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Effects of selected environmental conditions on growth and carrageenan quality of laboratory-cultured *Kappaphycus alvarezii* (Rhodophyta) in Fiji, South Pacific

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Abstract
The impacts of environmental conditions (temperature, salinity, and nutrients) on growth, semi-refined carrageenan yield, gel strengths, and viscosity were assessed on the red seaweed *Kappaphycus alvarezii* in laboratory culture. Results showed that *K. alvarezii* had a higher daily growth rate (0.94% day^{-1}) at higher temperature (30 °C). Its semi-refined carrageenan yield was high (75.79%) at a combination of low salinity (25 ppt) and high temperature (30 °C). Conversely, gel strengths made out of semi-refined carrageenan from *K. alvarezii* cultured at low temperature (24 °C) demonstrated a higher compression (5.84 N) and high penetration strength (0.29 N). Highest viscosity (289.50 cP) was attained at a combination of high temperature, low salinity, and high nutrient concentration. Gels made from carrageenan of *K. alvarezii* grown in a higher temperature (30 °C) mixed with pineapple juice showed higher compression strength demonstrating that carrageenan extracted from cultured *K. alvarezii* is a good thickening agent for fruit jellies or similar food products that do not require refrigeration. This could benefit communities in rural, non-electrified communities/areas of Fiji and other South Pacific Islands that could use *K. alvarezii* as an alternative gelling agent in the making of food products contributing towards their food and economic security.

Keywords *Kappaphycus alvarezii* · Rhodophyta · Cultivation · Daily growth rate · Carrageenan · Gel strength

Introduction

Seaweeds are sources of hydrocolloids such as carrageenan, agar, and alginate (Diyana et al. 2015). Carrageenans are obtained from marine Rhodophyceae (Chen et al. 2002; Tecante and Santiago 2012) and are primarily used as gelling, stabilizing, and thickening agents in the food, cosmetics, and pharmaceutical industries (Usov 2011). There are three types of carrageenan, namely *kappa*, *iota*, and *lambda*, which differ in their degree of sulfation (Yermak et al. 2017). Other differentiating factors between these three types of carrageenan are the presence of potassium ions in *kappa*-type which is used to make firm gels, and calcium ions in *iota*-type which produces elastic gels. *Lambda*-type carrageenan achieves a viscous solution without the intervention of any ions. Hydrocolloids are used in food formulations to improve quality and shelf-life. They are used as thickening agents in soups, gravies, salad dressing, and sauce and as gelling agents in jelly, jam, restructured foods, low-sugar/calorie gels, and marmalade (Saha and Bhattacharya 2010). Fruit juices are used as a dispersing medium in food thickeners and gelling agents such as carrageenan, agar, and alginate (Sopade et al. 2008).

Kappa-carrageenan is largely sourced from the red seaweed *Kappaphycus alvarezii* (Hayashi and Reis 2012), which is mainly cultivated in Indonesia, the Philippines, and some Pacific Islands (Gereniu et al. 2017; Ingle et al. 2018; Adharini et al. 2019). In the South Pacific Islands, *K. alvarezii* does not occur naturally. It was introduced for cultivation in Fiji and Kiribati in the late 1970s (Ram 1991) and, about 30 years later in 2003, it was introduced in the Solomon Islands (McHugh 2006). In Fiji, farming of *Kappaphycus* began in 1976 with specimens imported from

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Hawaii (Luxton et al. 1987; Eldredge 1994). A geographic expansion followed in 1984 and in 1987 (South 1993). Currently, *K. alvarezii* farms in Fiji are still operational after a chequered history of failures and successes (Prakash 1990; McHugh 2006), and environmental factors influenced by climate change likely affect the growth of cultivated *K. alvarezii* in this region.

Generally, there is a direct proportional relationship between growth rate and carrageenan yield of *Kappaphycus*; as growth rate increases, carrageenan yield also increases (Ohno et al. 1994; Hung et al. 2009). However, this relationship can be altered by multiple environmental factors, most notably seawater temperature, salinity, and nutrients (Orbita 2013). Orbita and Arnaiz (2014) investigated the effect of varying temperatures on carrageenan yield in *K. alvarezii* from the Philippines and found that yield increased at 26–27 °C and decreased at 28–29 °C. The effects of varying salinity were investigated in Brazil with mixed results; Hayashi et al. (2011) found a higher yield at 25 ppt, while Reis et al. (2011) reported a higher yield at 15 ppt. Changes in carrageenan yield in the presence of fixed amount of dissolved inorganic nitrogen (DIN) and dissolved reactive phosphorus (DRP) were investigated by Munoz et al. (2004), where 37.5 ± 1.1% yield was obtained at 5.9 to 10.45 μM L^{-1} DIN and 0.8 to 1.1 μM L^{-1} DRP. Rapid growth rates up to 3.76 ± 0.79% day^{-1} and high biomass production of *Kappaphycus* are usually associated with higher seawater temperatures (de Góes and Reis 2011). Chopin et al. (1995) reported that carrageenan production might be nitrogen-limited, but unlikely to be phosphorous-limited like in the red seaweed *Chondrus crispus*. Higher carrageenan yield does not necessarily imply better quality of carrageenan, whose quality is determined by its gel strength and viscosity (Webber et al. 2012).

Gel strength is an important parameter in the hydrocolloid industry; the structural and compositional characteristics of semi-refined carrageenan (SRC) are very sensitive to the gel forming process (Dewi et al. 2015). According to McHugh (2003), *K. alvarezii* heated in alkaline conditions driven by potassium hydroxide showed increased gel strength. This was ascribed to the hydroxide's ability to penetrate into the cell walls and reducing the amount of sulfate in carrageenan, thereby contributing to the increase of 3,6-anhydrogalactose (3,6-AG). Gel quality is associated with the physiological state of the seaweed, which can be influenced by anthropogenic factors such as the availability of nutrients, pollutants, warming seawater temperature, and ocean acidification (Ghaderiardakani et al. 2020). The viscosity of seaweed-derived hydrocolloids is affected by temperature, shear rate, pressure and time of shearing, total ionic concentration, and ion content of the system (Marcotte et al. 2001; Tecante and Santiago 2012).

Anthropogenic climate change resulting from the burning of fossil fuels since the start of the Industrial Revolution (1760-1840), along with deforestation and unsustainable agricultural practices, has had unequivocal impacts on the Earth's climate (Harley et al. 2006; Laffoley and Baxter 2016; IPCC, 2021). Under various carbon emission scenarios, unless drastic and concerted mitigation action takes place, global air and seawater temperatures are projected to further increase until the end of this century, with an associated increase in ocean acidification and change in world climate (IPCC 2022). The global human population currently at 7.7 billion is expected to reach 9.7 billion by 2050, and 10.5 billion by the year 2100 (United Nations Department of Economic and Social Affairs 2019). Such a large increase in population, 55% of which is expected to live in an urban setting by 2050 (OECD 2020), would generate a proportionately important amount of nitrogen-rich waste, most of which would end up in coastal waters and be taken up by marine plants.

