is a need for innovative polyculture systems that are adapted to local conditions and people's needs.

Viet Nam has an enormous geographic potential for aquaculture and is hence globally among the Top 3 producing countries in terms of marine and coastal animal aquaculture in general, as well as marine mollusks and crustaceans (biomass wet weight). Phycoculture plays an important - but currently minor - role in the country with the globally

---

[*] Corresponding author.
E-mail address: lara.stuthmann@leibniz-zmt.de (L.E. Stuthmann).
[1] joint senior-authorship

https://doi.org/10.1016/j.aqrep.2025.103224
Received 16 September 2025; Received in revised form 28 October 2025; Accepted 8 November 2025

13th highest production volume (FAO, 2024). Major species are red seaweeds *Gracilaria*, *Kappaphycus/Eucheuma* and relatively newly introduced species *Caulerpa lentillifera* (sea grapes) (Cai et al., 2021a; Quang et al., 2023; Tri et al., 2022).

The Khánh Hòa province in the Central South of Viet Nam encompasses a total coastline of $>$ 500 km with numerous bays and lagoons and hosts an area of 5198 ha used for aquaculture as of 2020 (Hasan et al., 2020). One of the species farmed in the province is the red seaweed *Kappaphycus alvarezii*, which is globally demanded for a variety of applications, including carrageenan extraction, human nutrition and as bio stimulant in agriculture (Nunes et al., 2024). The seaweed is cultivated in the Khánh Hòa province since 1993, using different cultivation methods, including longlines attached to rafts. Since losses to herbivory are a challenge for *Kappaphycus* cultivation (Hayashi et al., 2017), the use of cages or tubular nets is also known. The biomass is used for local markets and export, especially as for food or carrageen extraction (Diem Hong et al., 2010; Ohno et al., 1996). The Khánh Hòa province is also a hub for aquaculture of green seaweed *C. lentillifera*. The species is cultivated in shaded tidal ponds on the coasts of the province since ∼two decades (Stuthmann et al., 2023b). Sea grapes are valued for the special texture characterized by assimilators, consisting of vesiculate ramuli arranged around a central rachis and an overall beneficial nutritional composition (Stuthmann et al., 2023a; Syakilla et al., 2022). The seaweed́s popularity is growing globally in recent years and farm gate prices are currently rather high, compared to those for eucheumatoids, like *K. alvarezii* (Cai et al., 2021a; Stuthmann et al., 2023a; Terada et al., 2016b). Even though sea grapes are mostly cultivated in ponds or land-based raceway systems, *Caulerpa spp.* farming in lagoons and open water using plastic (screen) cages, cylindrical cages, trays and floating longlines in different water depths has been conducted with different levels of success (de Gaillande et al., 2017; Morris et al., 2014; Tanduyan et al., 2013; Titlyanov and Titlyanova, 2010).

C. lentillifera and *K. alvarezii* are both farmed in Van Phong Bay, the northern most bay in the Khánh Hòa province, providing the basic species´ compatibility for a polyculture. Besides, species compatibility results from the congregation of established processing procedure, retail chains for both species and especially the possibility to position *K. alvarezii* in a cultivation system above the benthic *C. lentillifera*. The farmers could diversify their respective cultivation system, generate additional income and achieve a higher bioremediation capacity, by exploiting the species complementarity. This includes complementary needs for the light and nitrogen supply, with sea grapes favoring rather low-light environments and nitrate over ammonia as a nitrogen source (Guo et al., 2015; Liu et al., 2016; Stuthmann et al., 2020). On the other hand, *K. alvarezii* is low-light adapted, but with regulative mechanisms to cope with changing intertidal conditions, evident by the cultivation on lines right below the surface (Terada et al., 2016b). However, appearance of infectious disease *ice-ice* of *K. alvarezii* grown at higher than optimal temperatures might be a hurdle for pond cultivation (Diem Hong et al., 2010a; Terada et al., 2016b). Besides, sea grapes are siphonous and hence sensitive to mechanical stress, potentially representing a challenge during a cultivation in the sea (Largo et al., 2016a).

This study presents a - to the best of our knowledge - first approach to establish a mono-trophic polyculture of *C. lentillifera* and *K. alvarezii* that is adapted to cultivation in Van Phong Bay, Khánh Hòa province. Three set-ups were tested in an *in-vivo* field trial: The cultivation in the in-shore environment on (1) longlines with integrated plastic cages and (2) joint cultivation of net cages, as well as (3) polyculture in tidal ponds locally used for sea grape cultivation. In this study, cost-efficient self-made plastic cages comparable to those described by Tanduyan et al. (2013) in a cylindric form were used, in order to minimize surface for currents and in two-level design for more space. The commercially available net cages were chosen based on the property that *K. alvarezii* can grow through the mesh. For a high applicability, the longline cultivation, using the tie-tie technique, was replicated based on the farming methods in Van Phong Bay.

We hypothesize, that *K. alvarezii* longline cultivation, as conducted in Van Phong Bay, is the most promising technique to integrate plastic cages wrapped with gauze for protection of delicate sea grapes. In order to investigate the potential of the different polyculture set-ups, especially in regard to their potential complementary light and nitrogen requirements, a compilation of suitable physiological (chlorophyll a fluorescence: F_v/F_m and F_v'/F_m') and growth (relative growth rate, RGR and net harvest) measurements were applied. Considering the economy of the set-ups, we included a small economic snap-shot of the respective material costs.

2. Material and methods

2.1. Study site and biomass

The experimental set-ups for this study were done consecutively at the aquaculture farm VIJA in Van Phong Bay, as well as at the Institute of Oceanography (IO) Viet Nam in Nha Trang (Fig. 1 C). The region has a weather regime mainly driven by the monsoon, with a wet (October - January) and a dry season (January/February - October). Various aquaculture species are grown in Van Phong Bay, including e.g. snails *Babylonia areolata*, shrimp, green mussels (*Perna viridis*), fin fish (sea bass, pompano) and spiny lobster (Fig. 1 F) (FAO, 2020; Hoang et al., 2009; Nghia et al., 2009; Phu et al., 2022a). Besides, commercial cultivation of *C. lentillifera* and *K. alvarezii* take place in different parts of the bay, respectively (Fig. 1 D, E). Whereas sea grapes are cultivated in land-based tidal ponds in the southern part, *K. alvarezii* is cultivated on longlines, attached to rafts in the calmer waters of the northern part of the bay. The initial biomass of both species was retrieved from a *Kappaphycus* farm and sea grapes farm VIJA on 13.05.22, respectively. The red and green algae were cultivated in nets in the bay at IO and in cultivations tanks, before the start of the experiments.

2.2. Experimental design

The experimental design consisted of three set-ups with different treatments, namely (1) the integration of the sea grapes in the longline cultivation of *K. alvarezii* fragments (n = 182) with the treatments of sea grapes being cultivated in plastic cages with (n = 6) and without gauze wrapping (n = 6) and (2) the joint cultivation of *K. alvarezii* and *C. lentillifera* in net cages with the treatment of *Kappaphycus* monocultivation (n = 6) and polycultivation of both species (n = 6) and (3) the integration of *K. alvarezii* in *C. lentillifera* cultivation ponds.

To test the feasibility of (1) the integration of sea grapes in longline cultivation of *K. alvarezii*, a number of 15 longlines were stretched between two main ropes of an approximate length of 50 m at the shore of IO Viet Nam (Fig. 2A). The set-up of longlines was replicated from the farm in Van Phong Bay in the waters of IO Viet Nam. Based on observations from the seaweed farm, 14 *K. alvarezii* fragments (initial weight of 64.1 ± 35.8 g) were attached in a distance of 20 cm using "tie-tie" technique at each line, respectively (Fig. 2 C, i). This led to an initial of 210 replicates of *Kappaphycus* fragments on longlines. For the integration of *C. lentillifera* twelve two-level plastic cages (height: 50 cm, diameter: 27.5 cm) were constructed from perforated plastic mesh (mesh width: 1.3 ×0.8 cm, Fig. 2D, F). Due to reports stating that strong currents prevent the successful sea grape cultivation in the open waters (Largo et al., 2016a), gauze wrapping was applied to six of the twelve plastic cages (Fig. 2G, n = 6). Two plastic cages, each one with and one without gauze wrapping, were attached to six longlines, respectively (initial sea grape stocking 250.7 ± 1.5 g). A stone and a plastic bottle (functioning as buoy) were used to stabilize the cages in the currents (Fig. 2A, E). For experimental measurements, the cages and the longlines were detached and brought to shore (Fig. 2G).

