Eucheumatoid seaweed farming under global change - Tomini Bay seaweed trial indicates *Eucheuma denticulatum* (*spinosum*) could contribute to climate adaptation

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Abstract. Farming of eucheumatoid seaweeds plays an important role in many tropical and equatorial coastal communities, supporting economic activity from local to global scales. Carbon capture has also been proposed as an added benefit of seaweed farming, potentially contributing to global climate change (GCC) mitigation. Historically, research and development of tropical/equatorial seaweed mariculture and downstream uses/products has concentrated on *Kappaphycus alvarezii*, while *Eucheuma denticulatum* has received much less attention. Comparative trials of *K. alvarezii* and *E. denticulatum* growth were conducted at Silampayang, Parigi Moutong District, situated close to the equator in the semi-enclosed Tomini Bay, Sulawesi, Indonesia. A medium scale (1 ha plot) longline culture method was used. Environmental parameters (water temperature, pH, dissolved oxygen, salinity, visibility, current speed and direction) were measured (2-8 times/day at 2-3 days intervals) at 8 stations along an inshore-offshore gradient. Weight and condition (SeaPlantNet scale) of 10 randomly selected thalli were recorded weekly. Water temperature during the study period was relatively high (28-33°C, mostly 30-31°C); conversely pH was relatively low (6.2-7.8). Harvested weight (at 45 days) was seven times higher for *E. denticulatum* than for *K. alvarezii*. Condition of *E. denticulatum* thalli was consistently green (healthy) while *K. alvarezii* thalli tended to suffer from pests and diseases including ice-ice. The fast growth and resistance to disease of *E. denticulatum* under conditions similar to those predicted to become more widespread due to GCC indicates potential for expanding culture of this species, particularly in equatorial regions. Such an expansion, accompanied by downstream research and development, could be considered as part of a GCC adaptation strategy.
Key Words: global climate change, mitigation and adaptation, eucheumatoid seaweeds, SeaPlantNet health scale, Sulawesi.

Introduction. The red seaweeds or Rhodophyta comprise many species of ecological importance, a growing number of which are also becoming valuable commodities, either wild-collected or farmed (Largo et al 2017). Over the past decade, the eucheumatoid carrageenophyte seaweeds (genera *Eucheuma* and *Kappaphycus*) have overtaken the brown seaweeds (dominated by the genera *Laminaria* and *Undaria*) in terms of global production tonnages (Hurtado et al 2019). The culture of these seaweeds plays an important role in many tropical and equatorial coastal communities, supporting economic activity from local to global scales (Neish et al 2017; Neish & Suryanarayan 2017; Hurtado et al 2019).

The taxonomy of algae in general and the Rodophyta in particular is the object of active research, especially since the advent of molecular biology methods (Lim et al 2017). This is certainly the case with the carrageenan-producing eucheumatoid seaweeds (Tan et al 2012; Lim et al 2017; Tan et al 2017). *Eucheuma cotonii* (Weber-van Bosse, 1913) has been reclassified and as a result renamed as *Kappaphycus alvarezii* (Doty) Doty ex P.C. Silva, 1996 (Guiry & Guiry 2020). However, this seaweed is still frequently referred to as 'cotoni' or 'cotonii' by farmers, traders and industry (Neish et al 2017). *Eucheuma spinosum* (Agardh, 1847) is now an invalid synonym of *E. denticulatum* (N.L. Burman) Collins & Hervey, 1917 but similarly still frequently referred to as *'spinosum'* in the trade (Neish et al 2017).

Seaweeds of the genera *Eucheuma* and *Kappaphycus* occur throughout the Indo-Pacific, especially in Southeast Asia (Hussein et al 2011; Tan et al 2012) and have been introduced to several regions of the world where they are not native (Neish et al 2017; Hurtado et al 2019). While research on and subsequent large scale production of eucheumatoid seaweeds began in the 1960-s and 1970's in the Philippines, Indonesia has been the major producer nation since around 2007 (Neish et al 2017).