Seaweed growth is primarily controlled by temperature, salinity, nutrient availability, irradiance, and water currents (Glenn and Doty 1990; Verges et al. 2014; Lee 2018). Anthropogenic global warming would have a direct impact on seaweed productivity, for instance from increased rainfall due to extreme weather events and, along the coastline of Pacific Islands, coastal eutrophication caused by deforestation and human population expansion (Harley et al. 2006). Overall, there is likely to be an increase in mean global ocean temperature of 1–4 °C by the year 2100 (IPCC 2021). Also, data from the US National Oceanic and Atmospheric Administration (NOAA) showed that the average global sea surface temperature of the upper few meters of the ocean has increased by approximately 0.13 °C per decade over the past 100 years (Laffoley and Baxter 2016). Hence, a 1 °C increase in sea surface temperature could pose harmful threats to marine species and ecosystems.

Predicted climate change impacts for Fiji, the Solomon Islands, and Kiribati include change in seawater temperature, salinity, and nutrient content of the ocean (Australian Bureau of Meteorology and CSIRO 2011). This would impact the production of *K. alvarezii* cultivated in some of the Pacific islands such as the Solomon Islands, where seaweed cultivation is a main source of income for families in remote areas, and contributes significantly towards national exports (Sabetian et al. 2019). Export of seaweeds is only possible when production of *K. alvarezii* is successful with a high growth rate and carrageenan yield.

The present study investigated the effects of varying temperature, salinity, and nutrient (nitrate) availability on the daily growth rate (DGR), semi-refined carrageenan (SRC) yield, and gel strength of cultivated *K. alvarezii* plants in a laboratory setting simulating various environmental parameters that could occur in future climate change scenarios. Such information is crucial to seaweed farmers in the South Pacific Islands to understand how climate change impacts

the functionality of *K. alvarezii* (Fache et al. 2019; IPCC 2019), coupled with an explosion of urban population (OECD 2020).

Materials and methods

Sample collection

Plants of *Kappaphycus alvarezii* were collected in February and March 2017 (austral summer) from a commercial seaweed farm at Kaba, Fiji (17°58′13.4″S and 178°44′59.6″E) where on-site seawater temperature was 29.0 °C (±1.3 °C), salinity 32.1 ppt (±2.8 ppt), and nitrate (referred as nutrient) concentration 0.2 mg L^{-1} (±0.05 mg L^{-1}). The seaweeds (approximately 4 kg) were transported to the University of the South Pacific's marine laboratory (Suva—18°14′93.0″S and 178°45′39.1″E) in Styrofoam boxes filled with seawater that was collected from the seaweed farm site. These were left to acclimatize for 3 days in a 60-L glass tank filled with seawater at ambient temperature sourced from the sea which was 10 m away from the marine laboratory. The laboratory seawater sourced from the sea was stored in a plastic tank (1000 L) to acclimatize to ambient temperature before being pumped into glass tanks ready for the experiment.

Manipulation of variables

Each of the three variables—temperature, salinity, and nutrient (nitrate)—was manipulated for 15 days with 12 replicates in each treatment (two glass tanks per treatment and each glass tank containing six replicates). A factorial design was used for the experiment, where the three independent variables were set as follows: temperature = 24 °C [T_L] and 30 °C [T_H]; salinity = 25 ppt [S_L] and 40 ppt [S_H]; nitrate concentration = 0.1 mg L^{-1} [N_L] and 0.5 mg L^{-1} [N_H], in a combination. An example of a combined treatment is $T_LS_LN_H$ and an experimental layout is shown in Fig. 1. A control was also set using the environmental parameters measured in the field during sample collection. A glass heater (Aqua One, 150 W) was attached to the glass tank to regulate the temperature at 30 °C; however, the glass heater was removed from the glass tank when the experiment was set at 24 °C. During the experiment, water change was done every second day, with the old seawater being drained out of the glass tank and replaced with fresh laboratory seawater. For salinity regulation, seawater was pumped to all the glass tanks using the laboratory seawater, which had a salinity of 29 ± 1.5 ppt. For treatments with 40 ppt salinity, rock salt was added to increase the salinity and for those treatments at 25 ppt salinity, freshwater was added to decrease salinity. Laboratory grade pelleted sodium nitrate ($NaNO_3$) was used to administer nitrate as nutrient. The concentration of

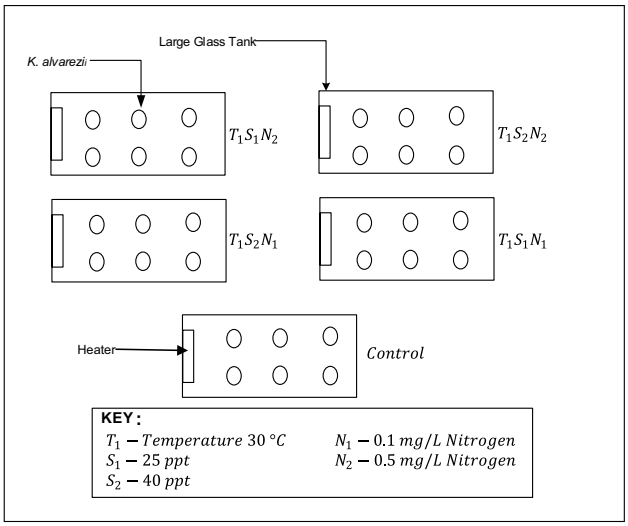

Fig. 1 Experimental layout

sodium nitrate added to the treatments was 0.1 mg L^{-1} and 0.5 mg L^{-1} and was administered once every second day. The irradiance was set at 20.47 µmol m^{-2} s^{-1} as measured by a HOBO (Pendant UA-002-08) data logger.

Measurement of daily growth rate (DGR)

Initial and final seaweed fresh weights were measured to calculate the daily average growth rate (DGR) (% day^{-1}) according to Yong et al. (2013) as per the formula below, where W_t is the final fresh weight (g), W_o is the initial fresh weight (g), and t is the number of culture days:

$$\mathrm{DGR}\left(\%\,\mathrm{day}^{-1}\right) = \left[\left(\frac{W_t}{W_o}\right)^{\frac{1}{t}} - 1\right] \times 100$$

Carrageenan extraction and measurement of gel strength

Carrageenan was extracted from the cultured seaweed using a modified semi-refined carrageenan method of Bono et al. (2014). In our study, cultured seaweeds were dried at 24 °C in an air-conditioned room for 24 h, prior to carrageenan extraction. The SRC yield (%) was calculated using the following formula from Mochtar et al. (2013):

$$\text{SRC yield}(\%) = \frac{\text{dry weight carrageenan (g)}}{\text{weight of extracted sample (g)}} \times 100$$

Extracted carrageenans were made into gels following the method of Thrimawithana et al. (2010). For each control sample, 1.5 g of SRC powder was dissolved in distilled