Besides, *C. lentillifera* were integrated in net cage cultivation of the red algae (2). Twelve net cages were purchased at a local fishing shop (height: 90 cm, diameter: 35 cm). The mesh size of the net (2 ×1.2 cm)

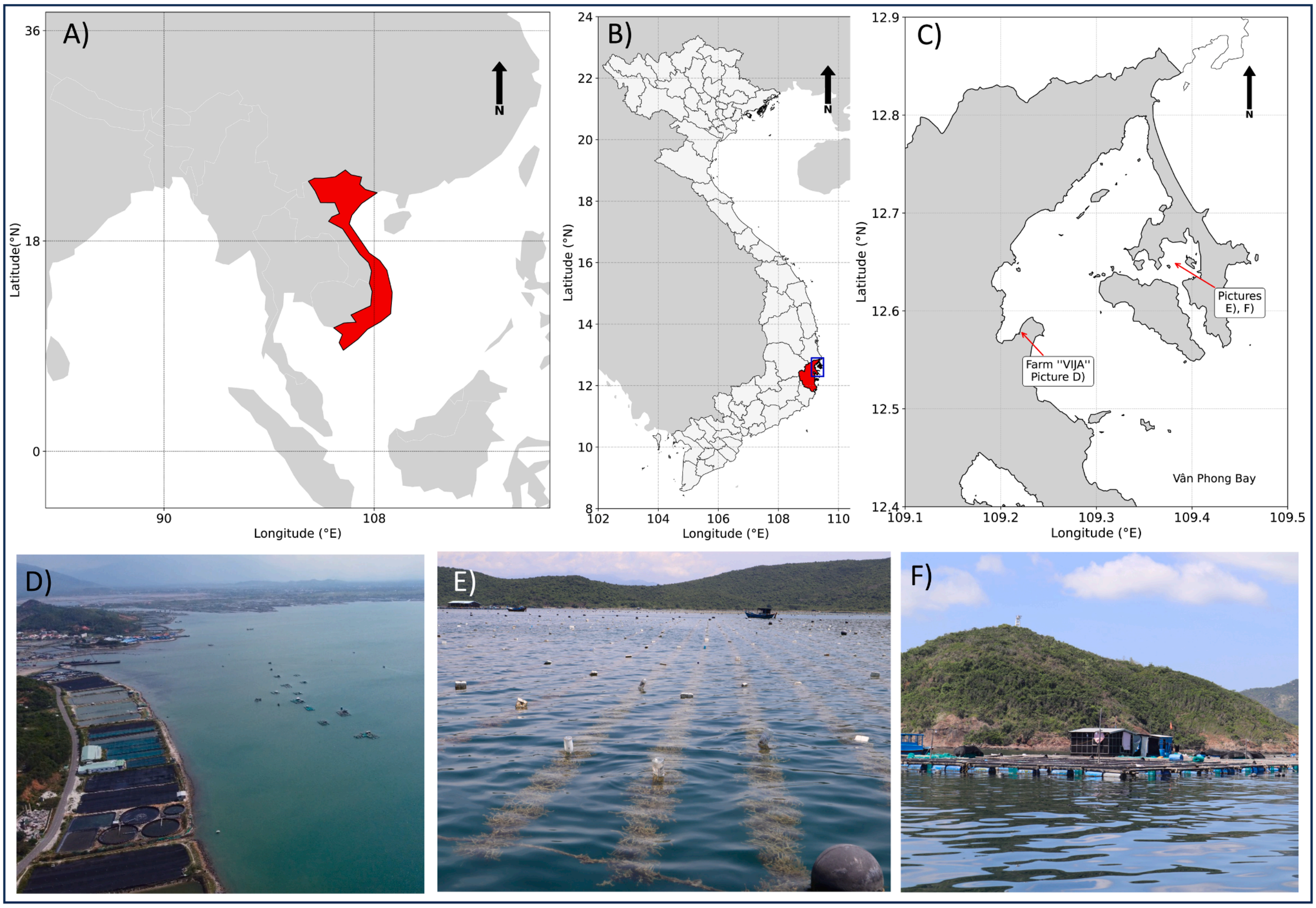

Fig. 1. Map of A) Viet Nam marked in with B) the Khánh Hòa province (red) and the location of Van Phong Bay annotated in blue. Map of C) Van Phong Bay with the sampling locations and in the north and south of the bay. Pictures show where aquaculture takes places D) along the coastline in tidal ponds, as well as in the bay area, like E) *Kappaphycus alvarezii* on longlines and F) lobster farming in cages. Note: Map lines delineate study areas and do not necessarily depict accepted national boundaries.

allowed *C. lentillifera* thalli to slip through and therefore the lower part was tied of and wrapped with gauze material (Fig. 2B). Six net cages used for the *K. alvarezii* mono-cultivation were not tied off (Fig. 2H, n = 6), leaving the fragments with more space, compared to the polyculture with sea grapes (Fig. 2L, n = 6). The net cages were stocked with the initial biomass (*C. lentillifera*: 350.3 ± 0.3 g; *K. alvarezii*: 695.8 ± 33.9 g), before attaching them to a rope in close proximity to the longlines (Fig. 2A).

In order to investigate the potential of *K. alvarezii* cultivation in sea grape ponds, *Kappaphycus* longlines were prepared in a similar manner than described for the first set-up. The lines were hung between bamboo sticks in a sea grape pond at farm VIJA. However, after two weeks, the *K. alvarezii* fragments showed strong signs of die-off and the experiment was stopped. The three different experimental set-ups were all run between May - July 2022. The start and of the experiments, as well as the quantification of response variables differ, due to logistic reasons. Please consult Supplements I and II for details on the exact experimental runs, respectively.

2.3. Environmental parameter

The environmental parameters salinity (S_A), temperature (C°), oxygen (% saturation) and pH were quantified using a Manta 2 multiparameter probe (Eureka, Texas, USA). Light irradiances of photosynthetically active radiation (PAR) were measured using a LI-1400 data logger with a 2-π and/or 4-π sensor (LICOR Biosciences, USA).

Water samples (20 mL) for analysis of nitrate and nitrite, ammonium and phosphate were filtered using a 0.45 µm syringe filter and stored in plastic bottles at −20°C until analysis. The analysis of the dissolved inorganic nitrate and nitrogen (NO_x) was determined following the procedures of García-Robledo et al. (2014), whereas quantification of phosphate was following the procedures of Ringuet et al. (2011). Ammonium was quantified following the procedures of Ringuet et al. (2011) and Yu et al. (1994). For the measurements of the absorbance an infinite 200 PRO microplate reader (TECAN, Austria) was used in all cases.

Environmental water parameters (salinity, temperature, pH, oxygen) were quantified at different depths (0–3 m) and times over the tidal cycle, light irradiances of PAR at different experimental set-ups and sea water samples for nutrient measurements at IO Viet Nam and the experimental pond at VIJA were quantified at different sampling days, respectively (Supplements II).

2.4. Growth, harvest and morphology

For quantification of the relative growth rate (RGR), the following formula was used:

$$\text{RGR } (\%\ \text{day}^{-1}) = ((\text{LN } (N_t) - \text{LN } (N_0))/\ t) * 100, \tag{1}$$

with N_t and N_0 being the fresh weight (FW) at time t and 0, respectively (Cai et al., 2021b). The net harvest (g g FW initial (in.)$^{-1}$ day^{-1}) was used as a measure for the harvest based on the biomass that was initially used as starter seedlings, considering the loss of *K. alvarezii*

