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Co-Culture of *Gracilariopsis longissima* Seaweed and *Penaeus monodon* Shrimp for Environmental and Economic Resilience in Poor South-East Asian Coastal Aquaculture Communities

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Abstract: A significant body of controlled laboratory research suggests different biological mechanisms by which the low-cost co-culture of seaweed and shrimp could improve sustainability whilst increasing income for the many poor pond farmers of South-East Asia. However, at the pond level, production and cost–benefit assessments remain largely lacking. Here, we studied the extensive co-culture of *Gracilariopsis longissima* seaweed and *Penaeus monodon* shrimp on pond production output, nutrient concentrations, and farm income on the north coast of Java, Indonesia. Co-culture showed 18% higher seaweed production during the first cycle (2261.0 ± 348.0 kg·ha^{-1}) and 27% higher production during the second (2,361.0 ± 127.3 kg·ha^{-1}) compared to monoculture. Shrimp production per cycle was 53.8% higher in co-culture (264.4 ± 47.6 kg·ha^{-1}) than in single-species cultivation (171.7 ± 10.4 kg·ha^{-1}). Seaweed agar content and gel strength did not differ between treatments, and neither did shrimp bacterial or heavy metals concentrations. The profit of co-culture was, respectively, 156% and 318% compared to single-species seaweed and shrimp cultivation. Co-cultivation lowered nutrient loading in the pond water and in the sediment and is argued to be a low-investment and environmentally friendly option for poor pond farmers to improve their income and financial resilience through product diversification.

Keywords: pond aquaculture; Indonesia; food security; plant–animal synergy; sustainable aquaculture

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1. Introduction

The concept of co-culturing plants in animal aquaculture has long been promoted as a sustainable way to remediate and mitigate environmental impacts, given that plants can absorb nutrients and thereby reduce nutrient loads which may otherwise be harmful to aquatic systems [1–5]. The idea of plants being used to mitigate excess nutrients, whether or not originating from aquaculture or other sources, remains as viable as ever [6–11]. In addition, there is also a considerable body of research that demonstrates a number of potential farm-level economic benefits of co-culturing aquatic plants and animals. However, most of such research has so far taken place in freshwater systems and with fish as the animal component [12]. Research on brackish or marine co-culture has generally been much more limited [13]. Even so, for controlled experimental systems, many biological benefits (or potential benefits) have also since been demonstrated. Examples include better feed conversion [14–17]; increased growth [9,14–25]; higher stocking density [15]; higher shrimp quality in terms of fatty acid profile [16,17] and pigmentation [14,16,18]; improved shrimp immune response to pathogens [19,21]; higher shrimp survival [9,21,23,26], possibly contributed to by shelter provision against predators and cannibalism [6,27] and reduced crowding [22]; higher mussel survival [28]; higher seaweed nitrogen assimilation [18,20,26,28]; phosphate assimilation [18,28]; protein content [17] and production [29]; and overall synergy between plant and animal [30].

While such results suggest promise for economic benefits from co-culture integration at the pond level, field trials for economic and environmental sustainability in outdoor brackish-water farm ponds are quite rare. Also, studies focusing on if and how the numerous demonstrable biological benefits at the laboratory or mesocosm level combine to generate economic benefits in the farm setting remain few. Moreover, when economic assessments are conducted, they are typically only partial, and consider only a subset of the cost and or revenue components, such as either shrimp [6,31] or seaweed yield [29,32], or feed costs [33], but rarely all factors jointly impacting financial feasibility. Laapo and Howara [34] and Tran et al. [35], respectively, performed cost–benefit analyses for milkfish–*Gracilaria* pond co-culture and tilapia–shrimp–seaweed pond polyculture, and were able to demonstrate high net positive returns even though the underlying biological and environmental mechanisms for improved returns were not studied. Economic analyses, such as those provided for a controlled aquaponics system by Castilho-Barros et al. [31], showed that with good management, an intensive co-culture system can also be economically viable. However, due to the high investment requirements, aquaponics and other intensive culture systems are not easily applicable to the millions of small-holder fish farmers that still account for 27.8% of worldwide farmed aquatic animal production [36]. Moreover, Ahmed et al. [37] conducted a socio-economic assessment for small-holder extensive co-culture of shrimp with mangroves in Bangladesh, and were unable to convincingly demonstrate higher profitability. This appeared to be because higher production was also accompanied by higher costs of co-culture. Based on farmer responses, Ahmed et al. [37] found evidence of the likely use of co-culture with mangroves as a risk mitigating strategy (via product diversification) by the farmers but not convincingly for higher profitability. Clearly, cost–benefit assessments of seaweed–shrimp integrated culture are dearly needed for a better evaluation of the many potential ways in which such co-culture might or might not make economic sense at the farm level under different environmental and socio-economic constraints impacting aquaculture in different countries.