In recent decades research and development of tropical/equatorial red seaweed mariculture and downstream uses/products, especially with respect to carrageenan, has concentrated on *K. alvarezii* (a kappa carrageenan producer), while *E. denticulatum* (an iota carrageenan producer) has received much less attention. However *E. denticulatum* was once a commodity of greater interest than *K. alvarezii* (Neish et al 2017), and interest in applications for this species appears to be growing, with recent research on non-carrageenan products from eucheumatoid seaweeds (Neish & Suryanarayan 2017; Tan et al 2017; Hessami et al 2018) as well as in other field such as the genome and gene expression (Hussein et al 2011; Othman et al 2019).

As the effects of global climate change (GCC) become ever more apparent, affecting both marine and terrestrial realms (Poloczanska et al 2013; Hoegh-Guldberg et al 2018) with serious economic consequences (DeFries et al 2019), the potential of so-called "Blue Carbon" marine ecosystems to absorb and sequester carbon could be critical to mitigation efforts (Duarte et al 2013). In addition to the now ubiquitously recognised and increasingly understood role of seagrasses, mangroves and saltmarshes in carbon capture, interest in marine macroalgae is also growing (Lovelock & Duarte 2019). It has been suggested that carbon capture could be a significant benefit of seaweed farming (Froehlich et al 2019), potentially making a significant contribution to GCC mitigation efforts (Turan & Neori 2010; Chung et al 2011; Duarte et al 2017). In addition to carbon capture, potential benefits in GCC mitigation include the production of low carbon footprint food, carbon-neutral bioenergy from seaweed, reduction in methane emissions through seaweeds as bovine feed additives, avoidance of adverse impacts through substituting seaweed for synthetic fertilisers; while potential contributions to adaptation include shoreline protection through absorption of wave energy, reduction of ocean acidification impacts on calcifiers through elevated daytime pH around seaweeds, and lessening the impacts of reduced oxygen absorption at higher temperatures through oxygen release (Turan & Neori 2010; Duarte et al 2017).

In this context, it is important to know how the various cultivated seaweeds respond to changing marine environments, including changes already occurring or likely to occur due to GCC. There are indications that eucheumatoid seaweeds are already suffering negative impacts from GCC (Aslan et al 2015; Largo et al 2017). In particular, the prevalence and virulence of the still poorly understood ice-ice disease seems to increase when temperatures exceed the optimum range for these species (Largo et al 2017). Research on photosynthesis and respiration at different temperatures (Glenn & Doty 1981) indicates that *E. denticulatum* may fare better at high seawater temperatures than *K. alvarezii*. However, reports on field studies (trials) with different species of eucheumatoid seaweeds with relatively comprehensive environmental data are limited.

This paper presents data collected during a comparative trial of *K. alvarezii* and *E. denticulatum* which was conducted in Tomini Bay, Indonesia, the largest semi-enclosed bay bisected by the equator.

Material and Method

Description of the study site. This study was conducted at Silampayang, Parigi Moutong District, Central Sulawesi Province This site is situated close to the equator in the semi-enclosed Tomini Bay, Indonesia (Figure 1). The trial took place in in September and October 2011, one year after a prolonged high temperature anomaly in Tomini Bay which resulted in widespread coral bleaching (Muslihuddin et al 2012).