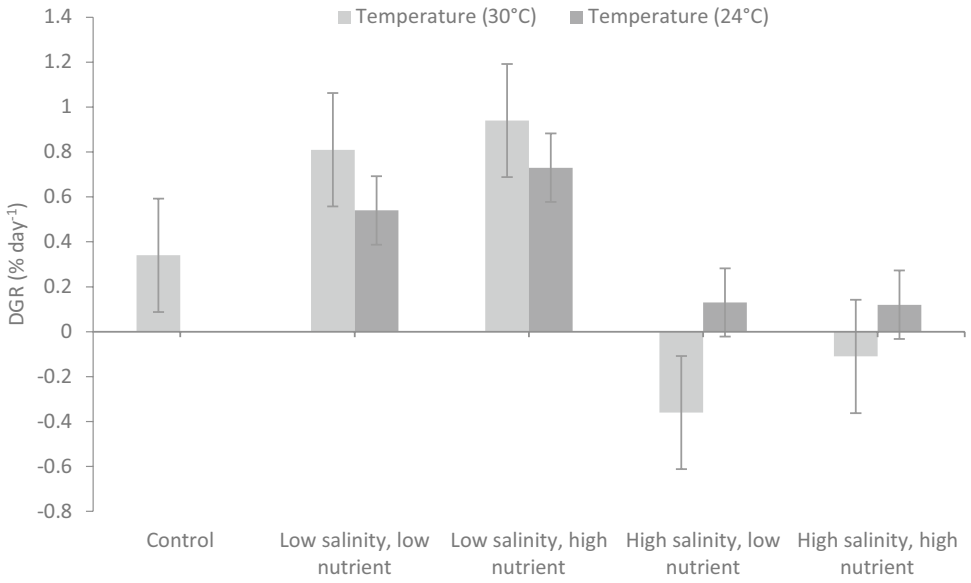

Fig. 2 Mean daily growth rate (DGR % day^{-1} ± standard error) of *Kappaphycus alvarezii* at four different combinations of temperature, salinity, and nutrient concentration. The gray bars represent 30 °C (T_H) and black bars represent 24 °C (T_L). The low salinity, low nutrient (S_LN_L) represents 25 ppt salinity and 0.1 mg L^{-1} nutrient; low salinity, high nutrient (S_LN_H) represents 25 ppt salinity and 0.5 mg L^{-1} nutrient; high salinity, low nutrient (S_HN_L) represents 40 ppt salinity and 0.1 mg L^{-1} nutrient; and high salinity, high nutrient (S_HN_H) represents 40 ppt salinity and 0.5 mg L^{-1} nutrient. For control, the temperature, salinity, and nutrient concentrations were kept matching the values recorded when samples were collected from field where temperature was 29.0 °C (±1.3 °C), salinity 32.1 ppt (±2.8 ppt), and nutrient concentration of 0.2 mg L^{-1} (±0.05 mg L^{-1}). The error bars represent the standard error of DGR per treatment and was calculated using 12 replicates

water with continuous magnetic stirring at 90 °C for 20 to 30 min, after which it was stabilized in a water bath at 80–90 °C. The diluted sample was transferred to a 50-mL plastic beaker for 20 to 30 min of cooling, and then sealed with plastic paraffin film for gel strength and viscosity measurements. Gel strength was measured using a digital texture analyzer (Shimadzu EZ Test) connected to RheoMeter software (version 2.04), and a KU-3 viscometer (Brookfield) to determine viscosity. A compression jig of 7 mm in diameter and a penetration jig of 4 mm in diameter were attached to a force transducer with a maximum applied force of 50 Newtons (N). The viscosity of the SRC gels was determined by a viscometer where a spindle number of 3 was used with a rotational speed of 60 rpm. After six complete revolutions of the spindle, the viscosity reading was recorded (Şen and Erboz 2010; Thrimawithana et al. 2010; Bono et al. 2014).

Pineapple fruit jelly confection

Pineapple fruit jelly was made the same way as SRC gels with some minor alterations. SRC powder was added to 100 mL of commercial pineapple fruit juice (sourced from a supermarket) instead of distilled water. The pH of the pineapple fruit juice was recorded as 3.74 using a pH meter (HANNA Instruments, pH211). Gels were cooled and sealed using plastic paraffin film (Parafilm) and stored at ambient temperature of 28 °C for 24 h prior to gel strength and viscosity analysis following the same methodology as for SRC gels.

Statistical analyses

Experiment-wide correlations were used to investigate the pairwise correlation between DGR, SRC yield, and gel strength, i.e., compression, penetration, and viscosity. The Shapiro-Wilk test was used to test for the normality of the data. Two-way ANOVAs were used to test for the effects of temperature, salinity, and nitrate concentration on DGR, SRC yield, gel strength, and viscosity of *K. alvarezii*. A post hoc test (Tukey HSD) was done to identify exactly which treatments showed a significant effect. For all the statistics, the significance level was set at 0.05. Statistical analyses were performed in R (R Core Team 2020).

Results

Daily growth rate (DGR)

The highest DGR (0.94% day^{-1}) was observed at 30 °C with a salinity of 25 ppt and nutrient as 0.5 mg L^{-1} ($T_HS_LN_H$) (Fig. 2). *Kappaphycus alvarezii* showed a

positive DGR in salinity of 25 ppt, while a loss in *K. alvarezii* biomass was observed at 40 ppt regardless of temperature and nutrient concentration (Fig. 2). A positive DGR was observed at 24 °C with 0.54% day^{-1} and 0.12% day^{-1} being the highest and lowest SRG respectively ($T_LS_LN_L$ and $T_LS_HN_H$, Fig. 2). Similarly, DGRs of 0.13% day^{-1} and 0.12% day^{-1} were noticed at 40 ppt salinity with 0.1 mg L^{-1} and 0.5 mg L^{-1} of nitrate at 24 °C respectively being the positive lowest DGR ($T_LS_HN_L$ and $T_LS_HN_H$, Fig. 2). Also, it was evident from the experiment that low salinity and low nutrient, and low salinity and high nutrient in both the experimental temperatures showed higher DGR compared to the control. There was a significant interactive effect of temperature, salinity, and nutrient on DGR of *K. alvarezii* ($F_{3,88} = 14.060$, $p < 0.001$).

Semi-refined carrageenan (SRC) yield

Higher SRC yields (ranging 75.79 to 58.31%) were obtained at 30 °C in all the combinations of treatments (Fig. 3), while at 24 °C, SRC yields were generally lower, except when salinity was 25 ppt and nutrient concentration at 0.5 mg L^{-1} (SCR yield 68.0% at $T_LS_LN_H$, Fig. 3). Highest SRC yield (75.79%) was recorded at 25 ppt salinity with 0.1 mg L^{-1} nutrient concentration at 30 °C ($T_HS_LN_L$, Fig. 3). The lowest SRC yield (52.70%) was obtained at 24 °C with 40 ppt salinity and 0.5 mg L^{-1} nutrient ($T_LS_HN_H$, Fig. 3). Salinity at 40 ppt with 0.1 mg L^{-1} nutrient and salinity at 40 ppt with 0.5 mg L^{-1} nutrient at 24 °C showed similar SRC yield ($T_LS_HN_L$ and $T_LS_HN_H$, respectively, Fig. 3). The temperature, salinity, and nutrient concentration had a significant interactive effect on the SRC yield of *K. alvarezii*, ($F_{3,16} = 207.70$, $p < 0.001$) with significant effects on temperature ($F_{1,16} = 565.90$, $p < 0.001$) and salinity plus nutrient ($F_{3,16} = 524.90$, $p < 0.001$). Higher carrageenan yields than control occurred with high salinity and low nutrient, and high salinity and high nutrient treatments at 30 °C.