Extensive shrimp culture of *Penaeus monodon* in large outdoor ponds with little or no fertilization or supplemental feeding remains the mainstay of small-holder shrimp production in many countries of South-East Asia [38]. For instance, in 2021, in Bangladesh, there were 186,275 ha of small shrimp ponds, with an average farm size of 1–4.5 ha and a 347 kg·ha^{-1} average annual output [38]. In Indonesia, the situation is somewhat different, as the traditional *P. monodon* culture collapsed in the 1990s due to the spread of White Spot Syndrome Virus, and shrimp farming largely switched to the lower-valued *P. vannamei*, which has greater tolerance to environmental degradation and disease. However, up to 15% of the farmers in Indonesia are still small, “independent” farmers using “traditional” technology while a much larger but unspecified group of farmers are small farmers that practice some form of semi-intensive culture system with some input of feed and chemicals [39]. Due to the spread of diseases and environmental degradation, in Indonesia today, there are roughly 250,000 ha of abandoned ponds [40]. As continued expansion of shrimp production will likely further the trend of large-scale mangrove destruction and is highly unsustainable [41], the urgency of developing effective ways for environmentally friendly pond rehabilitation has been stressed by others before [42,43]. Followed by shrimp price volatility, vulnerability to disease remains the second most important risk in small-scale shrimp culture [44]. In this, co-culture with seaweed shows promise as seaweeds have recently been shown to be able to have a strong inhibitory effect on shrimp pathogen virulence [45].

The purpose of this work was to compare pond yields for separate and integrated cultures of seaweed and shrimp along the north coast of Java, Indonesia. We chose *Penaeus monodon* as the shrimp of study because of its local preference by shrimp farmers. This species still accounts for about 19% of Indonesian shrimp production [46–48]. Typically, post larval shrimp are placed in ponds with a maximum density of 25 ind$\cdot$m^{-2} for semi-intensive farming and left to grow out to a marketable size, either with or without some form of additional feeding. Depending on the level of supplemental feeding, the time needed to reach a marketable size is approximately 120 d. The seaweed *Gracilariopsis longisssima* (Syn. *Gracilaria verrucosa* [49]) was chosen for our co-culture experiments. This is one of the three principal species cultured in Indonesia and typically used as a co-crop in saline and brackish ponds [50]. By measuring yields and product and water quality parameters, as well as the associated economic costs and benefits, we aimed to assess the potential for environmental remediation of combined culture and evaluate its net incremental effect of on pond profits.

2. Materials and Methods

2.1. Study Site and Pond Selection

Our co-culture experiments took place in the rural village of Kaliwlingi in the province of Brebes along the north coast of Central Java, Indonesia (6°48′16″ S; 109°2′1″ E) (Figure 1). Nine ponds (sizes: 2000–5000 m^2; approximate depths: 75 cm) were chosen based on availability and willingness of three farmers to cooperate. The water of the ponds was drained, the top layer (~15 cm) of pond sediment was removed, and the ponds were left to dry for 7–10 d until the sediment cracked (~20% moisture content) and became odorless [51]. Then, according to common practice, the ponds were treated with Saponin.

2.2. Physical Parameters and Nutrients of Pond Water and Sediment

Concentrations of organic carbon, nitrate (NO_3), and phosphate (PO_4) in the sediment and water were measured ex situ using Wavelength Dispersive X-ray Fluorescence (WDXRF) with a Rigaku Supermini200 every second week. Chlorophyll concentrations were measured according to the spectrophotometric method of Strickland & Parson [52]. Primary production (PP) was calculated following Beveridge's formula for annual pond PP [53], including correction for an average pond depth of 0.75 m:

$$\text{PP (gC m}^{-2}\cdot\text{day}^{-1}) = 56.5 \text{ chlorophyll-a(g}\cdot\text{m}^{-3})^{0.61} \cdot 0.75 \text{ m} \cdot 365 \text{ d}^{-1}$$

The total dissolved solids (TDS), salinity (digital ATAGO® PAL-06S; 1 ppt accuracy), temperature, and dissolved oxygen were determined using the Water Quality Checker (YSI® Pro 20; 0.1 °C and 0.01 ppm), and turbidity (in terms of Nephelometric Turbidity Units or NTUs) using the Thermo Scientific™ Orion™ AQUAfast AQ3010 and pH with the EZDO 7200 and its ORP sensor, three times a day (morning, noon, and afternoon), two days each week. Temperature and irradiance (PAR) were measured every 10 min using HOBO-loggers (Hobo UA 003-64 Onset) attached at a depth of 30 cm and above the pond for reference.