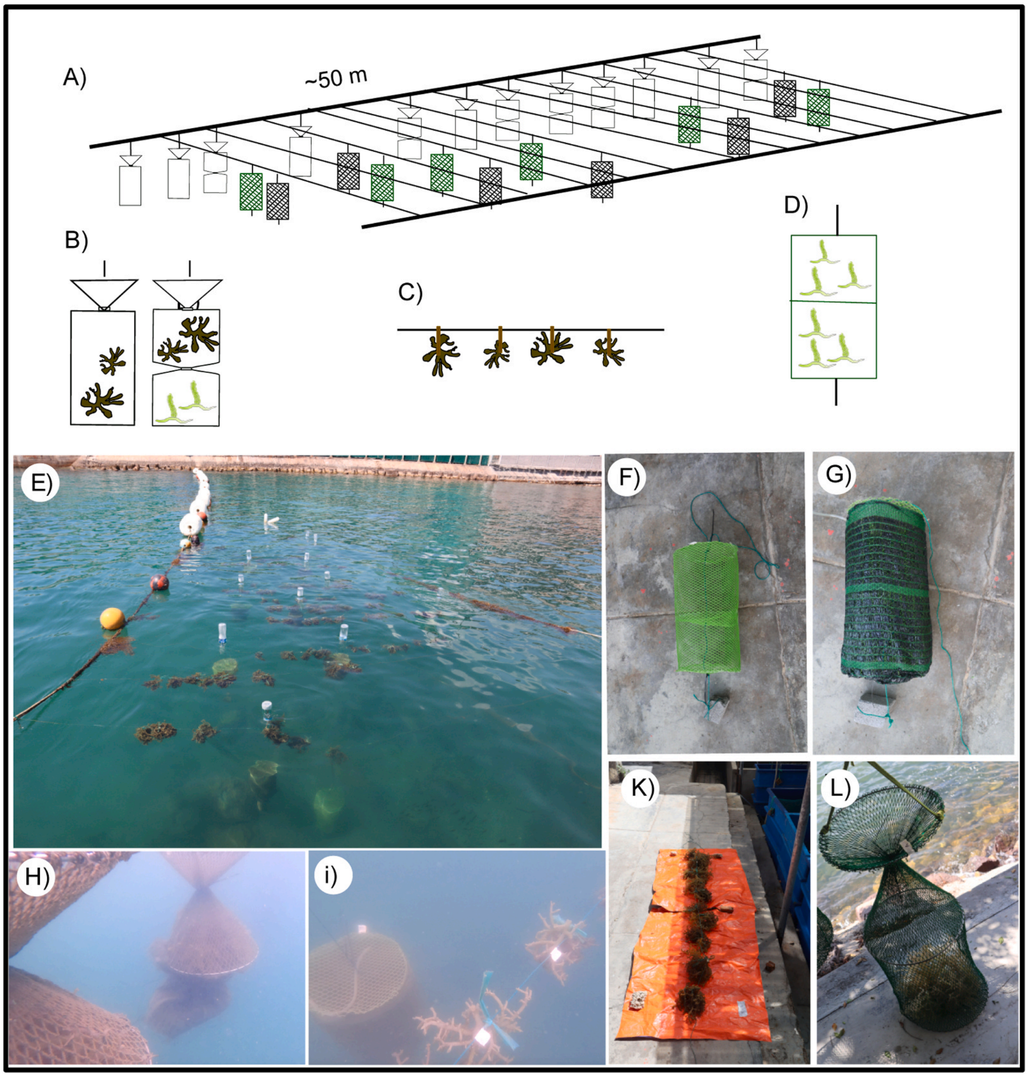

Fig. 2. A) Set-up of the field experiment in Nha Trang, Viet Nam, with the B) net cages for *Kappaphycus alvarezii* mono- and polyculture with *Caulerpa lentillifera* being attached to main rope and C) longlines with *K. alvarezii* fragments attached using the *tie-tie* technique. D) Plastic cages with *C. lentillifera* biomass were attached on longlines. Pictures of the E) set-up, the plastic cages F) without and G) with gauze wrapping, H) net cages, i) longlines and plastic cages in the water, K) *K. alvarezii* longlines during measurements on land and L) net cages on land are shown.

fragments (e.g. through wave action), as well as the time of growth (t).

It was calculated following the formula:

Net harvest (g g FW in.$^{-1}$ day^{-1}) = $(N_t - N_0) / (N_t * t)$

Morphological differences, as well as harvestable biomass for *C. lentillifera* were calculated as % Frond of total. It was quantified by separating and weighting the algae's fronds and stolons and calculated based on the formula:

$$\% \text{ Frond total} = \text{share Fronds (g)} * (100/ (\text{weight fronds (g)} + \text{weight stolons (g)}) \qquad (3)$$

The response variables RGR and % Frond of total were quantified at the end of the experiment, when not indicated differently.

2.5. *Chlorophyll a fluorescence measurement*

The maximum quantum efficiency of photosystem II (PSII, F_v/F_m) and the PSII maximum efficiency (F_v'/F_m') were quantified using a portable Diving-pulse-amplitude modulated (PAM) chlorophyll fluorometer (Walz, Effeltrich, Germany). The maximum quantum efficiency of PSII indicates changes in the efficiency of non-photochemical quenching. Hence, F_v/F_m values are widely used as a sensitive indicator of photosynthetic performance. Values below the specific optimum are interpreted as a sign of physiological stress, like photoinhibition (Maxwell and Johnson, 2000). For quantification of F_v/F_m the seaweeds were dark adapted for 7 min. The measurements of F_v'/F_m' were conducted at steady state light conditions in the respective cultivation set-up. Maximum quantum yield of PSII was measured at the end of the experiment, if not indicated differently in replicates of 4–7 (Supplements II). The diurnal change of F_v'/F_m' was quantified every second hour between 6 a.m. and 6 p.m. over the course of two days (Supplements II). A number of 4–6 replicated measurements were quantified for each cultivation set-up, depending on the prevailing environmental conditions. Simultaneously, the light irradiances of photosynthetically active radiation (PAR) in the air were quantified using a 2- and 4-π sensor, respectively.

2.6. *Initial investment estimation*

The cost of material was inquired at the local market in summer 2022, where farmers would likely also obtain their equipment. The monetary value was converted from Vietnamese dong (VND) to United States dollar (USD) using the rate 1000 VND = 0.043 USD.

2.7. Data analysis

The statistical analysis, as well as the graphical outputs were conducted using the software R in combination with R-studio (R Core Team, 2019) and the meta package tidyverse (Wickham et al., 2019). Outliers were identified using Grubb´s test through the webpage GraphPad (https:// www.graphpad.com/quickcalcs/Grubbs1.cfm, accessed on 15.03.2023; $p < 0.05$). Levene´s test (homogeneity of variance, $p > 0.05$) and Shapiro-Wilk test (normal distribution, $p > 0.05$) were conducted for each data set. Depending on the outcome of the test a parametric or non-parametric test was used to identify the effects on the response variables. A one-way ANOVA was used to test the effect of between-subject effects. Tukey´s honestly significant difference (HSD) *post-hoc* test was run afterwards. In case the requirements were not met, a Kruskal-Wallis test with a Dunn-Bonferroni *post-hoc* test was used. All statistical outputs are presented in the Supplements (III - V).

3. Results

3.1. Environmental parameters

The snapshot of environmental conditions in the experimental environments revealed potential trends of higher temperatures and salinities in the pond, compared to the experimental location in the sea (Table 1). Salinity and temperature at the experimental in-shore location were strongly influenced by the tidal cycle and throughout the water column with an inverse correlation: At high tide and at the largest depth the temperature values were lowest (~27 °C), whereas the salinity showed highest values (Supplements VI). The mean of nutrient levels (mean±SD, $n = 8$) in the period from May to June at the experimental site at IO showed values of 2.9 ± 2.1 µmol L^{-1} nitrate+nitrite, 4.8 ± 3.7 µmol L^{-1} ammonium and 0.8 ± 1.0 µmol L^{-1} phosphate. The irradiance levels of PAR at the experimental cultivation site of *K. alvarezii* and *C. lentillifera* with longlines, plastic cages and net cages varied strongly among the different treatments and throughout the water column. Values decreased from the surface to a level of 25 % at a water depth of two meters (Table 2). The *K. alvarezii* longlines, as well as the plastic and net cages provided considerable shade for the organisms below and inside, with the net cages showing the lowest irradiances present (Table 2).

3.2. Relative growth rates and morphology

K. alvareziis´ RGRs were overall significantly higher compared to *C. lentilliferas*´, when analyzed regardless of the respective cultivation method, but excluding the fragments integrated in the sea grape pond (Chi square=38.46, $p < 0.001$, df=1, Figs. 3, 4). The *K. alvarezii* fragments implemented in the experimental pond got white and spots and were considered dead after 14 days (Fig. 5A, B). The fragments at the longline showed the highest RGRs (4.4 ± 0.8 % day^{-1}), compared to the cultivation in net cages in mono- and polyculture with means of 2.1 ± 0.6 and 0.6 ± 0.5 % day^{-1}, respectively ($F(2,91)= 65.86$, $p < 0.001$). The RGRs of the longline cultivated fragments ranged from 2.4 % to 6.2 % day^{-1}. However, the cultivation at longlines led to high losses of fragments. Only a count of 168 (80 % of initial) and 82 (39 % of initial) fragments from the initially implemented 210 were still present after 21 and 41 days, respectively. The net harvest (g g FW, fresh weight initial (in.) day^{-1}) shows the farmers´ potential crop of *K. alvarezii* per day per g of initial seeded biomass, with lost fragments included in the calculation (Fig. 3B). The high RGRs of *K. alvarezii* fragments (Fig. 3A) remaining at the longlines caused, even though not statistically significant (Chi square=1.4531, $p = 0.1176$, df=2), still a trend of a higher mean net harvest (Fig. 3B).

Table 2
Irradiances of photosynthetically active radiation (PAR) quantified at the experimental cultivation site of *Kappaphycus alvarezii* and *Caulerpa lentillifera* at the Institute of Oceanography (IO), Nha Trang, Viet Nam using a 2-π sensor on 21.05.2022 in the time between 10:00 a.m. and 10:30 a.m. Data are presented as mean±standard deviation.

Location	Irradiances (µmol photons m^{-2} s^{-1})	Replicates (n)
Surface	921 ± 513	11
1 m depth	826 ± 384	11
2 m depth	234 ± 27	9
Below *K. alvarezii* longline	551 ± 323	4
C. lentillifera plastic cages without gauze	349 ± 245	6
C. lentillifera plastic cages with gauze	79 ± 68	6
Inside *K. alvarezii* net cages	278 ± 173	4
Inside *C. lentillifera* net cages	9 ± 7	6

The RGRs of *C. lentillifera* were negative throughout the cultivation experiment, ranging between means of −1.3 and −9.8 % day^{-1} (Fig. 4A). *C. lentilliferas*´ RGRs were affected by the cultivation method (plastic cage *vs* net cage; $F(1,10)= 8.78$, $p < 0.05$), as well as the status of gauze wrapping ($F(1,10)= 288.76$, $p < 0.001$). Sea grapes cultivated in the plastic cages without gauze wrapping lost the most weight (-9.8 ± 0.6 % day^{-1}), followed by net cage cultivated alga with gauze wrapping (-6.4 ± 0.8 % day^{-1}, Fig. 4A). However, the values for the cultivation in the plastic cages with gauze wrapping were, with a mean of -1.3 ± 0.8 % day^{-1}, significantly higher (Fig. 4A; $F(2,10)= 148.8$, $p < 0.001$). The morphology of sea grapes seemed to be affected by wave exposure: The presence of gauze wrapping led to a significantly higher proportion of fronds (46.4 ± 9.0 % Frond of total), compared to the algae without gauze as protection (26.4 ± 11.6 % Frond of total; $F(1,7) = 8.49$, $p < 0.05$, Fig. 4B). Additionally, thalli with lower wave exposure showed rather delicate stolons with considerably long fronds (Fig. 5C, D, F), compared to seemingly more sturdy thalli of sea grapes with higher wave exposure (Fig. 5E). Sea grapes that were cultivated as a pilot (without quantitative data) in tray cultivation at a sheltered place at the pier very close to the experimental cultivation site showed thalli morphologies that reminded of those from the pond cultivation (Fig. 5G). However, these are only observations and hence the results should be interpreted with care and investigated further.