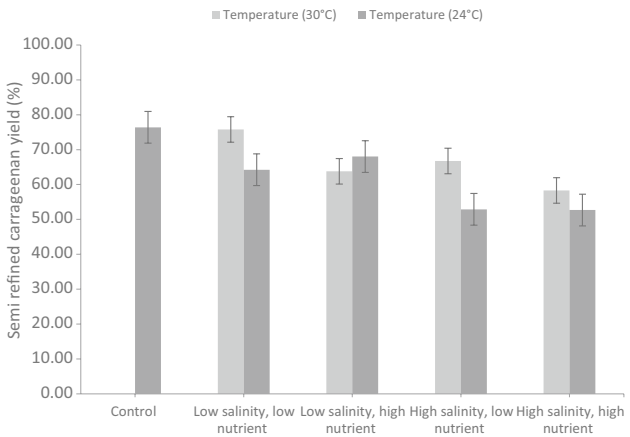

Fig. 3 Semi-refined carrageenan (SRC) yield (%) of *Kappaphycus alvarezii* at four different combinations of temperature, salinity, and nutrient concentration (same as Fig. 2). The error bars represent the standard error of SRC yield per treatment and was calculated on three replicates

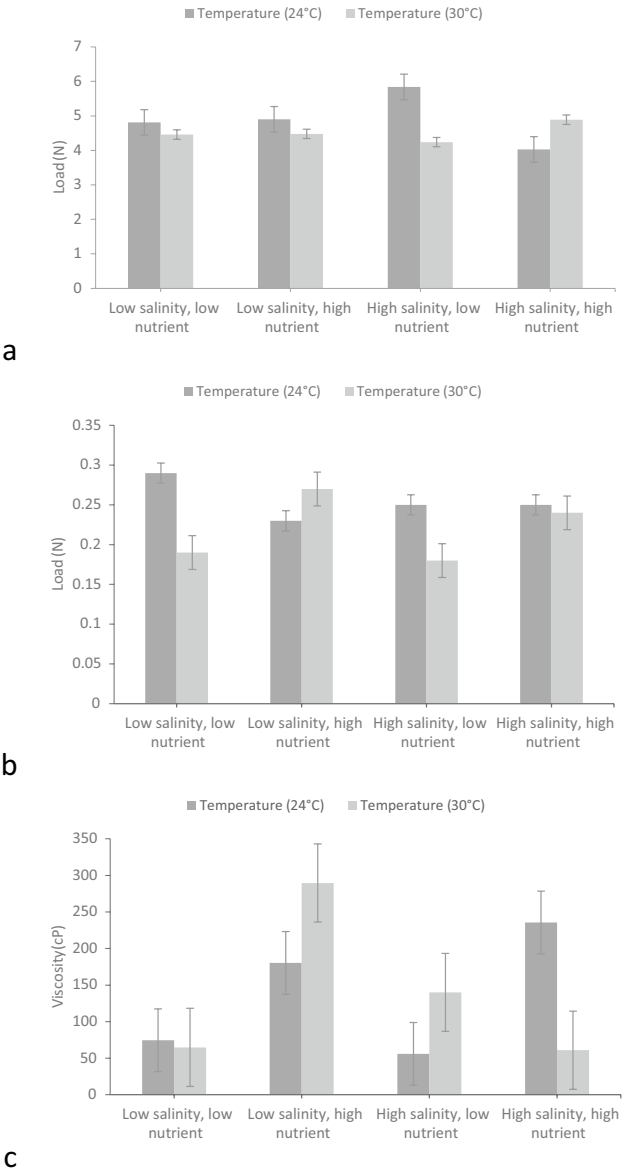

Fig. 4 Quality of gels of *Kappaphycus alvarezii* at four different combinations of temperature, salinity, and nutrient concentration (same as Fig. 2). **a** Compression strength; **b** penetration strength; **c** viscosity. The black bars represent 24 °C and gray bars represent 30 °C. The error bars represent the standard error of compression and penetration strength and viscosity. The standard error for **a** and **b** was calculated on three replicates and for **c**, it was calculated on four replicates

Carrageenan gel strength (compression, penetration) and viscosity

In general, higher compression strengths were recorded on lower temperature treatments, except for the combination of high salinity and high nutrients (Fig. 4a). The highest compression strength (5.84 N) was observed with a combination of low temperature, high salinity, and low nutrients ($T_LS_HN_L$). Temperature, salinity, and nutrient concentrations had significant interactive effects on compression strength of the SRC gels ($F_{3,28} = 3.350$, $p = 0.033$). The highest penetration strength (0.29 N) was obtained with a combination of low temperature, high salinity, and low nutrients ($T_LS_HN_L$, Fig. 4b). The highest viscosity (289.5 cP) was obtained with a combination of high temperature, low salinity, and high nutrient concentration ($T_HS_LN_L$, Fig. 4c). Salinity and nutrients had a significant effect on the viscosity of the SRC gels formed ($F_{3,40} = 16.930$, $p < 0.003$). The interaction between temperature, salinity, and nutrient also had a significant effect on viscosity of SRC gels ($F_{3,40} = 13.910$, $p < 0.002$).

Pineapple fruit gels

Compression strength

The compression strength of *K. alvarezii* pineapple fruit gels when compared to normal gel (made in distilled water) showed that there was an increased compression strength in all the treatments except for three, i.e., temperature of 24 °C with (i) 25 ppt and 0.1 mg L^{-1}, (ii) 40 ppt and 0.1 mg L^{-1}, and (iii) 40 ppt and high 0.5 mg L^{-1} treatments (Table 1). The highest compression strength was 6.34 N with treatment conditions of high temperature (30 °C), low salinity (25 ppt), and low nutrient concentration (0.1 mg L^{-1}) (Table 1). Generally, the compression strength of the obtained gels was higher at higher temperatures. There was a significant interactive effect of salinity and nutrient concentration on the compression strength of SRC gels mixed with pineapple juice ($p < 0.05$).

Penetration strength

The SRC gels of *K. alvarezii* made with pineapple juice showed higher penetration ability at 30 °C than at 24 °C when compared with normal gels (Table 1). The general trend was that at 30 °C, the penetration strength was more than at 24 °C for carrageenan gels made in fruit juice except for the treatment combination of 24 °C, 40 ppt, and 0.1 mg L^{-1}, where the penetration strength remained the same in both types of gel. Comparing compression and penetration strengths of carrageenan gels made in pineapple juice, a greater positive impact of the pineapple juice was seen on compression strength than on penetration strength.