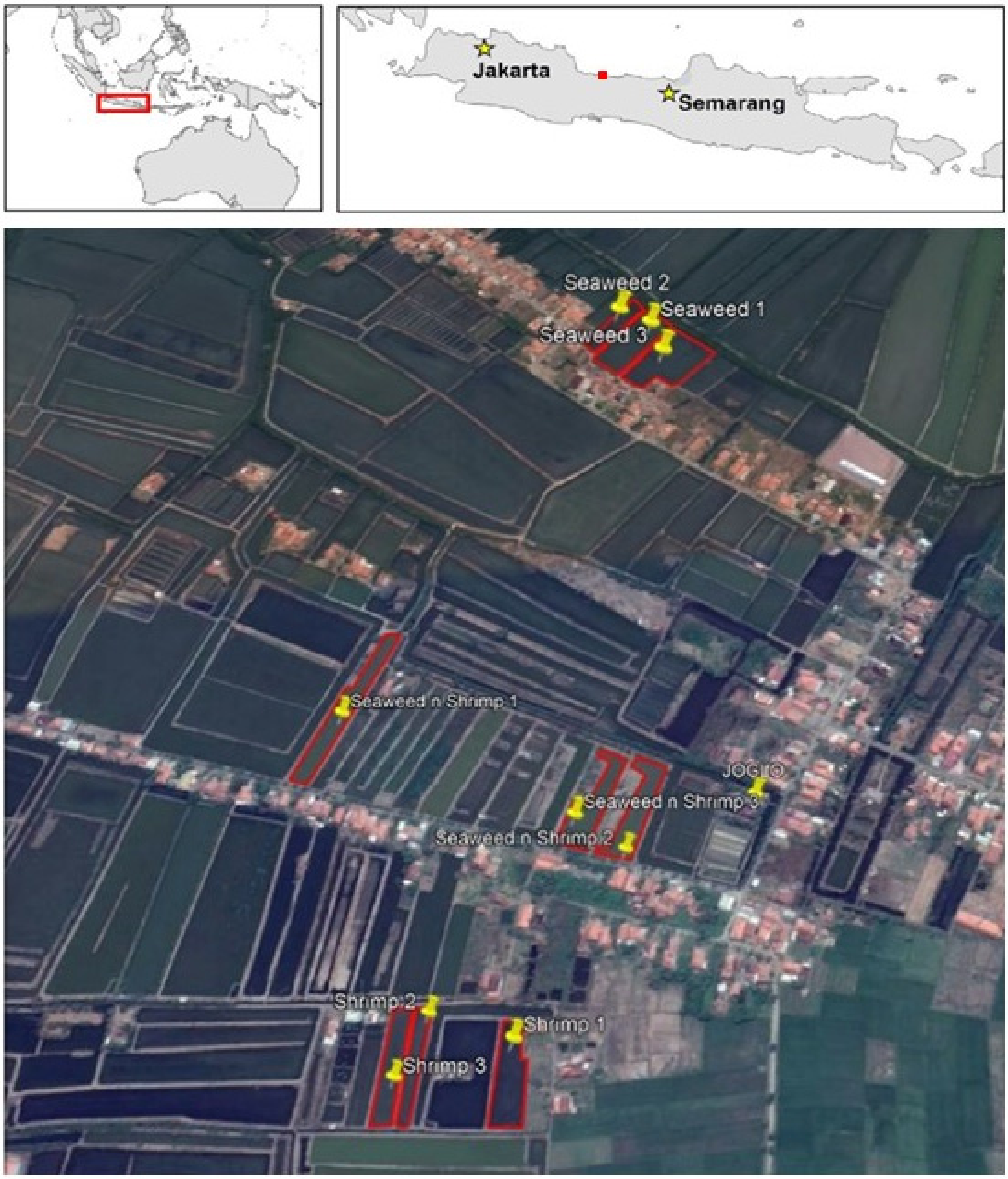

Figure 1. Map of study area in the rural village of Kaliwlingi, Brebes, north coast of Central Java, Indonesia, showing the layout of the ponds used.

At the end of the experiment, three sediment samples per pond were taken to determine the CNP-composition and presence of heavy metals (As, Pb, Hg, and Cd) using Wavelength Dispersive X-ray Fluorescence (WDXRF) with a Rigaku Supermini200 at the Diponegoro University laboratory facilities. The level of detection (LOD) for all heavy metals was $\geq$0.008 mg$\cdot$g^{-1}.

2.3. Experimental Design for Growth and Yield

The growth and yield of *P. monodon* and *G. longissima* were measured over a 122 d cultivation period, without supplemental feeding or fertilization. Seaweed and shrimp were cultured separately and/or jointly using identical stocking rates for either of the two in order to assess potential differences in production under the three different culture scenarios. Throughout the text, we refer to the three culture settings or treatments as "Shrimp", "Seaweed", and "Combined". Each scenario was executed in triplicate. As the cultivation period of seaweed is much shorter compared to the shrimp, two cultivation cycles of 45 d each were applied for seaweed during the course of the experiment. The difference in days was used for the manual harvest of the seaweed and its restocking. The initial stocking, at a density of 100 $g \cdot m^2$ which was chosen for practical reasons (seeding time and availability of seed material and costs), took place shortly prior to the broadcast stocking of the shrimp. At the end of each cycle, the seaweed was harvested, weighed, and air dried on netting hung above the ground using bamboo sticks. After harvest, the ponds were restocked, and the second "hanging method" was used, whereby seaweed seedlings are attached to ropes and hang freely in the water column. Seaweed was weighed and sampled prior to the (re)stocking moments and at harvest to assess dry matter content and the total yield. In addition to total production per cycle in terms of weight yield, important quality parameters for seaweed (in terms of agar content and gel strength) were measured.

Penaeus monodon post larvae of ~12 weeks old (0.15 g) were seeded in the ponds at a density of 10 post larvae$\cdot m^{-2}$. For comparison, the optimum stocking densities for intensive farming, semi-intensive, and extensive (non-fed) cultivation, respectively, are 45, 25, and 4.8 post larvae$\cdot m^{-2}$ [54,55]. Our stocking level was chosen as the intermediate between the optima for semi-intensive and extensive (non-fed) cultivation based on local expert input and to potentially enhance the differences between the treatments. Shrimp were weighed prior to stocking and at harvest. Ten randomly caught individuals were weighed every second week.

2.4. Calculation of Biological and Economic Yield

Specific growth rates (SGR) in %$\cdot day^{-1}$ were calculated using the formula given below, in which d = day, T = number of days of cultivation, W_0 = initial wet weight, and W_t = wet weight at harvest:

$$SGR\ (\%\cdot day^{-1}) = [\ln(W_t) - \ln(W_0)]/T \cdot 100\%$$

The prices obtained by the farmers were used to assess generated revenue (R). Variable cost estimates (V) for pond preparation, seeding, pond maintenance, harvest, and product treatment up to the point of sale to middlemen were obtained from the farmers. Price per kg for seaweed (dried) was $0.35 (IDR 5000.-), and for the shrimp, this was $6.37 (IDR 90,000.-). All cost and yield figures were standardized to productivity per hectare for one cycle of shrimp and two cycles of seaweed cultivation.