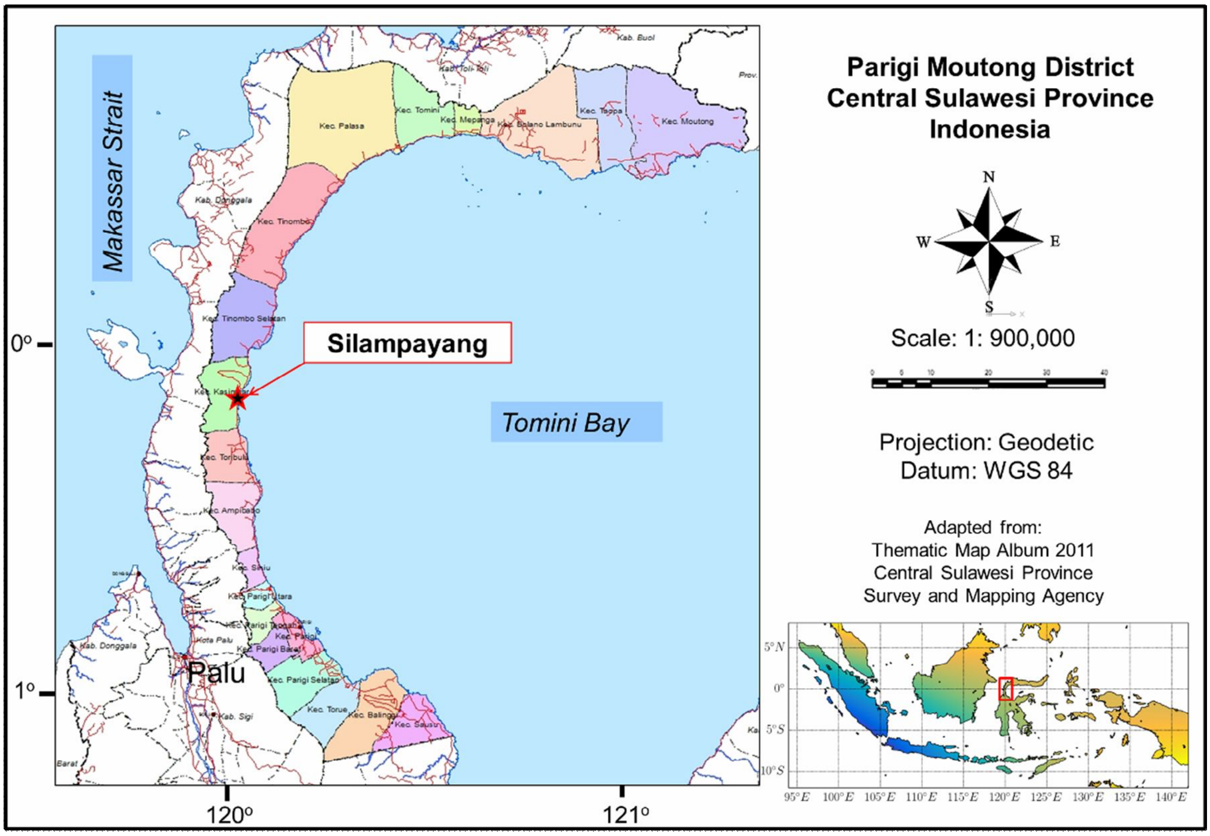


Figure 1. Administrative map of Central Sulawesi Province, Indonesia showing the study site Silampayang) in Parigi Moutong District, on the coast of Tomini Bay.

A medium scale (100 m x 100 m = 1 ha) longline culture plot was used (Figure 2). Environmental parameters (Table 1) were measured at 8 stations along an inshore-offshore gradient (Table 2). Measurements were made at 0.5 m (planting depth) twice a day on three days. On one day in each week, measurements were made eight times/day at 3 hour intervals, also at 0.5 m depth. Temperature data were also collected weekly at depths of 0.5-5 m (0.5 m intervals). Water samples were collected using a Nansen bottle and parameters measured immediately (on-board).

Figure 2. The 1 hectare cultivation plot. Lines of *K. alvarezii* and *E. denticulatum* were distributed randomly throughout the plot, with 1 m spacing between lines, and 20 cm between seeds.

Table 1

Water quality monitoring parameters and equipment

Parameter	*Unit*	*Equipment*
Water temperature	ºC	Glass alcohol thermometer (Precision 0.05ºC)
pH		pH meter (Lutron pH-201)
Dissolved oxygen (DO)	ppm	DO meter (Lutron DO-5509)
Visibility	m	Secchi disc[a]
Salinity	ppt	Refractometer (Vee Gee STX-3)
Current speed	$cm\ s^{-1}$	Cruciform drogue[b]
Current direction	Degrees	Compass (Eiger hand-held)

[a] Custom made, specifications in English et al (1997); [b] Obtained from local chandlery: plastic float and metal vanes, attached to a reel.