Viscosity

Gels made from *K. alvarezii* cultured at 24 °C and mixed with pineapple juice showed higher viscosity compared to the cultured conditions (Table 1). These results indicate that temperature had a significant effect on the viscosity of the SRC gels made with pineapple juice ($p < 0.001$). There was generally increased viscosity with gels mixed in pineapple juice.

Correlations between variables

There was a positive correlation between DGR and viscosity ($r = 0.55$, $p = 0.027$). However, there were no significant pairwise correlations between DGR, viscosity, and

Table 1 The gel strength (compression and penetration) and viscosity of pineapple fruit gel and normal gel (made in distilled water) made from the extracted semi-refined carrageenan of *K. alvarezii*. Experimental low and high temperatures were 24 °C and 30 °C; low salinity and high salinity were 25 ppt and 40 ppt; and low and high nutrient concentrations were 0.1 mg L^{-1} and 0.5 mg L^{-1}

Treatments	Compression (N)		Penetration (N)		Viscosity (cP)	
	Pineapple juice gel	Normal gel	Pineapple juice gel	Normal gel	Pineapple juice gel	Normal gel
High temperature, low salinity, low nutrient	6.34	4.46	0.28	0.19	112.00	64.75
High temperature, low salinity, high nutrient	5.76	4.48	0.29	0.27	127.50	289.50
High temperature, high salinity, low nutrient	4.97	4.24	0.26	0.18	90.75	140.00
High temperature, high salinity, high nutrient	5.51	4.89	0.27	0.24	108.75	61.00
Low temperature, low salinity, low nutrient	4.49	4.81	0.18	0.29	203.50	74.50
Low temperature, low salinity, high nutrient	4.76	4.90	0.19	0.23	227.00	180.25
Low temperature, high salinity, low nutrient	4.82	5.84	0.25	0.25	182.50	56.00
Low temperature, high salinity, high nutrient	4.29	4.03	8.00	0.25	136.50	235.50

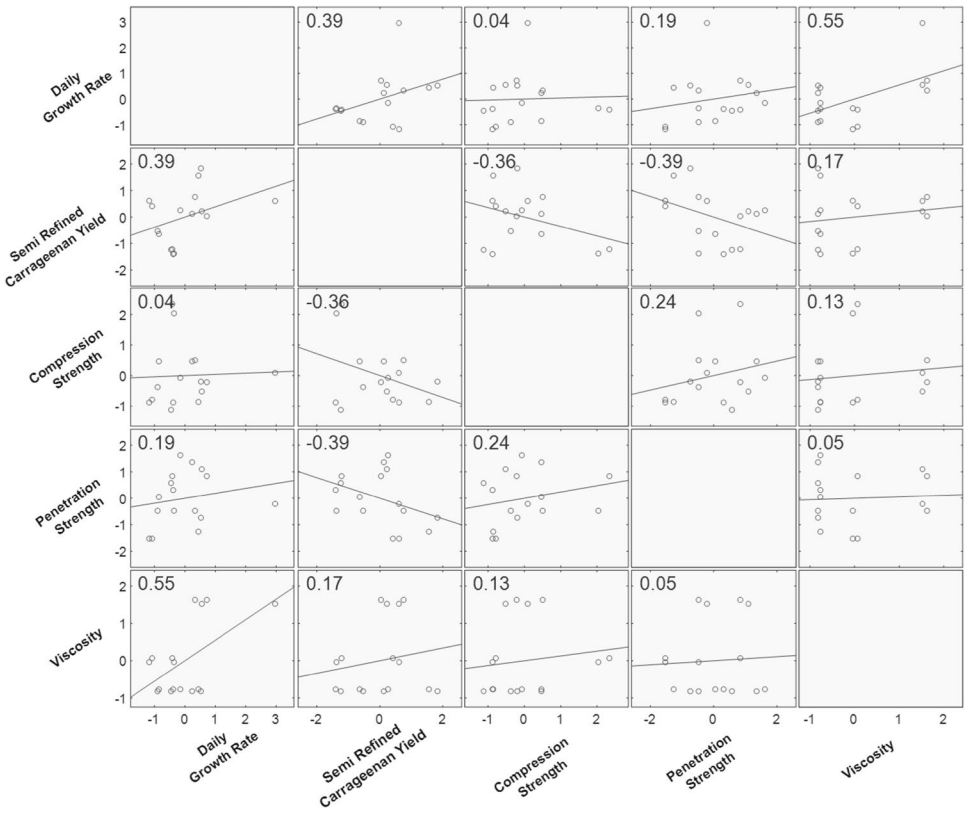

Fig. 5 Correlation matrix showing the correlation between daily growth rate (DGR), semi-refined carrageenan (SRC) yield, gel strength (i.e., compression and penetration), and gel viscosity regardless of the different treatments

the other four variables (SRC yield, compression, penetration, and viscosity). There was no significant pairwise correlation since the data plots (Fig. 5) are scattered. Also, there were no statistical differences in DGR, SRC, gel strength, and gel viscosity found from the correlation coefficient stated in Fig. 5 between the two variables. Notably, a negative correlation was seen between SRC yield and compression strength as well as between SRC yield and penetration strength (Fig. 5).

Discussion

Changing temperature, salinity, and nitrate concentration

The experimental upper maximum cultured temperature of 30 °C used in this research approached the annual average sea surface temperature for Fiji of about 29 °C (Naidu et al. 2017). Our results (Fig. 2) showed that *K. alvarezii* cultured at 25 ppt salinity had positive DGR while the treatment cultured at 40 ppt had loss of biomass, at both temperatures, 24 °C and 30 °C. This would imply that *K. alvarezii* can tolerate low salinity and thrive at 30 °C. In addition to the effects of climate change due to increased concentrations of carbon dioxide in the atmosphere, the chemistry of coastal waters in Fiji is also affected by the El Niño Southern Oscillation (ENSO), manifested in El Niño and La Niña events (Singh et al. 2011) which in turn can affect the growth and mariculture of seaweeds though either drought (El Niño), increased precipitation (La Niña), and resulting variations in surface salinity. Under certain circumstances, increased precipitation coupled with land deforestation can lead to heavy leaching of nutrients from fertilizer-enriched soils into the ocean, contributing to increase in the nitrate, phosphate, and potassium levels available to coastal seaweeds, along with a decrease in salinity affecting seaweed growth and carrageenan quality (Harper et al. 2007).