3.3. Chlorophyll a fluorescence measurement

The F_v/F_m values of *K. alvarezii* between longline and net cage cultivation were similar with means ranging from 0.55 ± 0.08–0.59 ± 0.04 (Chi square=1.481, $p = 0.4768$, df=2; Table 3). F_v/F_m values of *C. lentillifera* showed significantly smaller values, when cultivated in plastic cages without gauze wrapping, compared to plastic and net cages with additional gauze (0.46 ± 0.09, $F(2,11)= 8.448$, $p < 0.01$; Table 3).

Table 1
Environmental parameters absolute salinity (S_A), oxygen saturation (% saturation), pH, temperature (°C) presented as mean±standard deviation (SD) quantified at the Institute of Oceanography (IO), Nha Trang, Viet Nam and at the pond VIJA, where the cultivation experiment took place, respectively. The measurements at the IO and VIJA were conducted on a single day and over eight days, respectively.

Location	Salinity	Oxygen	pH	Temperature	Replicates
	(S_A)	(% Saturation)		(°C)	(n)
Experimental site IO	32.7 ± 1.2	109.0 ± 7.8	8.5 ± 0.04	28.8 ± 0.8	106
Experimental site pond	33.7 ± 0.04	79.2 ± 4.7	8.4 ± 0.02	30.6 ± 0.1	10

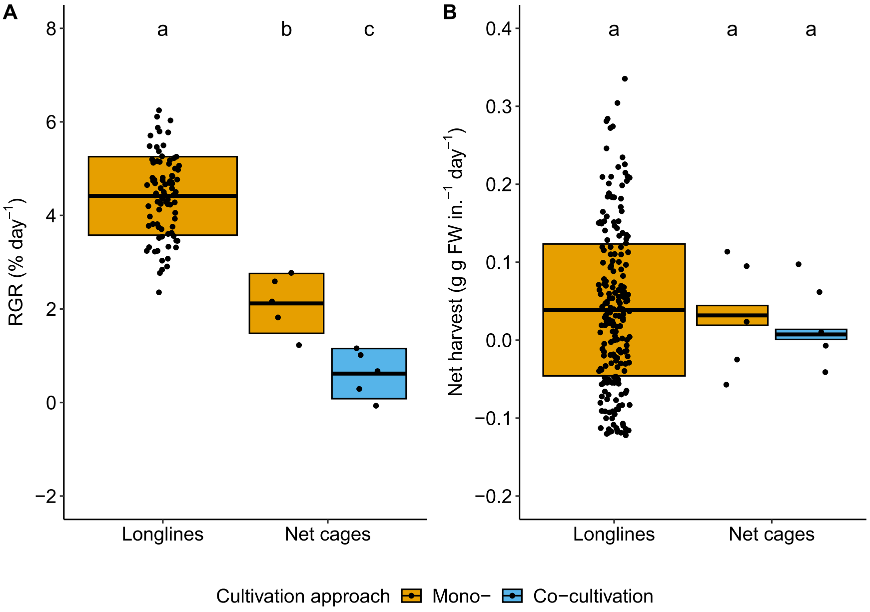

Fig. 3. Relative growth rates (RGR, % day^{-1}, of A) *Kappaphycus alvarezii* cultivated at the Institute of Oceanography (IO), Nha Trang, Viet Nam on longlines and in net cages with and without *C. lentillifera* after 41 and 33 days of cultivation and n = 82 and n = 5, respectively. Only the fragments that were still present after 41 days were considered. B) Net harvest per day (g g FW, fresh weight initial (in.) day^{-1}) of *K. alvarezii* cultivated on longlines (n = 210) and in net cages with (n = 5) and without (n = 5) *C. lentillifera*. Also missing fragments were included. Data are presented as mean±standard deviation, indicated by the middle line and the box, respectively. Black dots indicate individual data points. To avoid overlap of data points a small amount of noise was added to each point using the jitter function in RStudio. Different letters indicate statistical differences between the treatments (One-Way ANOVA with Tukeys HSD *post hoc* test and Kruskal Wallis test).

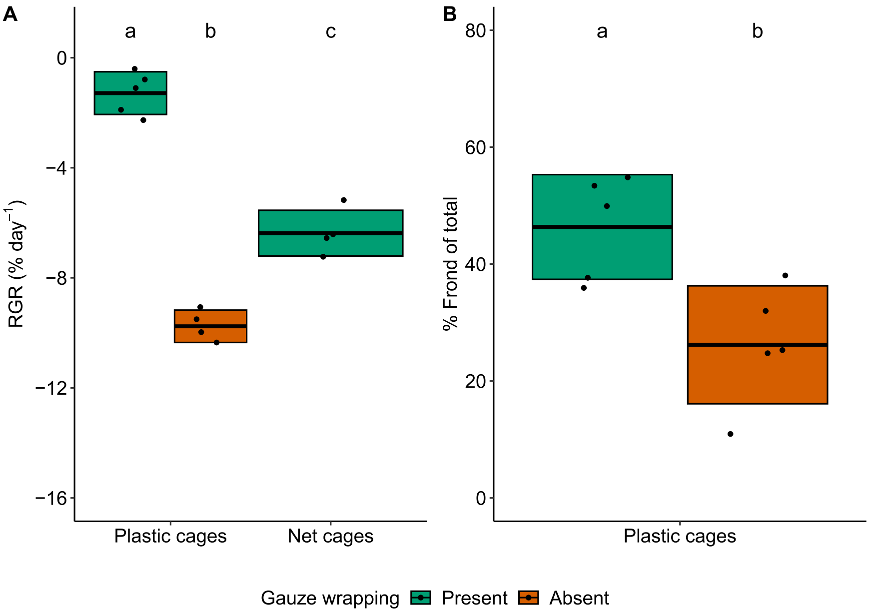

Fig. 4. Relative growth rates (RGR, % day^{-1}) of A) *Caulerpa lentillifera* cultivated at the Institute of Oceanography (IO), Nha Trang, Viet Nam in plastic cages with and without gauze wrapping and in net cages after 24 and 33 days of cultivation (n = 4–5), respectively and B) the % Frond of total of *C. lentillifera* in plastic cages with and without gauze wrapping. Data are presented as mean ± standard deviation, indicated by the middle line and the box, respectively. Black dots indicate individual data points. To avoid overlap of data points a small amount of noise was added to each point using the jitter function in RStudio. Different letters indicate statistical differences between the treatments (One-Way ANOVA with Tukeys HSD *post-hoc* test).

The intensity of irradiances of PAR changed over the day during the diurnal measurements (Fig. 6A). Following this pattern, the corresponding F_v'/F_m' values of the red seaweed showed a midday depression in accordance with the highest PAR values (Fig. 6C). F_v'/F_m' values of *C. lentillifera* fluctuated the most for the algae cultivated in plastic cages without gauze wrapping with lowest values around noon (Fig. 6B).

3.4. *Costs of material*

The net cages cultivation was most expensive for *K. alvarezii*, as well as *C. lentillifera* cultivation regarding the costs for material (Table 4). The cultivation of *K. alvarezii* at longlines was the most efficient in terms of material costs.