Fixed costs, such as the costs of obtaining the ponds or renting ponds, depreciation costs, and capital costs were assumed to be equal and of no differential effect in our assessment. Variable production costs (V) were then subtracted from the generated revenues to determine the Contribution Margin (C) for comparative cost–benefit ratios, assuming equal fixed costs. Most often, the Profit Margin for a product being considered is used to decide whether or not to include that product in a product portfolio. Thereby, the profit margin is the measure of the total difference between revenue from sales and all costs, both variable and fixed. However, to better understand how a specific addition of a product can or cannot contribute to profits of a running operation, it is better to look at the contribution margin as we have here [56]. Hence, our economic assessment only addressed the incremental cost–benefit of co-culture over monoculture for farmers that were already involved in these activities. Individual and synergistic contributions of shrimp and seaweed to total pond revenues were calculated, following Alam et al. [57], as follows:

$$\text{Contr. seaweed (\%)} = \text{yield seaweed (IDR)}/\text{yield seaweed and shrimp (IDR)} \cdot 100\%$$

$$\text{Contr. shrimp (\%)} = \text{yield shrimp (IDR)}/\text{yield seaweed and shrimp (IDR)} \cdot 100\%$$

2.5. Product Quality and Food Safety Assessment

For the harvested *Gracilariopsis*, two key quality criteria, namely agar content and gel strength, were determined following Rejeki et al. [58] After drying, 500 g of seaweed was pre-treated with 5 L of NaOH 6% (*w*/*w*) at 85 °C for 3.5 h. After ample washing, the samples were neutralized with 200 mL of acetic acid 0.5% (*w*/*w*) for 1h at room temperature. Extraction using 200 mL distilled water at 85 °C for 2 h was followed by filtering while still hot using a 100% cotton cloth. The mixture allowed to gel at room temperature for 24 h. Based on the air-dried weight, agar yields were calculated. Gel strength was measured using the Brookfield CT3 4500. Dried agar starch (1.5 g) was dissolved in 100 mL distilled water by magnetic stirring for 20–30 min at 90 °C. Stabilization of the solution was performed in an 80–90 °C water bath for 15min in order to reduce and remove irregularities [58]. Then, 22 mL samples were left overnight at 28 °C, after which, gel strength was measured using a Rheometer following Bono et al. [59].

At the end of the experiment, nine samples of shrimp per pond were analyzed for bacterial contamination (total plate count in colony-forming units per gram, CFU·g^{-1}) according to the Standard Nasional Indonesia procedures (SNI 2332.3:2015 [60]), for *Escherichia coli*, according to SNI 2332:1-2015 [61], for *Salmonella* and for *Vibrio cholerae* according to SNI 01-2332.2-4 2006 [62], all by the Central Java Laboratory of the Ministry of Fisheries in Semarang. Heavy metals in shrimp were assessed using the same protocol as for the sediments, as described above.

2.6. Statistical Analysis

Statistical analysis was performed using Graph Pad Prism (V8.2.1) software. Comparison between ponds within treatments was performed using Welch's one-way ANOVA (under assumption of a Gaussian distribution and variable standard deviations). Gel strength, bacterial presence (total plate count), seaweed production, and carbon, nitrate, and phosphate content of both the water and the sediment were likewise compared using an unpaired Welch's *t*-test. When concentrations were below the level of detection, the minimum detection level was set as the measured level. All samples were pooled per pond and the different ponds were treated as experimental replicates. Throughout the text, mean values are followed by standard deviations (±SD).

3. Results

3.1. Water and Sediment Parameters

Table 1 provides the comparisons of water quality parameters for the three different experimental treatments divided across the three sets of ponds. The total dissolved solids (TDS) were, respectively, 19.29 ± 2.20, 21.67 ± 2.63, and 23.79 ± 1.51ppt for the treatments of Combined, Shrimp, and Seaweed. The ponds with the Combined culture showed the lowest salinity of 24.9 ± 2.9‰, whereas those with the monocultures Shrimp and Seaweed had higher salinities of, respectively, 28.6 ± 3.6‰ and 31.6 ± 1.8‰. These differences were likely due to different proximities to the main marine tidal water channels of the village. Although significant, all were within the optimal range for both growth (20–35 psu) and survival (10–35 psu) of *P. monodon* [63]. *Gracilariopsis* grows decidedly better at the higher range of salinities observed within our ponds. As in our experiments, the ponds with only seaweed happened to be those also optimal for seaweed, this choice would have the effect of minimizing potential differences between the chosen treatments. Temperature measurements (both by hand and by continuous monitoring) did not show substantial differences between the ponds. The average temperature was 31.4 ± 2.2 °C, with a minimum of 27.0 °C and a maximum temperature measured of 36.0 °C. Overall, the average DO of the ponds was 3.67 ± 0.59 ppm in the morning, increasing to 5.15 ± 1.05 ppm during midday and ending at 5.44 ± 1.03 ppm by the end of the afternoon. The largest consistent differences in DO in the ponds were due to the diel cycle of photosynthesis, but there were also smaller significant differences between the three treatments (Table 1). An explanation for this remains wanting, but could be due to an artefact caused by differences in the timing of sampling. Turbidity for Combined, Shrimp, and Seaweed cultures was, respectively 18.89 ± 12.23, 23.04 ± 12.20, and 17.21 ± 8.31 NTUs. The differences were significant between Shrimp and Combined ($p < 0.001$), and between Shrimp and Seaweed ($p < 0.001$), but not between Seaweed and Combined ($p = 0.077$) (Table 1). These results were likely due to bioturbation caused by the shrimp. Mean chlorophyll-a concentrations neither differed significantly between ponds nor between treatments. A slight increase in chlorophyll-a was observed over time for the Shrimp and Combined treatments.