Daily growth rate (DGR)

In this study, higher *K. alvarezii* DGR values were recorded at 30 °C (0.94% day^{-1}) than at 24 °C, which agrees with published data on the known optimum temperature range of 28–32°C for the highest growth rate (0.015% day^{-1}) in *K. alvarezii* (Terada et al. 2016). Rapid growth rate of 3.76 ± 0.79% day^{-1} and high biomass production of *Kappaphycus* are usually associated with high seawater temperature (de Góes and Reis 2011). The DGR obtained in this study was within the range of growth rates obtained by Ohno et al. (1994) and Hurtado et al. (2001) which were of 0.13–8.12% day^{-1} and 0.2–4.2% day^{-1} respectively. Moreover, the maximum photosynthesis rate for eucheumatoids, which include *K. alvarezii*, occurs at 30 °C (Ask and Azanza 2002).

Loss of biomass in *K. alvarezii* occurred at 40 ppt and positive DGR was observed at 25 ppt at 30 °C. Both the selected salinity levels were outside the range of tolerance known for the species (i.e., from 30 to 35 ppt, in de Góes and Reis 2011). However, our findings of an increased DGR obtained at 25 ppt salinity indicate that Fijian *K. alvarezii* is able to tolerate salinity levels below 30 ppt in a laboratory culture situation. Ding et al. (2013) reported that at high salinity (40 ppt), the chromatoplast structure can be damaged by massive accumulation of excess of salt particles into the cells, thus affecting the efficiency of photosynthetic activity and overall seaweed growth. Xiao et al. (2019) found that the growth rate for any given cultivated seaweed biomass density increased with 1/3 the power of irradiance. That paper also opined that seaweeds growing under high nutrients and sufficient supply of irradiance sustained a high growth rate even though occupying only 2% of the space. This agrees with our results, where it was observed that DGR was higher in treatments with more nutrient concentration, regardless of temperature (Fig. 2).

Semi-refined carrageenan (SRC)

For SRC yield, higher values were observed at 25 ppt salinity. This is likely the effect of the inverse relationship between salinity and carrageenan yield, where an increase in the former leads to a decrease in the latter, and vice versa (de Góes and Reis 2011). Hayashi et al. (2011) argued that when *K. alvarezii* is subjected to low salinity for an extended period of time, this results in phycocolloid deposition in the cell wall, which tends to provide additional structural support for turgid cells, hence increasing the yield. In particular, Hayashi et al. (2011) showed that highest carrageenan yield (35.3%) was obtained at 25 ppt salinity and lowest carrageenan yield was obtained at higher salinities such as 45 ppt (25.4%). In our study, *K. alvarezii* cultured at 0.5 mg L^{-1} nutrient with high salinity at both low and high temperatures yielded lower SRC compared to other treatments (Fig. 3). This may be due to the effect of accumulated nitrogen compounds in the tissues of the seaweeds that lowered the carbon to nitrogen ratio, hence reducing the carrageenan content (Rui et al. 1990). The low carrageenan content in seaweeds due to increased nitrogen availability has been described by Neish et al. (1977) and Chopin et al. (1995) as the Neish effect.

Long-term environmental stress may result in the seaweeds adapting to changing environmental conditions at the genomic level (Morgan-Kiss et al. 2006; Ghaderiardakani et al. 2020). In contrast, short-term physiological alterations also happen where seaweeds acclimatize in response to short-term transitory changes in the environmental conditions (Borowitzka 2018; Ghaderiardakani et al. 2020). Under short-term stress, seaweeds do not have enough time to adapt and need to develop new survival strategies. This short-term stress could affect *K. alvarezii* carrageenan yield and quality. Experimental studies serve as the baseline to understand the impacts and outcomes of various climate change and environmental scenarios on marine species.

Carrageenan gel strength

According to Ohno et al. (1994), the gelling properties of *K. alvarezii* increased when cultured in lower seawater temperature, which agrees with our results. This was evident in the high gel strength for *K. alvarezii* grown at 24 °C compared to 30 °C. According to de Góes and Reis (2011), *K. alvarezii* cultured at 24.6 °C showed gel strength of 395.1 ± 100.6 g cm^{-2}. Additionally, compression and penetration strengths for SRC gels were higher for *K. alvarezii* cultured at 0.5 mg L^{-1} nutrient with 25 ppt salinity (Fig. 4a and b). On the other hand, in our results, *K. alvarezii* cultured at 30 °C showed high gel strength for 0.5 mg L^{-1} nutrient concentration with 40 ppt salinity. This observation agrees with previously published work reporting that an increase in gel strength of carrageenan occurs at increasing nitrogen availability (Craigie et al. 1984; Bird 1988; Rui et al. 1990).

Viscosity

In our study, *K. alvarezii* cultured at 24 °C with 40 ppt salinity and 0.5 mg L^{-1} nutrient concentration showed higher SRC gel viscosity (Fig. 4c), possibly because viscosity strongly increases with increasing salinity. According to Iglauer et al. (2011), cations appear to influence viscosity of carrageenan gels, resulting in stronger molecular aggregations and double-helix formation of *kappa*-carrageenans, resulting in higher viscosity. This could explain why our results at the lower salinity (cation) concentration of 25 ppt with 0.1 mg L^{-1} nutrient generally showed a lower viscosity. The viscosity of carrageenans is also reported to decrease with higher seawater temperature (Iglauer et al. 2011); however, this is the opposite to what was observed in our study. Such a difference could be explained by other interacting factors such as salinity and nutrient concentrations acting simultaneously.

Pineapple fruit gels

In our study, greater gel strength was observed for *K. alvarezii* at 30 °C when made in pineapple fruit juice compared to that in distilled water (Table 1). This could be because carrageenan acted as a gelling agent in the fruit juice (Saha and Bhattacharya 2010), while the cooling process in extracting SRC caused the carrageenan to become strongly cross-linked and form aggregates, hence achieving greater gel strength (Kaya et al. 2015). The pH also plays an important role in gel strength, leading to hardness and

rigidity at a pH of 3.5 (Yamamoto and Cunha 2007; Picone and Cunha 2011). Pineapple fruit juice is strongly acidic, with a pH of 3.74; hence, our results agree with previously published data on the effects of low pH on increased gel strength.

Conclusions and recommendations

Our results suggest that projected impacts of both anthropogenic climate change and natural (ENSO) events until the end of this century would not be significantly detrimental to the cultivation of *K. alvarezii*, and possibly other red seaweeds, grown in the Pacific Island region. This information is important to seaweed farmers in small island nations in the Pacific and could encourage an increase in seaweed farming as an adaptation measure for climate change and sea-level rise. This is especially applicable to low-lying atoll communities with very little arable land, whose already minimal to non-existent agricultural sector had been negatively impacted by climate change through coastal erosion and sea-level rise. Further research is required to better define the temperature thresholds for optimal growth, high yield, and quality of carrageenan in several other genera of commercial seaweeds such as *Gracilaria* and *Hypnea* growing in Pacific Islands. Extrapolating the results of our research to the local seawater temperature and salinity conditions of other island nations within the Pacific region would provide tailored solutions to optimise their seaweed cultivation and yield in the face of climate change impacts.