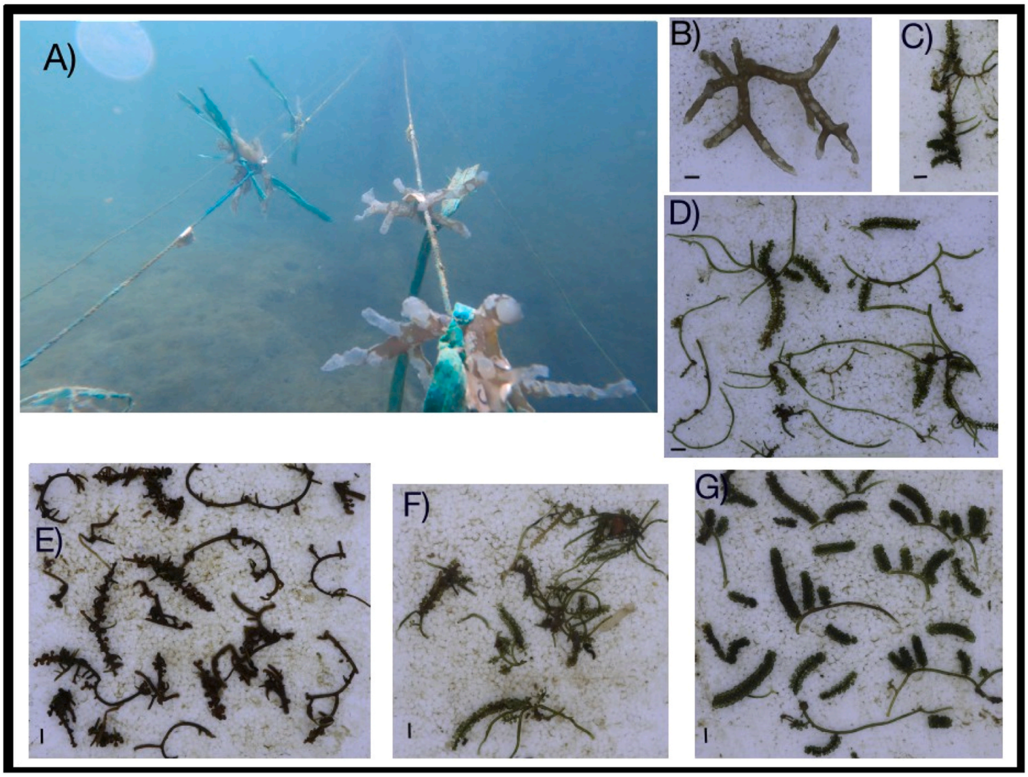

Fig. 5. Pictures of *Kappaphycus alvarezii* A) at longlines and B) in close-up after 15 days in the sea grape pond and *Caulerpa lentillifera* C) after 15 days in net cage cultivation and at the end of the experiment when cultivated in plastic cages D) with and E) without gauze wrapping and F) net cages. G) Sea grapes after tray cultivation at a sheltered place.

Table 3
F_v/F_m values of *Kappaphycus alvarezii* and *Caulerpa lentillifera* in different cultivation methods at the Institute of Oceanography (IO), Nha Trang, Viet Nam, calculated after the total experimental run (days) and in replicate numbers (n). The data are expressed as mean±standard deviation. Different letters indicate significant differences between the means. Tested with a one-way ANOVA or Kruskal-Wallis test with a *Post-hoc* test.

Species	Set-up	Run	F_v/F_m	n
		days		
K. alvarezii	Longline	41	0.55 ± 0.08^a	83
	Net cages mono-cultivation	33	0.56 ± 0.05^a	5
	Net cages polyculture	33	0.59 ± 0.04^a	5
C. lentillifera	Plastic cages no gauze	24	0.46 ± 0.09^a	5
	Plastic cages gauze	24	0.66 ± 0.05^b	5
	Net cages	33	0.65 ± 0.11^b	4

4. Discussion

The close proximity of *K. alvarezii* and *C. lentillifera* cultivation sites in Van Phong Bay with established production chains, as well as their complementary light and nutrient demands suggested a high potential for a mono-trophic seaweed polyculture. This research confirms the hypothesis, that the integration of sea grapes in *K. alvarezii*′s longline cultivation is the most promising technique, with potential especially for the cultivation of sea grapes in shaded plastic cages. The results suggest that irradiances of PAR, water movement and temperature are essential yield determinants for site selection that should be considered with strong attention when working towards an up-scaling of the system and future designs of polycultures.

The RGRs of *K. alvarezii* fragments in the inshore area correspond to values quantified previously for *K. alvarezii* in Nha Trang and Cam Ranh Bay (Diem Hong et al., 2010; Hung et al., 2019, 2009). However, the experiments took place during the warmest months in the Khánh Hòa province (ISPONRE, 2009) and even higher growth rates are expected during the cold season (Diem Hong et al., 2010; Hung et al., 2019, 2009). The considerably warm temperatures (Table 1) and low water motion in the pond have likely caused the whitening and softening of *Kappaphycus*′ thalli (Fig. 5 A, B) and prevented their survival. The symptoms are well-documented signs of the ice-ice syndrome (Tahiluddin and Eldani-Tahiluddin, 2024). The syndrome is driven by unfavorable environmental conditions, especially increased temperatures and bacterial infection, and can lead to decreased biomass and carrageenan yields (Ward et al., 2022). In general, water motion is an important parameter for successful *K. alvarezii* cultivation and significantly correlated to growth (Ask and Azanza, 2002; Glenn and Doty, 1992; van Oort et al., 2025). However, the experimental location of the *Kappaphycus* longline culture was characterized by very strong water movements, especially driven by winds in the afternoon and influx from a river explaining the changes in salinities (3.1). The strong motions caused the majority of *K. alvarezii* fragments at longlines to be lost. Loss of fragments was regularly reported and usually caused by herbivory or wave action (van Oort et al., 2025). Different cultivation structures, including nets and cages, are developed to counteract such losses (Kasim et al., 2024; Kasim and Mustafa, 2017). However, although the net cages in this experiment prevented the loss of fragments, the RGR′s of longline cultivated seaweeds were so high, that even the net harvest showed a trend of higher values (Fig. 3B). This is in line with research of van Oort et al., who found that the longline cultivation outperformed the tube-net and cage methods during an experiment in Indonesia with fouling of mud and epiphytes reported as the major reason (van Oort et al., 2025). In this experiment, the significant decrease of RGR and net harvest of fragments cultivated in net cages in polyculture with sea grapes (Fig. 3), indicates that a space limitation might have restricted the seaweed growth. This could be adjusted by lower initial seedling weight.

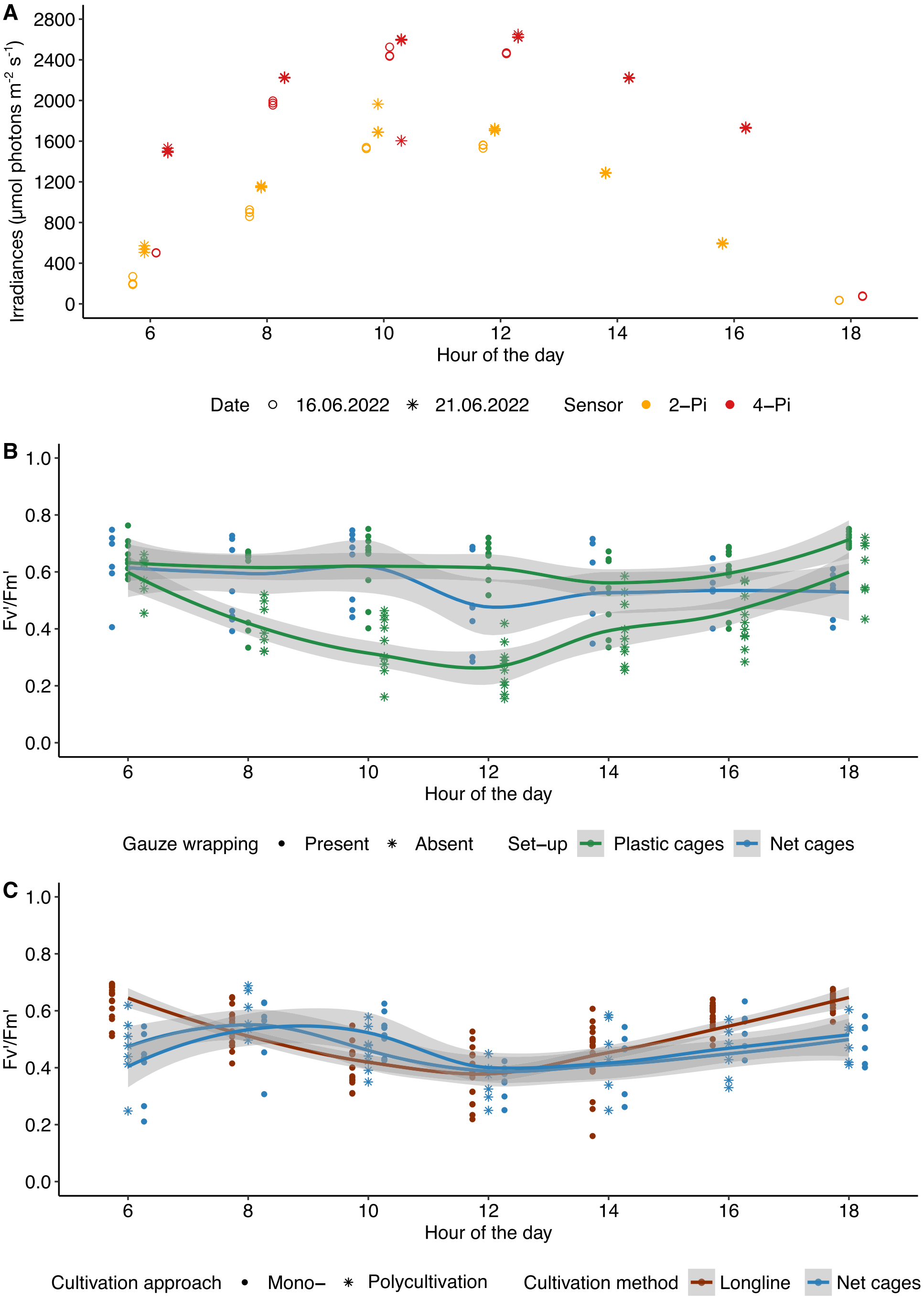

Fig. 6. Diurnal measurements between 6 a.m. and 6 p.m. (for 12 h of the day) of A) light irradiance (µmol photons m^{-2} s^{-1}) using a 2- and 4-π sensor at two different dates in June 2022 at the experimental two-layer cultivation at the Institute of Oceanography (IO) in Nha Trang, Viet Nam, as well as the maximum efficiency of photosystem II in a steady state light environment (F_v'/F_m) of B) *Caulerpa lentillifera* in plastic and net cages and with or without gauze wrapping and C) *Kappaphycus alvarezii* on longlines or in net cages.