Table 2

Water quality monitoring stations along a transect perpendicular to the coastline, from seawards of the trial site (station 1) to the shoreward margin (Station 8) of the community seaweed farming area situated between the trial site and the shoreline

Station	*Coordinates*[a]	
	Latitude S	*Longitude E*
1	0º 04’ 30.0”	120º 02’ 22.5”
2	0º 04’ 29.1”	120º 02’ 20.4”
3	0º 04’ 29.8”	120º 02’ 17.1”
4	0º 04’ 29.4”	120º 02’ 14.4”
5	0º 04’ 27.7”	120º 02’ 12.4”
6	0º 04’ 26.8”	120º 02’ 09.5”
7	0º 04’ 26.5”	120º 02’ 07.6”
8	0º 04’ 25.8”	120º 02’ 04.9”

[a] Garmin GPSMAP 76CSx (datum WSG 84).

Seaweed seeds (weight approximately 50 g) were attached to polyethylene rope at 20 cm intervals (Figure 3a). Weight and condition of 10 randomly selected thalli were recorded weekly (Figure 3b). These thalli were marked with numbered tags. These procedures were the same for both seaweed species.

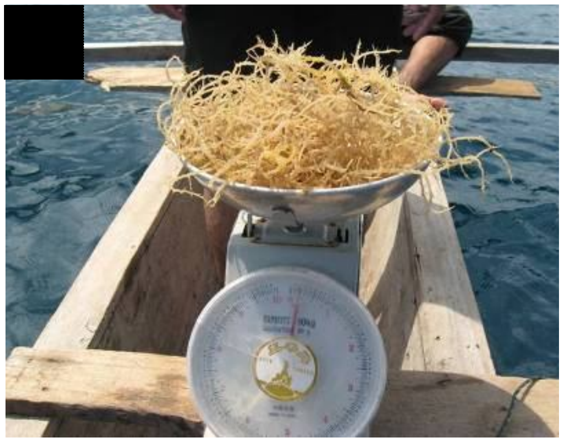


Figure 3. Seaweed trial: a. a longline newly planted with *E. denticulatum* (50 g seeds); b. weighing a healthy (GN) *E. denticulatum* thallus on day 7 of the trial.

Seedling condition was measured using the SeaPlantNet scale (Neish 2008). This qualitative scale is shown in Figure 4, together with examples of some condition categories observed.