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Author contribution AS: data curation, formal analysis, funding acquisition, investigation, writing—original draft. AN: writing, mentoring—review and editing. JL: conceptualization, supervision, writing—review and editing. SP: conceptualization, supervision, writing—review and editing. All authors read and approved the final manuscript.

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Data availability All data available as supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

References

Adharini RI, Suyono EA, Jayanti AD, Setyawan AR (2019) A comparison of nutritional values of *Kappaphycus alvarezii*, *Kappaphycus striatum*, and *Kappaphycus spinosum* from the farming sites in Gorontalo Province, Sulawesi, Indonesia. J Appl Phycol 31:725–730

Ask EI, Azanza RV (2002) Advances in cultivation technology of commercial eucheumatoid species: a review with suggestions for future research. Aquaculture 206:257–277

Australian Bureau of Meteorology and CSIRO (2011) Climate change in the Pacific: scientific assessment and new research. Volume 1: Regional Overview. Volume 2: Country Reports. Australian Bureau of Meteorology, Commonwealth Scientific and Industrial Research Organisation, Canberra, p 257

Bird KT (1988) Agar production and quality from *Gracilaria sp.* strain G — 16: effects of environmental factors. Bot Mar 31:33–38

Bono A, Anisuzzaman S, Ding OW (2014) Effect of process conditions on the gel viscosity and gel strength of semi-refined carrageenan (SRC) produced from seaweed (*Kappaphycus alvarezii*). J King Saud Univ - Eng Sci 26:3–9

Borowitzka MA (2018) The 'stress' concept in microalgal biology—homeostasis, acclimation and adaptation. J Appl Phycol 30:2815–2825

Chopin T, Gallant T, Davison I (1995) Phosphorus and nitrogen nutrition in *Chondrus crispus* (Rhodophyta): effects on total phosphorus and nitrogen content, carrageenan production, and photosynthetic pigments and metabolism. J Phycol 31:283–293

Chen Y, Liao ML, Dunstan DE (2002) The rheology of K+-κ-carrageenan as a weak gel. Carbohydr Polym 50:109–116

Craigie J, Wen Z, Van der Meer J (1984) Interspecific, intraspecific and nutritionally-determined variations in the composition of agars from *Gracilaria* spp. Bot Mar 27:55–62

de Góes HG, Reis RP (2011) Temporal variation of the growth, carrageenan yield and quality of *Kappaphycus alvarezii* (Rhodophyta, Gigartinales) cultivated at Sepetiba bay, southeastern Brazilian coast. J Appl Phycol 24:173–180

Dewi EN, Ibrahim R, Suharto S (2015) Morphological structure characteristic and quality of semi refined carrageenan processed by different drying methods. Procedia Environ Sci 23:116–122

Ding L, Ma Y, Huang B, Chen S (2013) Effects of seawater salinity and temperature on growth and pigment contents in *Hypnea cervicornis* J. Agardh (Gigartinales, Rhodophyta). BioMed Res Int 2013:594308. https://doi.org/10.1155/2013/594308

Diyana FA, Abdullah A, Shahrul HZA, Chan K (2015) Antioxidant activity of red algae *Kappaphycus alvarezii* and *Kappaphycus striatum*. Int Food Res J 22:1977–1984

Eldredge L (1994) Perspectives in aquatic exotic species management in the Pacific Islands. Vol 1. South Pacific Comission, Noumea, New Caledonia.

Fache E, Dumas P, De Ramon N'Yeurt A (2019) An interdisciplinary overview of some climate-related narratives and responses in the Pacific. J Soc Océan 149:199–210

Gereniu CRN, Saravana PS, Getachew AT, Chun BS (2017) Characteristics of functional materials recovered from Solomon Islands red seaweed (*Kappaphycus alvarezii*) using pressurized hot water extraction. J Appl Phycol 29:1609–1621

Ghaderiardakani F, Quartino ML, Wichard T (2020) Microbiome-dependent adaptation of seaweeds under environmental stresses: a perspective. Front Mar Sci 16:575228

Glenn EP, Doty MS (1990) Growth of the seaweeds *Kappaphycus alvarezii, K. striatum* and *Eucheuma denticulatum* as affected by environment in Hawaii. Aquaculture 84:245–255

Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Tornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environ Conservat 34:325–333

Hayashi L, Faria GS, Nunes BG, Zitta CS, Scariot LA, Rover T, Felix MR, Bouzon ZL (2011) Effects of salinity on the growth rate, carrageenan yield, and cellular structure of *Kappaphycus alvarezii* (Rhodophyta, Gigartinales) cultured in vitro. J Appl Phycol 23:439–447

Hayashi L, Reis RP (2012) Cultivation of the red algae *Kappaphycus alvarezii* in Brazil and its pharmacological potential. Rev Bras Farmacogn 22:748–752

Hung L, Hori K, Nang H, Kha T, Hoa L (2009) Seasonal changes in growth rate, carrageenan yield and lectin content in the red alga *Kappaphycus alvarezii* cultivated in Camranh Bay, Vietnam. J Appl Phycol 21:265–272

Hurtado A, Agbayani R, Sanares R, Castro-Mallare M (2001) The seasonality andeconomic feasibility of cultivating *Kappaphycus alvarezii* in Panagatan Cays, Caluya, Antique, Philippines. Aquaculture 199:295–310

Iglauer S, Wu Y, Shuler P, Tang Y, Goddard WA (2011) Dilute iota-and kappa carrageenan solutions with high viscosities in high salinity brines. J Petrol Sci Eng 75:304–311

Ingle K, Vitkin E, Robin A, Yakhini Z, Mishori D, Golberg A (2018) Macroalgae biorefinery from *Kappaphycus alvarezii*: conversion modelling and performance prediction for India and Philippines as examples. BioEnergy Res 11:22–32

IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner HO, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (Eds.) Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. https://www.ipcc.ch/sr15/chapter/spm/

IPCC (2019) Summary for policymakers. In: Pörtner HO, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds.) IPCC special report on the ocean and cryosphere in a changing climate. https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/03_SROCC_SPM_FINAL.pdf

IPCC (2021) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds.) Climate change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar6/wg1/downloads/report/IPCC_AR6_WGI_SPM_final.pdf

Kaya AO, Suryani A, Santoso J, Rusli MS (2015) The effect of gelling agent concentration on the characteristic of gel produced from the mixture of semi-refined carrageenan and glukomannan. Int J Sci: Basic Appl Res 20:313–324

Laffoley D, Baxter JM (eds) (2016) Explaining ocean warming: causes, scale, effects and consequences. Full report. IUCN, Gland, Switzerland

Lee RE (2018) Phycology, 5th edn. Cambridge University Press, Cambridge

Luxton D, Robertson M, Kindley M (1987) Farming of *Eucheuma* in the South Pacific Islands of Fiji. Hydrobiologia 151:359–362

Marcotte M, Hoshahili ART, Ramaswamy H (2001) Rheological properties of selected hydrocolloids as a function of concentration and temperature. Food Res Int 34:695–703