However, fouling of the nets was observed (Fig. 2H) and could have contributed to a decreased growth in net cages compared to the longline as well. *K. alvarezii* fragments on longlines and *C. lentillifera* in plastic cages without gauze wrapping were exposed to the highest irradiances (Table 1) and their F_v'/F_m' values showed a typical midday depression (Fig. 6 C) in accordance with the highest values of PAR (Fig. 6A) (Jiang et al., 2018; Terada et al., 2016b, 2016a). The pattern was less pronounced for fragments in net cages and fouling could have caused an additional shading effect. F_v'/F_m' measurements varied considerably within the same species and treatment, which can be attributed to differences in the microenvironments of the algae (Terada et al., 2016a). However, the decrease of F_v'/F_m' at high midday irradiances is likely a regularity process limiting the transport of electrons through PSII, acting as a protective mechanism from excess light energy through thermal dissipation. The recovery of F_v'/F_m' in the afternoon at lower irradiances and similar values of F_v/F_m values between treatments (Table 3) suggest photoadaptation (Häder et al., 1998; Terada et al., 2016b, 2016a). Hence, the study suggests that water temperature and water movement are the most profound yield determinants of *K. alvarezii* in the context of this cultivation site.

Even though, *C. lentillifera* did not show positive RGRs, the net biomass loss was minimal in the plastic cages with gauze wrapping

Table 4
Costs (as United States dollar, USD) of material for different polyculture set-ups sourced from markets in Nha Trang, Viet Nam. United States dollar (USD) was converted from Vietnamese dong (VND) using the rate 1000 VND = 0.043 USD.

			Longlines (per m)	Plastic cages without gauze	Plastic cages with gauze	Net cages
Material	unit	USD/unit	Units needed for respective cultivation method			
Gauze material	1 m	0.87	-	1	-	-
Perforated plastic	1 m	1.28	-	1.5	1.5	-
Plastic line	1 m	0.3	1	-	-	-
Tie-tie rope	100 g	0.043	1	-	-	-
Net cages	1 piece	3.63	-	-	-	1

(Fig. 4A) and the share of frond was high (Fig. 4B). Sea grapes are a siphonous species (Zubia et al., 2020) and their fragile thalli can be sensitive to strong physical forces, like water currents. Largo et al. (2016) cultivated *C. lentillifera* as an extractive species in an open water integrated multi-trophic aquaculture (IMTA) system in The Philippines using baskets. Even though slight growth was observed during the first three weeks, the seaweeds disintegrated during stormy waters and waves (Largo et al., 2016b). The high loss of biomass in the plastic cages without gauze wrapping was likely caused by the higher exposure to the strong waves during stormy weather and high tidal ranges in the bay. This is also indicated by the observed differences in morphologies between cultivation methods and set-ups (Figs. 5C-G, 3.2). *Caulerpa spp.* are known to be morphologically plastid as a response to different environmental parameters, among others temperature, salinity (Estrada et al., 2020) as well as light and water movement (Calvert, 1976). *C. lentillifera* cultivated without gauze wrapping were exposed to the highest irradiances (Table 2) and significantly decreased F_v/F_m indicate that they suffered from photoinhibition (Stuthmann et al., 2020). Hence, in regard to the sea grapes, water motion and light irradiances were the most yield determining in the context of this study site.

Growth data, as well as the investment costs (Table 4) suggest that the *K. alvarezii* longline cultivation with sea grapes in plastic cages is more promising that the net cage. Plastic cages were self-made and the investment costs were low, compared to the commercially available net cages (Table 4). However, this comparison did not evaluate the cultivation management, including time rates for planting and harvesting. Research comparing tubular netting and tie-tie technique of *K. alvarezii* from Marambaia Bay, Brazil found that tubular netting method was considerably more effective and the cultivation management was > 50 % faster (de Góes and Reis, 2011). However, the authors included an additional net to protect longline cultivation from herbivory. Future research needs to consider the cultivation management as well.

The main obstacle for a successful polyculture was the strong water movement at the experimental location. However, the waters are considerably calmer at the *K. alvarezii* production site in the north of Van Phong Bay, due to the land-locked position (Fig. 1C) and farmers employ already successfully the tie-tie longline cultivation. This study did not investigate the bioremediation potential of the seaweed polyculture. However, the complementary N preferences of the species could enhance the nutrient take up from fed aquaculture, like spiny lobsters, in Van Phong Bay (Fig. 1F) and potentially mitigate negative impacts (Phu et al., 2022b). In sight of the water depth in Van Phong Bay, sea grapes could be implemented below the longlines in the water column according to favorable irradiance levels in order to avoid the use of gauze-wrapping. The gauze wrapping was essential to shade the sea grapes and prevent photooxidation, indicated by significantly decreased F_v/F_m values when cultivated without gauze, as well as to protect the delicate fronds from high water movement. Salinity levels deeper in the water column are also expected to be higher and more stable, potentially enabling sea grape cultivation also during the rainy season (Ly, 1999). This could lead to a year-around supply of fresh sea grapes. Considering the economical favorable thallus structure of sea grapes farmed in trays at the sheltered area of the experimental site (Fig. 5G), different cages and tray-systems for sea grape farming could be investigated. However, taking the importance of sustainability principles in the aquaculture sector in account, as well as Viet Nam's efforts to reduce marine plastic pollution, alternatives to plastic should be considered, especially when establishing new phycoculture systems (Dang et al., 2021; Trang et al., 2023).

5. Conclusion

This study provides a basis for a mono-trophic seaweed polyculture in Van Phong Bay, Viet Nam, combining *K. alvarezii* and sea grapes (*C. lentillifera*). Integration of sea grapes in *K. alvarezii* longline cultivation, particularly in shaded plastic cages, proved to be the most efficient method. The yield determinants of highest importance for the polyculture were water movement, temperature, irradiances of PAR, as well as fouling and they should be considered for future site selections. *K. alvarezii* cultivation in the pond environment failed due to appearance of ice-ice syndrome, possibly related to high temperatures and lack of water movement. While K. *alvarezii* showed high growth at longlines, fragment loss following high wave action posed a challenge. Calmer waters in the north of Van Phong Bay might provide a better cultivation ground for the polyculture. Further research should explore the upscaling in Van Phong Bay, the bioremediation potential of the system, as well as sustainability concerns regarding the use of plastics further.

CRediT authorship contribution statement

Aaron Johannes Cordes: Writing – review & editing, Investigation. **Andreas Kunzmann:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Hoang Trung Du:** Writing – review & editing, Resources. **Karin Springer:** Writing – review & editing, Supervision, Funding acquisition. **Beatrice Brix da Costa:** Writing – review & editing, Investigation. **Lara Elisabeth Stuthmann:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis.

Funding

This work was supported by Leibniz Centre for Tropical Marine Research inhouse funding and AJ Cordes was supported by Kellner&-Stoll-Stiftung.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Aaron Johannes Cordes reports financial support was provided by Kellner-Stoll Foundation for Climate & Environment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to the staff of Institute of Oceanography and the sea grape farm VIJA for the support in the field and to Mia Pribbernow for the help with the sampling handling. The authors would like to thank that team of Institute of Oceanography (IO) Viet Nam, the colleagues from the Marine Labs at ZMT Bremen for their support with measurements. Special thanks to the seaweed farmers of VIJA and *Kappaphycus* in Van Phong Bay.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2025.103224.

Data Availability

The data related to this study are uploaded with the following DOI https://doi.org/10.6084/m9.figshare.29940989.v1 and can be accessed with the following link https://figshare.com/articles/dataset/Relative_growth_rates_RGRs_Net_weight_light_irradiances_environemntal_data_salinity_pH_oxygen_saturation_temperature_and_nutrient_measurements_related_to_the_publication_of_Stuthmann_et_al_/29940989.

References

Ask, E.I., Azanza, R.V., 2002. Advances in cultivation technology of commercial eucheumatoid species: a review with suggestions for future research. Aquaculture 206, 257–277. https://doi.org/10.1016/S0044-8486(01)00724-4.

Boyd, C.E., D'Abramo, L.R., Glencross, B.D., Huyben, D.C., Juarez, L.M., Lockwood, G.S., McNevin, A.A., Tacon, A.G.J., Teletchea, F., Tomasso, J.R., Tucker, C.S., Valenti, W. C., 2020. Achieving sustainable aquaculture: historical and current perspectives and future needs and challenges. J. World Aquac. Soc. 51, 578–633. https://doi.org/10.1111/jwas.12714.