Table 1. Average water parameters (±SD). Significance is for the overall comparison between treatments.

	Combined	**Shrimp**	**Seaweed**	**Significance** [1]
Total diss. sol. (ppt)	19.29 ± 2.20	21.67 ± 2.63	23.79 ± 1.51	***
Salinity (‰)	24.94 ± 2.91	28.37 ± 3.73	31.42 ± 2.05	***
pH	7.53 ± 0.59	7.77 ± 0.63	7.41 ± 0.50	NS
Temperature (°C)	31.61 ± 2.08	31.26 ± 2.30	31.38 ± 2.11	NS
Dissolved oxygen (%)	4.8 ± 1.11	5.08 ± 1.36	4.77 ± 4.36	***
Turbidity (NTU)	18.89 ± 12.23	23.04 ± 12.20	17.21 ± 8.31	***
Chl-a ($mg \cdot m^{-3}$)	1.71 ± 0.94	2.06 ± 1.41	2.12 ± 0.99	NS
Primary prod. ($gC \cdot m^{-2} \cdot d^{-1}$)	0.18 ± 0.07	0.20 ± 0.08	0.21 ± 0.06	NS

[1] 1-way ANOVA, NS > 0.05; *** < 0.001.

Nitrate, phosphate, and carbon concentrations are shown in Table 2. The nitrate content of the pond waters decreased for all treatments, but only significantly for the two monocultures (Shrimp: $p = 0.013$, Seaweed: $p = 0.010$). In contrast, nitrate concentrations in the pond sediment increased for Shrimp and Combined while remaining almost the same for Seaweed, but no significant effects could be demonstrated. Phosphate concentrations in pond waters varied over time, but no significant decrease was found. However, phosphate content in the sediment decreased significantly during culture for all treatments (*p*-values for Shrimp: 0.005, Seaweed: 0.003, and Combined: 0.003). All three culture systems effectively consumed phosphate. For the water, organic carbon content remained equal for the ponds with only Shrimp, but increased (insignificantly) for the Combined culture ($p = 0.082$) and increased significantly for Seaweed ($p = 0.013$). The carbon content of the sediment increased for Shrimp and Combined but decreased for Seaweed, but only insignificantly.

Table 2. Nitrate, phosphate, and carbon concentrations at the beginning and end of the experiment in both the water and pond sediment. Values are averages for the ponds ±SD.

		Water		**Sediment**	
	Treatment	**Start (T0)**	**End (T6)**	**Start (T0)**	**End (T6)**
Nitrate ($mg \cdot L^{-1}$)	Seaweed	0.97 ± 0.14	0.37 ± 0.05	2.93 ± 0.50	3.03 ± 1.69
	Shrimp	1.29 ± 0.19	0.73 ± 0.12	2.54 ± 2.50	2.71 ± 0.99
	Seaweed + Shrimp	0.78 ± 0.07	0.47 ± 0.38	2.73 ± 1.88	2.86 ± 0.76
Phosphate ($mg \cdot L^{-1}$)	Seaweed	0.03 ± 0.03	0.02 ± 0.00	0.32 ± 0.03	0.04 ± 0.02
	Shrimp	0.07 ± 0.05	0.02 ± 0.00	0.34 ± 0.05	0.02 ± 0.00
	Seaweed + Shrimp	0.04 ± 0.01	0.02 ± 0.00	0.32 ± 0.04	0.02 ± 0.00
Carbon ($mg \cdot L^{-1}$)	Seaweed	0.48 ± 0.02	0.53 ± 0.11	3.89 ± 0.24	3.70 ± 0.32
	Shrimp	0.76 ± 0.12	0.67 ± 0.22	1.08 ± 0.21	1.43 ± 0.61
	Seaweed + Shrimp	0.66 ± 0.11	0.68 ± 0.14	1.29 ± 0.24	1.59 ± 0.32

None of the sediment samples had levels of Hg and Cd exceed the levels of detection. However, for As and Pb, mean concentrations were above detection levels in sediment (Table 3). The heavy metal contents in the shrimp were all below the standard allowable limits of the current Indonesian National Standards [64] and European Union standards [65]. The limits for these two regulations are, respectively, <1 mg·kg^{-1} (As, Hg and Cd) and <0.5 mg·kg^{-1} for Pb. The comparisons of heavy metals concentrations between treatments were neither clear cut nor significant.

Table 3. Heavy metal content (mg·g^{-1}) in the cultivated shrimp and the pond sediments. All values marked as "0.008" are those below the level of detection (LOD). Averages were calculated using the LOD of 0.008 mg·g^{-1}.