McHugh DJ (2003) A guide to the seaweed industry FAO Fisheries Technical Paper 441. Food and Agriculture Organization of the United Nations, Rome pp 51–72

McHugh DJ (2006) The seaweed industry in the Pacific Islands. ACIAR Working Paper No. 61. Australian Centre for International Agricultural Research, Canberra. 55 pp

Mochtar AH, Parawansa I, Ali MSS, Jusoff K, Reta R, Astuti SD, Azis N, Muchdar A, Palad MS, Hikma N, Kasmawati M, Nirwan (2013) Effects of harvest age of seaweed on carrageenan yield and gel strength. World Appl Sci J 26:13–16

Morgan-Kiss RM, Priscu JC, Pocock T, Gudynaite-Savitch L, Huner NPA (2006) Adaptation and acclimation of photosynthetic microorganisms to permanently cold environments. Microbiol Molec Biol Rev 70:222–252

Munoz J, Freile-Pelegrín Y, Robledo D (2004) Mariculture of *Kappaphycus alvarezii* (Rhodophyta, Solieriaceae) color strains in tropical waters of Yucatán, México. Aquaculture 239:161–177

Naidu R, Muller-Karger F, McCarthy M (2017) Mapping of benthic habitats in Komave, coral coast using WorldView-2 satellite imagery. In: Filho WL (ed) Climate change impacts and adaptation strategies for coastal communities. Springer, Cham, pp 337–356

Neish A, Shacklock P, Fox C, Simpson F (1977) The cultivation of *Chondrus crispus*. Factors affecting growth under greenhouse conditions. Can J Bot 55:2263–2271

OECD (2020) Cities in the world: a new perspective on urbanisation. OECD Urban Studies. OECD Publishing, Paris

Ohno M, Largo DB, Ikumoto T (1994) Growth rate, carrageenan yield and gel properties of cultured kappa-carrageenan producing red alga *Kappaphycus alvarezzi* (Doty) Doty in the subtropical waters of Shikoku, Japan. J Appl Phycol 6:1–5

Orbita MLS (2013) Growth rate and carrageenan yield of *Kappaphycus alvarezii* (Rhodophyta, Gigartinales) cultivated in Kolambugan, Lanao del Norte, Mindanao, Philippines. Advn Ag Bot 5:128–139

Orbita MLS, Arnaiz JA (2014) Seasonal changes in growth rate and carrageenan yield of *Kappaphycus alvarezii* and *Kappaphycus striatum* (Rhodophyta, Gigartinales) cultivated in Kolambugan, Lanao del Norte. Adv Ag Bot 6:134–144

Picone CSF, Cunha RL (2011) Influence of pH on formation and properties of gellan gels. Carbohydr Polym 84:662–668

Prakash J (1990) Fiji. In: Adams T, Foscarini R (eds). Proceedings of the regional workshop on seaweed culture and marketing. FAO South Pacific Aquaculture Development Project, Suva. iv + 86 p.

Ram V (1991) The seaweed industry in Fiji, with specific reference to *Eucheuma* (Rhodophyta). The University of the South Pacific Marine Studies Programme Technical Report Series 1991/2. The University of the South Pacific, Suva, p 19

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria

Reis RP, Loureiro RR, Mesquita FS (2011) Does salinity affect growth and carrageenan yield of *Kappaphycus alvarezii* (Gigartinales/Rhodophyta)? Aquacult Res 42:1231–1234

Rui L, Jiajun L, Chaoyuan W (1990) Effect of ammonium on growth and carrageenan content in *Kappaphycus alvarezii* (Gigartinales, Rhodophyta). Hydrobiologia 204:499–503

Sabetian A, Breen D, Vavia A, Chan C, Garofe W, Robinson M, Misiga S, Diake S, Teri J, Masu R, Panda R, Sulu R, Schwartz AM, Walter R, Fenigolo J, White L (2019) SINOPSIS–The Solomon Islands National Ocean Planning Spatial Information System: spatial decision support tools for seaweed aquaculture planning in

the Solomon Islands. New Zealand Institute for Pacific Research (NZIPR), Auckland, p 68

Saha D, Bhattacharya S (2010) Hydrocolloids as thickening and gelling agents in food: a critical review. J Food Sci Technol 47:587–597

Şen M, Erboz EN (2010) Determination of critical gelation conditions of κ-carrageenan by viscosimetric and FT-IR analyses. Food Res Int 43:1361–1364

Singh A, Delcroix T, Cravatte S (2011) Contrasting the flavors of El Niño-Southern Oscillation using sea surface salinity observations. J Geophys Res 116:C06016

Sopade P, Halley P, Cichero J, Ward L, Liu J, Varliveli S (2008) Rheological characterization of food thickeners marketed in Australia in various media for the management of dysphagia. III. Fruit juice as a dispersing medium. J Food Eng 86:604–615

South G (1993) Seaweeds. In: Wright, A. & Hill, L., eds. Nearshore marine resources of the South Pacific: information for fisheries development and management. Canada: Institute of Pacific Studies, Suva, Forum Fisheries Agency, Honiara and International Centre for Ocean Development 683–710

Tecante A, Santiago MDCN (2012) Solution properties of κ-carrageenan and its interaction with other polysaccharides in aqueous media. In: De Vicente J (ed) Rheology. InTech, Rijeka, pp 241–264

Terada R, Vo TD, Nishihara GN, ShioyaK Shimada S, Kawaguchi S (2016) 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 App Phycol 28:457–467

Thrimawithana T, Young S, Dunstan D, Alany R (2010) Texture and rheological characterization of kappa and iota carrageenan in the presence of counter ions. Carbohydr Polym 82:69–77

United Nations, Department of Economic and Social Affairs, Population Division (2019) World population prospects 2019: Highlights. ST/ESA/SER.A/423

Usov AI (2011) Polysaccharides of the red algae. Adv Carbohydr Chem Biochem 65:115–217

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA et al (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Roy Soc B 281:20140846

Webber V, Carvalho SMD, Ogliari PJ, Hayashi L, Barreto PLM (2012) Optimization of the extraction of carrageenan from *Kappaphycus alvarezii* using response surface methodology. Food Sci Technol (Campinas) 32:812–818

Yamamoto F, Cunha R (2007) Acid gelation of gellan: effect of final pH and heat treatment conditions. Carbohydr Polym 68:517–527

Yermak IM, Mischchenko NP, Davydova VN, Glazunov VP, Tarbeeva DV, Kravchenko AO, Pimenova EA, Sorokina IV (2017) Carrageenans-sulfated polysaccharides from red seaweeds as matrices for the inclusion of echinochrome. Mar Drugs 15:337

Yong YS, Yong WTL, Anton A (2013) Analysis of formulae for determination of seaweed growth rate. J Appl Phycol 25:1831–1834

Xiao X, Agusti S, Lin F, Xu C, Yu Y, Pan Y, Li K, Wu J, Duarte CM (2019) Resource (light and nitrogen) and density-dependence of seaweed growth. Front Mar Sci 6:618