Cai, Y., Li, G., Zou, D., Hu, S., Shi, X., 2021. Rising nutrient nitrogen reverses the impact of temperature on photosynthesis and respiration of a macroalga *Caulerpa lentillifera* (Ulvophyceae, Caulerpaceae). J. Appl. Phycol. 33, 1115–1123. https://doi.org/10.1007/s10811-020-02340-9.

Cai, J., Lovatelli, A., Aguilar-Manjarrez, J., Cornish, L., Dabbadie, L., Desrochers, A., Diffey, S., Garrido Gamarro, E., Geehan, J., Hurtado, A., Lucente, D., Mair, G., Miao, W., Potin, P., Przybyla, C., Reantaso, M., Roubach, R., Tauati, M., Yuan, X., 2021. Seaweeds and microalgae: an overview for unlocking their potential in global aquaculture development. FAO. https://doi.org/10.4060/cb5670en.

Calvert, H.E., 1976. Culture studies on some Florida species of *Caulerpa*: Morphological responses to reduced illumination. Br. Phycol. J. 11, 203–214. https://doi.org/10.1080/00071617600650481.

R. Core Team, 2019. A Language and Environment for Statistical Computing.

Dang, V.H., Gam, P.T., Xuan Son, N.T., 2021. Vietnam's regulations to prevent pollution from plastic waste: a review based on the circular economy approach. J. Environ. Law 33, 137–166. https://doi.org/10.1093/jel/eqaa028.

Diem Hong, D., Minh Hien, H., Thi Hoai Thu, N., Thi Thu Hang, D., Quang Nang, H., 2010. Establish cultivation by mixing crops of different strains of *Eucheuma* and *Kappaphycus* species. J. Mar. Biosci. Biotechnol. 4, 24–30.

Duarte, C.M., Bruhn, A., Krause-Jensen, D., 2022. A seaweed aquaculture imperative to meet global sustainability targets. Nat. Sustain 5, 185–193. https://doi.org/10.1038/s41893-021-00773-9.

Estrada, J.L., Bautista, N.S., Dionisio-Sese, M.L., 2020. Morphological variation of two common sea grapes (*Caulerpa lentillifera* and *Caulerpa racemosa*) from selected regions in the Philippines. Biodiversitas 21, 1823–1832. https://doi.org/10.13057/biodiv/d2105 08.

FAO, 2020. Strengthening, Empowering and Sustaining Small-Scale Aquaculture Farmers' Associations, Strengthening, Empowering and Sustaining Small-Scale Aquaculture Farmers' Associations. FAO. https://doi.org/10.4060/ca7741en.

FAO, 2024. The State of World Fisheries and Aquaculture 2024, The State of World Fisheries and Aquaculture 2024. FAO. https://doi.org/10.4060/cd0683en.

Frankic, A., Hershner, C., 2003. Sustainable aquaculture: developing the promise of aquaculture. Aquac. Int. 11, 517–530. https://doi.org/10.1023/B:AQUI.0000013264.38692.91.

de Gaillande, C., Payri, C., Remoissenet, G., Zubia, M., 2017. *Caulerpa* consumption, nutritional value and farming in the Indo-Pacific region. J. Appl. Phycol. 29, 2249–2266. https://doi.org/10.1007/s10811-016-0912-6.

García-Robledo, E., Corzo, A., Papaspyrou, S., 2014. A fast and direct spectrophotometric method for the sequential determination of nitrate and nitrite at low concentrations in small volumes. Mar. Chem. 162, 30–36. https://doi.org/10.1016/j.marchem.2014.03.002.

Glenn, E.P., Doty, M.S., 1992. Water motion affects the growth rates of *Kappaphycus alvarezii* and related red seaweeds. Aquaculture 108, 233–246. https://doi.org/10.1016/0044-8486(92)90109-X.

de Góes, H.G., Reis, R.P., 2011. An initial comparison of tubular netting versus tie–tie methods of cultivation for *Kappaphycus alvarezii* (Rhodophyta, Solieriaceae) on the south coast of Rio de Janeiro State, Brazil. J. Appl. Phycol. 23, 607–613. https://doi.org/10.1007/s10811-010-9647-y.

Guo, H., Yao, J., Sun, Z., Duan, D., 2015. Effect of temperature, irradiance on the growth of the green alga *Caulerpa lentillifera* (Bryopsidophyceae, Chlorophyta). J. Appl. Phycol. 27, 879–885. https://doi.org/10.1007/s10811-014-0358-7.

Häder, D.-P., Lebert, M., Figueroa, F.L., Jiménez, C., Viñegla, B., Perez-Rodriguez, E., 1998. Photoinhibition in Mediterranean macroalgae by solar radiation measured on site by PAM fluorescence. Aquat. Bot. 61, 225–236. https://doi.org/10.1016/S0304-3770(98)00068-0.

Hasan, M.R., Bueno, P.B., Corner, R.A., 2020. Strengthening, empowering and sustaining small-scale aquaculture farmers' associations. Rome.

Hayashi, L., Reis, R.P., dos Santos, A.A., Castelar, B., Robledo, D., de Vega, G.B., Msuya, F.E., Eswaran, K., Yasir, S.Md, Ali, M.K.M., Hurtado, A.Q., 2017. The Cultivation of *Kappaphycus* and *Eucheuma* in Tropical and Sub-Tropical Waters. Tropical Seaweed Farming Trends, Problems and Opportunities. Springer International Publishing, Cham, pp. 55–90. https://doi.org/10.1007/978-3-319-63498-2_4.

Hoang, D.H., Sang, H.M., Kien, N.T., Bich, N.T.K., 2009. Culture of *Panulirus ornatus* lobster fed fish by-catch or co-cultured *Perna viridismussel* in sea cages in Vietnam. Spiny lobster aquaculture in the Asia–Pacific region. Proc. Int. Symp Nha Trang Vietnam 118–125.

Hung, L.D., Hoa, L.T., Hau, L.N., Trung, D.T., 2019. The lectin accumulation, growth rate, carrageenan yield, and quality from the red alga *Kappaphycus striatus* cultivated at Cam Ranh Bay, Vietnam. J. Appl. Phycol. 31, 1991–1998. https://doi.org/10.1007/s10811-018-1692-y.

Hung, L.D., Hori, K., Nang, H.Q., Kha, T., Hoa, L.T., 2009. Seasonal changes in growth rate, carrageenan yield and lectin content in the red alga *Kappaphycus alvarezii* cultivated in Cam Ranh Bay, Vietnam. J. Appl. Phycol. 21, 265–272. https://doi.org/10.1007/s10811-008-9360-2.

ISPONRE, 2009. Viet Nam Assessment Report on Climate Change. Hanoi.

Jiang, H.S., Zhang, Y., Yin, L., Li, W., Jin, Q., Fu, W., Zhang, T., Huang, W., 2018. Diurnal changes in photosynthesis by six submerged macrophytes measured using fluorescence. Aquat. Bot. 149, 33–39. https://doi.org/10.1016/j.aquabot.2018.05.003.

Kang, Y.H., Kim, S., Choi, S.K., Lee, H.J., Chung, I.K., Park, S.R., 2021. A comparison of the bioremediation potential of five seaweed species in an integrated fish-seaweed aquaculture system: implication for a multi-species seaweed culture. Rev. Aquac. 13, 353–364. https://doi.org/10.1111/raq.12478.

Kasim, M., Mustafa, A., 2017. Comparison growth of *Kappaphycus alvarezii* (Rhodophyta, Solieriaceae) cultivation in floating cage and longline in Indonesia. Aquac. Rep. 6, 49–55. https://doi.org/10.1016/j.aqrep.2017.03.004.

Kasim, M., Sara, L., Nurdiana, Ernaningsih, Tamsil, A., Jalil, W., Mustari, T., Paena, M., 2024. Novel methods protecting *Kappaphycus alvarezii* herbivores overview development economic prospects. Trop. Phyconom. Coal. Dev. 277–287. https://doi.org/10.1007/978-3-031-47806-2_22.

Largo, D.B., Diola, A.G., Marababol, M.S., 2016a. Development of an integrated multi-trophic aquaculture (IMTA) system for tropical marine species in southern cebu, Central Philippines. Aquac. Rep. 3, 67–76. https://doi.org/10.1016/j.aqrep.2015.12.006.

Largo, D.B., Diola, A.G., Marababol, M.S., 2016b. Development of an integrated multi-trophic aquaculture (IMTA) system for tropical marine species in southern cebu, Central Philippines. Aquac. Rep. 3, 67–76. https://doi.org/10.1016/j.aqrep.2015.12.006.

Liu, H., Wang, F., Wang, Q., Dong, S., Tian, X., 2016. A comparative study of the nutrient uptake and growth capacities of seaweeds *Caulerpa lentillifera* and *Gracilaria lichenoides*. J. Appl. Phycol. 28, 3083–3089. https://doi.org/10.1007/s10811-016-0858-8.

Ly, N.X., 1999. Culture technologies for some economically important seaweeds. Site Train. MangroveFriendly Aquac. Hai Phong City 214–240.

Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence—a practical guide. J. Exp. Bot. 51, 659–668. https://doi.org/10.1093/jexbot/51.345.659.