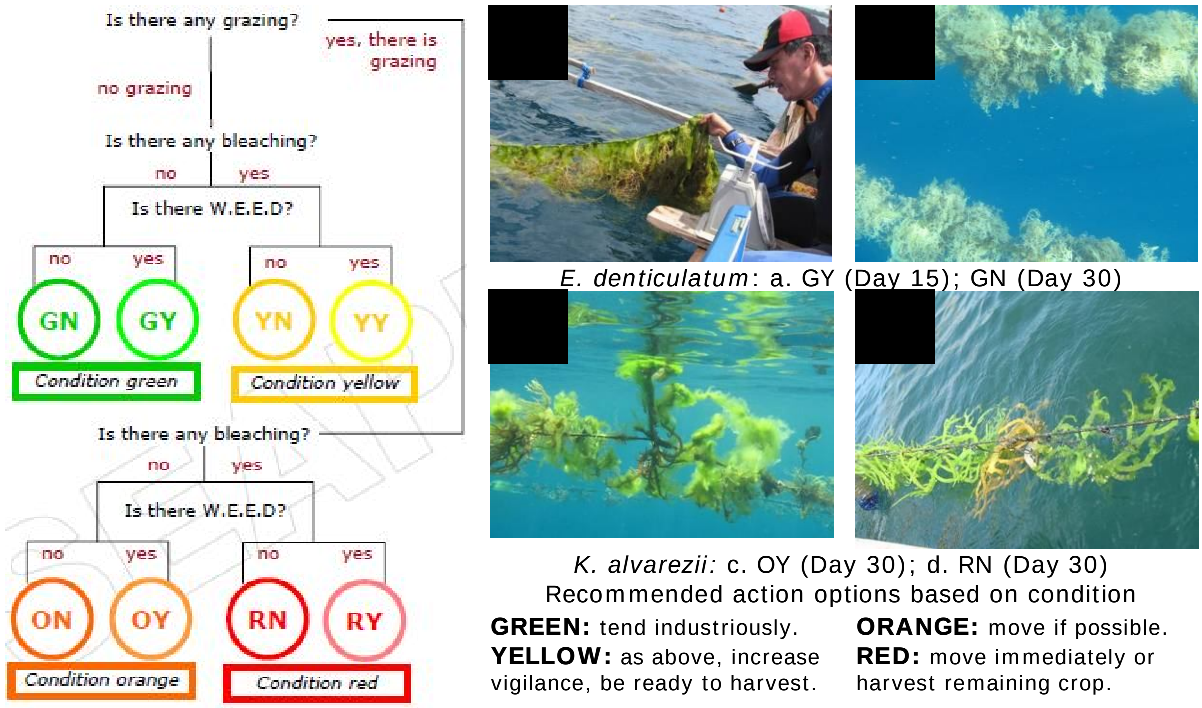


Figure 4. The SeaPlantNet scale (Neish 2008) with some examples from the study site.

Data were tabulated and analysed graphically in Microsoft Excel 2007. The results were analysed descriptively with reference to relevant literature and historical data. The sampled seedling weight for the two species cultivated was compared at weekly intervals using the Student t-test for independent samples. The statistical analyses were conducted in R version 3.6.0, in the RStudio version 1.1.456 environment.

Results

Seedling growth. The mean harvested weight (at 45 days) was seven times higher for *E. denticulatum* (2720 g/thallus) than for *K. alvarezii* (124 g/thallus) (Figure 5). The variability was high, with standard deviation for *E. denticulatum* in range of 6.7-20% and for *K. alvarezii* of 7.4-33.5%. Nonetheless, the difference between the means was highly significant ($p < 0.001$) for all time periods (Day 7, Day 15, Day 30 and Day 45).

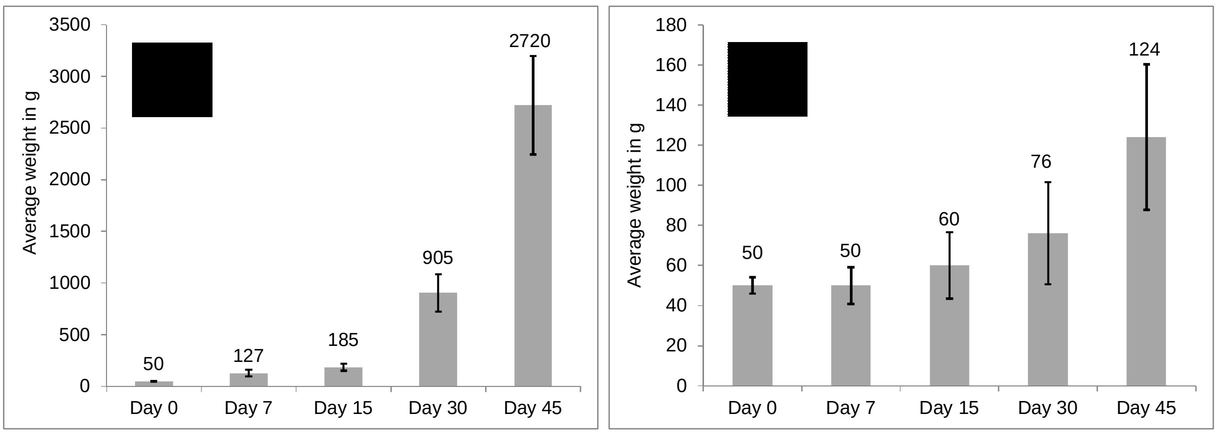


Figure 5. Growth of seaweed seedlings during the trial: a. *E. denticulatum*; b. *K. alvarezii*.
The figures above the bars are mean seed weight; error bars indicate standard deviation (SD).

Seedling condition. The condition varied over time but was consistently better, on average, for *E. denticulatum* than for *K. alvarezii*. The observed conditions covered a wider range than that exhibited by the sampled seedlings in Table 3. Examples of the various condition categories observed during the trial are shown in Figure 6.