Source	Treatment	Replicate.	Arsenic (As)	Lead (Pb)	Mercury (Hg)	Cadmium (Cd)
Shrimp	Combined	1	0.011 ± 0.002	0.008 ± 0.000		0.051 ± 0.002
		2	0.020 ± 0.001	0.008 ± 0.000	0.008	0.047 ± 0.006
		3	0.008 ± 0.000	0.043 ± 0.006		0.143 ± 0.021
		Mean	0.013 ± 0.005	0.020 ± 0.018	0.008 ± 0.000	0.080 ± 0.048
	Shrimp	1	0.008 ± 0.000	0.012 ± 0.001	0.017 ± 0.002	0.056 ± 0.002
		2	0.034 ± 0.005	0.008 ± 0.000	0.008 ± 0.000	0.023 ± 0.006
		3	0.008 ± 0.000	0.024 ± 0.004	0.008 ± 0.000	0.027 ± 0.003
		Mean	0.017 ± 0.013	0.015 ± 0.008	0.011 ± 0.004	0.036 ± 0.016
Sediment	Combined	1	0.005 ± 0.001	0.008 ± 0.000		
		2	0.038 ± 0.005	0.008 ± 0.000	0.008	0.008
		3	0.008 ± 0.000	0.018 ± 0.002		
		Mean	0.017 ± 0.016	0.011 ± 0.005	0.008 ± 0.000	0.008 ± 0.000
	Shrimp	1	0.018 ± 0.003	0.008 ± 0.000		
		2	0.021 ± 0.004	0.018 ± 0.003	0.008	0.008
		3	0.008 ± 0.000	0.064 ± 0.044		
		Mean	0.016 ± 0.006	0.030 ± 0.034	0.008 ± 0.000	0.008 ± 0.000
	Seaweed	1	0.008 ± 0.000	0.008 ± 0.000		
		2	0.008 ± 0.000	0.048 ± 0.009	0.008	0.008
		3	0.008 ± 0.000	0.008 ± 0.000		
		Mean	0.008 ± 0.000	0.021 ± 0.021	0.008 ± 0.000	0.008 ± 0.000

3.2. Production

The SGR of seaweed in co-culture was significantly higher (3.62 ± 0.02) than compared to monoculture (3.30 ± 0.08%·day^{-1}) (Table 4). The mean seaweed yield for the monoculture was 1923 ± 25.2 and 1858 ± 34.8 kg·ha^{-1}, respectively, for the two subsequent cultivation periods. For the co-cultivation, seaweed yield was higher, respectively, 2261 and 2361 kg·ha^{-1}, notwithstanding the less optimal salinity regime. Seaweed production for both the first harvest experiment ($p < 0.01$) and the second harvest experiment ($p < 0.05$) was significantly higher when co-cultivation was used. Combined cultivation yielded 18% more seaweed than only Seaweed during the first cycle and 27% more during the second cycle. Shrimp yield was higher when co-cultivation was applied (+53.8%). Shrimp yield was 171.7 kg·ha^{-1} for monoculture and 263.89 kg·ha^{-1} for Combined (Figure 2). Due to the low replication of these field trials (only three replicates per system), test power was relatively low and this apparently large difference was not statistically significant. However, the apparent differences in yield were consistent with demonstrated differences in the SGR of the shrimp, which were 4.44 ± 0.06 and 4.79 ± 0.16 for Shrimp and Combined, respectively ($p = 0.026$, Table 4). In addition, there was a significantly large difference in survival (of about 30%) for shrimp between the Shrimp and the Combined culture settings (Table 4).

Table 4. The specific growth rate (SGR) for both shrimp and seaweed and overall survival rate (SR) for the shrimp in the three different culture treatments compared. (*) indicates $p < 0.05$ for comparison between treatments.

SGR (% Day^{-1})	Treatment		
	Shrimp	Seaweed	Combined
Shrimp	4.4 ± 0.06 *	-	4.79 ± 0.16 *
Seaweed	-	3.30 ± 0.08 *	3.62 ± 0.02 *
Shrimp SR (%):	61 ± 2.45 *	-	80 ± 3.76 *

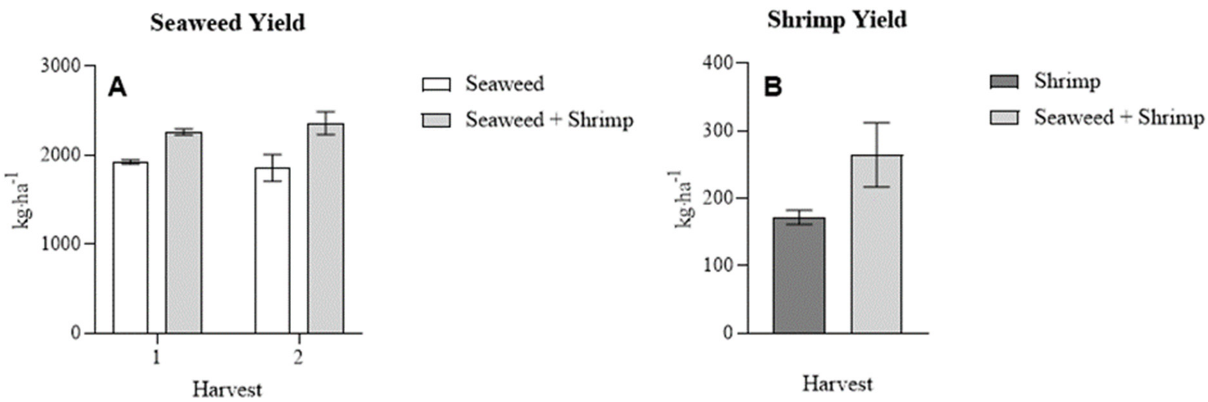

Figure 2. Yields (kg·ha^{-1}) of (**A**) seaweed and (**B**) shrimp per harvest and per treatment.

The largest differences in economic effect between the different culture types was seen in the revenue·ha^{-1} (Table 5). The contribution margin of the Combined culture was, respectively, 156% and 318% of the contribution margin of cultivating either only seaweed or shrimp. For Combined, the contribution of seaweed and shrimp to overall pond production was, respectively, 49% and 51%.