Morales-Nin, B., Zimmermann, F., Merino, G., Antelo, L.T., Murillas-Maza, A., Moksness, E., 2024. Challenges on blue food provision. Front. Ocean Sustain. 2. https://doi.org/10.3389/focsu.2024.1271783.

Morris, C., Bala, S., South, G.R., Lako, J., Lober, M., Simos, T., 2014. Supply chain and marketing of sea grapes, *Caulerpa racemosa* (Forsskål) J. Agardh (Chlorophyta: Caulerpaceae) in Fiji, Samoa and Tonga. J. Appl. Phycol. 26, 783–789. https://doi.org/10.1007/s10811-014-0254-1.

Neori, A., Chopin, T., Troell, M., Buschmann, A.H., Kraemer, G.P., Halling, C., Shpigel, M., Yarish, C., 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. Aquaculture 231, 361–391. https://doi.org/10.1016/j.aquaculture.2003.11.015.

Nghia, N.D., Lunestad, B.T., Trung, T.S., Son, N.T., Maage, A., 2009. Heavy metals in the farming environment and in some selected aquaculture species in the Van Phong Bay and Nha Trang Bay of the Khanh Hoa Province in Vietnam. Bull. Environ. Contam. Toxicol. 82, 75–79. https://doi.org/10.1007/s00128-008-9561-z.

Nunes, A., Azevedo, G.Z., de Souza Dutra, F., dos Santos, B.R., Schneider, A.R., Oliveira, E.R., Moura, S., Vianello, F., Maraschin, M., Lima, G.P.P., 2024. Uses and applications of the red seaweed *Kappaphycus alvarezii*: a systematic review. J. Appl. Phycol. https://doi.org/10.1007/s10811-024-03270-6.

Ohno, M., Nang, H.Q., Hirase, S., 1996. Cultivation and carrageenan yield and quality of *Kappaphycus alvarezii* in the waters of Vietnam. J. Appl. Phycol. 8, 431–437. https://doi.org/10.1007/BF02178588.

van Oort, P.A.J., Julianto, B., Latama, G., Siradjuddin, I., Rukminasari, N., Walyandra, Z. Z., Ibrahim, I.A., Verhagen, A., van der Werf, A.K., 2025. Yield determinants of *Kappaphycus alvarezii* seaweed in South Sulawesi, Indonesia. J. Appl. Phycol. https://doi.org/10.1007/s10811-025-03446-8.

Phu, L.H., Kim-Hong, P.T., Chung, T.Van, Binh, T.Van, Dung, L.T., Ngoc, P.H., Thu, N.H., Thu, N.T.T., Anh, N.T.H., Nguyen, A.L., Minh-Thu, P., 2022b. Environmental concerns for sustainable mariculture in coastal waters of South-Central Vietnam. Sustainability 14, 8126. https://doi.org/10.3390/su14138126.

Phu, L.H., Kim-Hong, P.T., Chung, T.Van, Binh, T.Van, Dung, L.T., Ngoc, P.H., Thu, N.H., Thu, N.T.T., Anh, N.T.H., Nguyen, A.L., Minh-Thu, P., 2022a. Environmental concerns for sustainable mariculture in coastal waters of South-Central Vietnam. Sustainability 14, 8126. https://doi.org/10.3390/su14138126.

Quang, N.Van, Binh, T.T., Anh, N.T., 2023. Mariculture development in Vietnam: present status and prospects. Minist. Sci. Technol. Vietnam 65, 11–20. https://doi.org/10.31276/VMOSTJOSSH.65(3).11-20.

Ringuet, S., Sassano, L., Johnson, Z.I., 2011. A suite of microplate reader-based colorimetric methods to quantify ammonium, nitrate, orthophosphate and silicate concentrations for aquatic nutrient monitoring. J. Environ. Monit. 13, 370–376. https://doi.org/10.1039/C0EM00290A.

Stekoll, M., Pryor, A., Meyer, A., Kite-Powell, H.L., Bailey, D., Barbery, K., Goudey, C.A., Lindell, S., Roberson, L., Yarish, C., 2024. Optimizing seaweed biomass production - a two kelp solution. J. Appl. Phycol. https://doi.org/10.1007/s10811-024-03296-w.

Stuthmann, L.E., Brix da Costa, B., Springer, K., Kunzmann, A., 2023a. Sea grapes (*Caulerpa lentillifera* J. Agardh, Chlorophyta) for human use: structured review on recent research in cultivation, nutritional value, and post-harvest management. J. Appl. Phycol. 35, 2957–2983. https://doi.org/10.1007/s10811-023-03031-x.

Stuthmann, L.E., Du, H.T., Brix da Costa, B., Kunzmann, A., Springer, K., 2023b. Sea grape (*Caulerpa lentillifera*) aquaculture in Van Phong Bay, Viet Nam: evaluation of the post-harvest quality. J. Appl. Phycol. https://doi.org/10.1007/s10811-023-03030-y.

Stuthmann, L.E., Springer, K., Kunzmann, A., 2020. Cultured and packed sea grapes (*Caulerpa lentillifera*): effect of different irradiances on photosynthesis. J. Appl. Phycol. 33, 1125–1136. https://doi.org/10.1007/s10811-020-02322-x.

Syakilla, N., George, R., Chye, F.Y., Pindi, W., Mantihal, S., Wahab, N.A., Fadzwi, F.M., Gu, P.H., Matanjun, P., 2022. A review on nutrients, phytochemicals, and health benefits of green seaweed, *Caulerpa lentillifera*. Foods 11, 2832. https://doi.org/10.3390/foods11182832.

Tahiluddin, A.B., Eldani-Tahiluddin, M.-H.S., 2024. Ice-ice disease in cultivated eucheumatoid seaweeds: the perspectives of farmers. Eur. J. Phycol. 59, 423–435. https://doi.org/10.1080/09670262.2024.2383623.

Tanduyan, S.N., Gonzaga, R.B., Bensig, V.D., 2013. Off bottom culture of *Caulerpa lentillifera* in three different water levels in the marine waters of San Francisco, Cebu, Philippines. Galax. J. Coral Reef. Stud. 15, 123–132. https://doi.org/10.3755/galaxea.15.123.

Terada, R., Vo, T.D., Nishihara, G.N., Matsumoto, K., Kokubu, S., Watanabe, Y., Kawaguchi, S., 2016a. The effect of photosynthetically active radiation and temperature on the photosynthesis of two Vietnamese species of *Sargassum*, *S. mcclurei* and *S. oligocystum*, based on the field and laboratory measurements. Phycol. Res 64, 230–240. https://doi.org/10.1111/pre.12143.

Terada, R., Vo, T.D., Nishihara, G.N., Shioya, K., Shimada, S., Kawaguchi, S., 2016b. The effect of irradiance and temperature on the photosynthesis and growth of a cultivated red alga *Kappaphycus alvarezii* (Solieriaceae) from Vietnam, based on in situ and in vitro measurements. J. Appl. Phycol. 28, 457–467. https://doi.org/10.1007/s10811-015-0557-x.

Thomas, M., Pasquet, A., Aubin, J., Nahon, S., Lecocq, T., 2021. When more is more: taking advantage of species diversity to move towards sustainable aquaculture. Biol. Rev. 96, 767–784. https://doi.org/10.1111/brv.12677.

Titlyanov, E.A., Titlyanova, T.V., 2010. Seaweed cultivation: methods and problems. Russ. J. Mar. Biol. 36, 227–242. https://doi.org/10.1134/S1063074010040012.

Trang, C.T.T., Cong, N.Van, Da, P.T., Thanh, N.X., Kha, P.T., Tu, T.A., 2023. Management of buoyant materials in aquaculture for brackish and salt water in Quang Ninh province (Vietnam). Bull. Mar. Sci. 99, 467–485. https://doi.org/10.5343/bms.2022.0069.

Tri, N.N., Tu, N.P.C., Nhan, D.T., Tu, N.V., 2022. An Overview of Aquaculture Development in Viet Nam. Proceedings of International Conference on Fisheries and Aquaculture. The International Institute of Knowledge Management, pp. 53–71. https://doi.org/10.17501/23861282.2021.7105.

Ward, G.M., Kambey, C.S.B., Faisan, J.P., Tan, P., Daumich, C.C., Matoju, I., Stentiford, G.D., Bass, D., Lim, P., Brodie, J., Poong, S., 2022. Ice-Ice disease: an environmentally and microbiologically driven syndrome in tropical seaweed aquaculture. Rev. Aquac. 14, 414–439. https://doi.org/10.1111/raq.12606.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. J. Open Source Softw. 4, 1686. https://doi.org/10.21105/joss.01686.

Yu, J., Ishimaru, T., Murano, M., Otsuki, A., 1994. Some improvements in the salicylate-dichloroisocyanurate method for determining ammonia in Seawater. La Mer. 32, 119–122.

Zubia, M., Draisma, S.G.A, Morrissey, K.L., Varela-Álvarez, E., De Clerck, O., 2020. Concise review of the genus *Caulerpa* J.V. Lamouroux. J. Appl. Phycol. 32, 23–39. https://doi.org/10.1007/s10811-019-01868-9.