Table 5. Overview of revenue generation (R), variable costs (V), and the resulting contribution margin (C) for monocultures and co-cultivation based on prices and cost structures for Kaliwlingi village, Brebes, Indonesia. Values in USD ($) and calculated using the exchange rate of USD/ IDR = 1:14,129.50. "pm" = pro memoria.

		Seaweed	Shrimp	Combined
Revenues Seaweed Yield (kg·ha^{-1})	1st harvest (Mean ± SD)	1923.3 ± 25.2	-	2161.0 ± 348.0
	2nd harvest (Mean ± SD)	1858.3 ± 150.7	-	2361.0 ± 127.3
Shrimp yield (kg·ha^{-1})		-	171.7 ± 10.4	264.4 ± 47.6
Mean Revenue ($)	1st harvest	680.61		800.14
	2nd harvest	657.61		835.53
	Shrimp		1093.46	1680.88
	Subtotal	1338.22	1093.46	3316.54
Fixed costs ($)		pm	pm	pm
Variable costs ($·ha^{-1})	Pond prep. labor	28.31	28.31	28.31
	Pond prep. pump rent	21.23	21.23	21.23
	Pond prep. consumables	7.08	7.08	7.08
	Stocking material	159.24	212.32	371.56
	Seeding–labor	14.15	7.08	21.23
	Harvest–labor	70.77	70.77	141.55
	Drying–labor	14.15		14.15
	Drying–materials	17.69		17.69
	Subtotal	332.64	346.79	622.81
Contribution Margin ($·ha^{-1})		1005.58	746.66	2693.73

3.3. Product Quality Aspects

Seaweed agar content increased significantly only for the Seaweed and Combined treatments during the first round of cultivation (p = 0.02), but not during the second cultivation cycle (p = 0.554). No differences in gel strength were found during the first cultivation cycle. For the second cycle, a slight reduction was measured for the gel strength of the Combined treatment, but this was only significant for the hanging method ($p < 0.05$). No significant difference could be established in gel strength between the hanging and broadcast method (Table 6).

Table 6. Gel strength, agar content, and specific growth rate (SGR) for seaweed in either mono or combined culture with shrimp (mean ± SD). Only three samples were taken from the batch used for stocking (*). Note also that SGR for seaweed was determined only for the combined deployment methods (**).

Treatment	Time in d and (Cycle)	Gel Strength $g \cdot cm^{-2}$	n	Agar Content (%)	n	SGR $\% \cdot d^{-1}$
Stocking material	0 (1)	20.2 ± 4.1	6	13.59 ± 0.75 *	3	-
Seaweed	30 (1)	35.7 ± 8.1	9	21.15 ± 0.06	9	2.4 ± 0.15
Combined	30 (1)	19.3 ± 13.1	9	21.62 ± 0.10	9	2.1 ± 0.55
Restocking material	0 (2)	41.3 ± 5.8	3	25.54 ± 0.16	9	-
Seaweed	30 (2)	43.8 ± 18.0	9	22.24 ± 0.20	9	3.2 ± 0.03
Combined (hanging)	30 (2)	16.2 ± 9.2	9	24.70 ± 0.26	9	3.7± 0.2 **
Combined (broadcast)	30 (2)	16.7 ± 11.5	9	22.43 ± 0.20	9	

At harvest, the presence of pathogenic bacteria, *E. coli*, in all shrimp was below 3 $MPN \cdot g^{-1}$ (MPN = Most Probable Number), while *Salmonella* and *V. cholerae* were not detected. The total plate counts of samples were comparable within ponds, ranging from about 3.7 $logCFU \cdot g^{-1}$ to 4.4 $logCFU \cdot g^{-1}$. Bacterial load appeared lower in ponds with Combined culture or only Seaweed (4 ± 3.85 $logCFU \cdot g^{-1}$) than in ponds with only Shrimp (4.3 ± 3.75 $logCFU \cdot g^{-1}$); however, the difference was not statistically significant (p = 0.145).

4. Discussion

While the many potential biological benefits in terms of sustainability, synergistic production effects, and possible economic advantages of combined plant and animal production have been well studied under controlled laboratory and/or culture basin conditions, few of these have been investigated and/or demonstrated under outdoor farm culture conditions. For the advantages of co-culture, as demonstrated in the confines of the laboratory setting, to achieve wider application, making the step from the laboratory to the farmer's pond is essential. In our experiments, we set out to verify if production and economic advantages could be convincingly demonstrated under real farm conditions. Our field experiments at the farm level did show the practical difficulty in fully controlling and/or randomizing for all environmental variables when working with farmers. This is because, notwithstanding our care in selection of the most comparable ponds, there remained some modest yet consistent differences in pond conditions between the three different sets of replicate ponds. Thus, while our results provide empirical corroboration of laboratory-based expectations under field conditions, they still fail to provide rigorous field proof of possible differences between the three different culture forms studied. Our choice for placing the seaweed monoculture treatment in the ponds that were most similar to seawater conditions, and thus most favorable to *Gracilariopsis* growth, likely inadvertently minimized potential contrasts between the different culture options studied. Another point to keep in mind is that our cost–benefit analysis was only partial as it only included the main variable costs of culture and excluded several fixed costs that were assumed to be largely equal and obligatory (e.g., pond ownership or rental, and depreciation). Therefore, our comparison is not a full assessment of economic viability based on the overall *profit margin* but strictly an incremental comparison between options using the *contribution margin* as a criterium. As stressed by Gallo [55], if a product being considered has a positive contribution margin, then its production contributes to fixed costs and profit, even if its conventionally calculated profit margin is negative. As in the small subsistence family farms being studied, ponds are practically an obligatory form of income generation; the contribution margin is the most relevant criterium to use for farmer decision-making.

In Indonesia, seaweed culture and extensive shrimp culture in ponds largely occur side by side but separately. This work shows that they can be combined in the same pond with synergistic benefits to both. More specifically, and notwithstanding the various above-discussed limitations and constraints, our results largely confirm what has been suggested from controlled tank or basin experiments previously. In particular, our results showed: (a) the expected reduction in nutrient contents of pond waters, particularly nitrate concentrations; (b) a large synergistic effect on growth (SGR) of both shrimp and seaweed and higher survival of shrimp under combined culture conditions; (c) a large positive effect on cost–benefit ratios for combined culture over monoculture, notwithstanding higher labor costs for including seaweed; and (d) no compromise of product quality as measured for seaweed, in terms of seaweed agar contents and gel strength, and for shrimp, in terms of bacterial and heavy metals concentrations. Even so, much more work will be needed to validate the higher productivity, functioning, and broader effects on product quality for co-culture under different field circumstances and with different species combinations.

As productivity of shrimp farming has been steadily declining, pond farmers have been transitioning to seaweed cultivation, which, today, has become a major activity in Indonesia's coastal areas [66]. Co-culture could tap into plant–animal synergy and be of benefit to both the seaweed and shrimp sectors and both environmental and economic sustainability. The available evidence further indicates clearly that the benefits of co-culture are also possible in partially fed or fertilized culture systems [31,34,35,67]. In addition, co-culture could help bolster farm economic resilience by affordably mitigating market risks through product diversification [1,37]. Given the pressing need worldwide for more sustainable food production, further work to assess and understand the potential co-culture under field settings is urgently needed.

Our study did not address the specific biological pathways leading to the higher effective growth of shrimp and/or seaweed, but such topics are very interesting for further study. Shrimp are principally known as detritivores [67] but it may be that in co-culture with seaweed, shrimp will feed significantly from within the seaweed clumps that provide additional surface on which food like filamentous algae and other natural food sources grow [67] and thereby have more food available. As co-culture with seaweed changes the pond plankton community for the better by inhibiting the abundance of harmful species [68], some demonstrable differences in shrimp diet are certainly to be expected. Also, higher shrimp survival, as we found in co-culture, might be due to a reduced impact of cannibalism or predation by wading herons and egrets, but this remains to be investigated.

While Pb and Cd concentrations in shrimp tissue were lower in the Shrimp monoculture treatment, As and Hg were lower in the Combined treatment ponds. Seaweed capacity for bio-absorption of As and Hg may sequester these heavy metals and thereby reduce their uptake by the shrimp through digestion and osmoregulation [69]. These heavy metals are known to be efficiently bound by carboxylates, sulphates, and hydroxyls found in gracilariid cell walls [70]. In contrast, the remobilization of Pb and Cd from the sediment to the water column as a result of the physical presence of the seaweed on the bottom, in contact with the sediment, is probably what produced the rise in levels in the Combined treatment. It has been found that when seaweed is cultivated on the bottom, Pb and Cd rapidly re-enter the water and might then be more easily absorbed by shrimp due to their strong affinity for sediment particles [11,71]. Additionally, compared to other heavy metals, shrimp have a greater propensity to accumulate Pb and Cd. This is believed to be because of particular physiological mechanisms in their excretion and metabolic systems [72].

The value of co-culture of seaweed with shrimp under the cost and price structure affecting the small subsistence shrimp and seaweed farmers in our study area in Indonesia mirrors the results previously found by others [34,35]. We therefore argue that in light of the accumulated evidence, co-culture should likely be broadly beneficial to small family farms culturing *Gracilariopsis* and/or *Penaeus* in brackish ponds in Indonesia, and possibly even other similar species. Thus, for those who do not yet practice co-culture, our results may serve as convincing stimulus to take the small steps needed to combined shrimp and seaweed cultures. For those who already have access to ponds and are practicing either seaweed or shrimp monoculture, the incremental investment costs to expand their operation towards co-culture are fairly minimal. This makes co-culture relatively easier to achieve for poor farmers than any capital-intensive technology-transformation to an intensive culture system [73–75] would. Hence, with proper information campaigns and training [76,77], co-culture can probably be achieved on a wide scale, at a low cost, and fairly quickly result in much needed socio-economic benefits to poor coastal communities. In Indonesia, any such efforts would strongly align with the national ambition of becoming the world's leading producer of agar-agar and carrageenan products [78,79] and can be highly recommended for improved sustainability.

While functioning market and supply chains exist in all but the most rural and distant coastal areas of the Indonesian archipelago, this is certainly not the case for a significantly contrasting country like Bangladesh. There, seaweed culture remains practically unknown, and processing and market chains for small-scale producers to make use of would first need to be developed [80,81]. In other words, implementing seaweed culture in Bangladesh, would be much more complicated than in a country like Indonesia, even though co-culture might be a cautious first step to developing such an industry, as has been pinpointed by others as being of significant potential to Bangladesh [81–84]. So, while our findings certainly seem to have wider applicability, the recommended roadmap and specifics for successful implementation of seaweed and shrimp co-culture may differ significantly depending on the environmental and socio-economic situation of the country or region being considered.

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