Table 3

Condition of sampled seaweed seedlings at weekly intervals during the trial (ten thalli per species, in descending condition order)

Eucheuma denticulatum condition					*Kappaphycus alvarezii condition*				
Day 0	*Day 7*	*Day 15*	*Day 30*	*Day 45*	*Day 0*	*Day 7*	*Day 15*	*Day 30*	*Day 45*
GN	GN	GN	GN	GN	GN	OY	YY	YY	YY
GN	GN	GN	GN	GN	GN	RY	YY	YY	YY
GN	GN	GN	GN	GN	GN	RY	YY	YY	YY
GN	GN	GN	GN	GN	GN	RY	YY	YY	YY
GN	GN	GN	GN	GN	GN	RY	YY	YY	YY
GN	GN	GN	GY	GN	GN	RY	YY	OY	OY
GN	GY	GN	GY	GN	GN	RY	YY	OY	OY
GN	GY	GY	GY	GY	GN	RY	OY	OY	OY
GN	GY	GY	GY	GY	GN	RY	RY	RY	OY
GN	GY	GY	GY	GY	GN	RY	RY	RY	RY

Figure 6. Examples of seaweed condition during the trial. a. *Eucheuma denticulatum* on Day 45 (GN); b. *E. denticulatum* on Day 30 (GY); c. *Kappaphycus alvarezii* infested with *"bulubabi"* epiphyte (dark spots) on Day 15 (YY); d. *K. alvarezii* recovering with new shoots on Day 45 (GN).

Condition of nearly all *E. denticulatum* thalli was consistently Green (healthy), with (GY) or without (GN) epiphytes, although a few thalli with some signs of grazing (ON and OY) were seen. The *K. alvarezii* thalli tended to suffer from pests and diseases including ice-ice, epiphytic green algae, mainly *Ulva* sp. (similar to *E. denticulatum*), and a condition called "*bulubabi*" by local farmers. However, by the final week (Day 40-45) some of the thalli which had suffered from predation but not from ice-ice or "bulubabi" had healed and started to grow and initiate new shoots. Examples of the various condition categories observed during the trial are shown in Figure 6. The prevalence of the epiphyte "*bulubabi*" (Figure 6c) was highest close to the shore (close to stations 6-8), with none observed in the most seaward area (around stations 1-3).

Environmental parameters. The temperature profile data measured at 0.5 m depth intervals showed differences between stations and weeks but no difference with depth below 1 m (Table 4). Samples taken at 10 m depth at the stations furthest offshore (where the water depth was 15-30 m) also showed no difference compared with the temperatures at 1-5 m depth. The temperature at 0.5 m depth and (to a lesser extent) at 1 m depth varied with time of day, being warmest in the late afternoon and coldest in the early hours of the morning before dawn. In general the depth profile was uniform from 0-5 m from around mid-morning until early afternoon.

Table 4

Temperature (ºC) profile data (1-5 m depth) at 8 stations at weekly intervals during the 45 day trial

Depth (m)	*Day 0*	*Day 7*	*Day 15*	*Day 30*	*Day 45*
0-0.5	31-32	31-32	31	30.5-31	30-31.5
1	31-32	31-31.5	31	30	31
1.5 to 5 m[a]	31-31.5	31	31	30	31

[a] Measured at 0.5 m intervals; the range shown is between stations, the coolest being furthest offshore (Station 1) and the warmest closest to shore (Station 8), as below 1 m the temperature was uniform at each station.

Water temperature at 0.5 m depth during the study period was relatively high (28-33°C, mostly 30-31°C) with an overall 24 hour average of 30.5°C; conversely pH was relatively low (6.2-7.8). The mean values measured at each station are shown in Table 5. The inshore stations (6-8) had higher variability (reflected in higher standard deviation values) for all parameters measured. The most extreme values were also recorded in theses stations, including the highest temperatures (Figure 7) as well as the lowest pH, DO and salinity (Figure 8). Current direction changed with the daily tidal cycle and was similar across the area (Figure 9a). Low current speeds were also more frequent and occurred during a greater proportion of the tidal cycle in the inshore areas (Figure 9b).

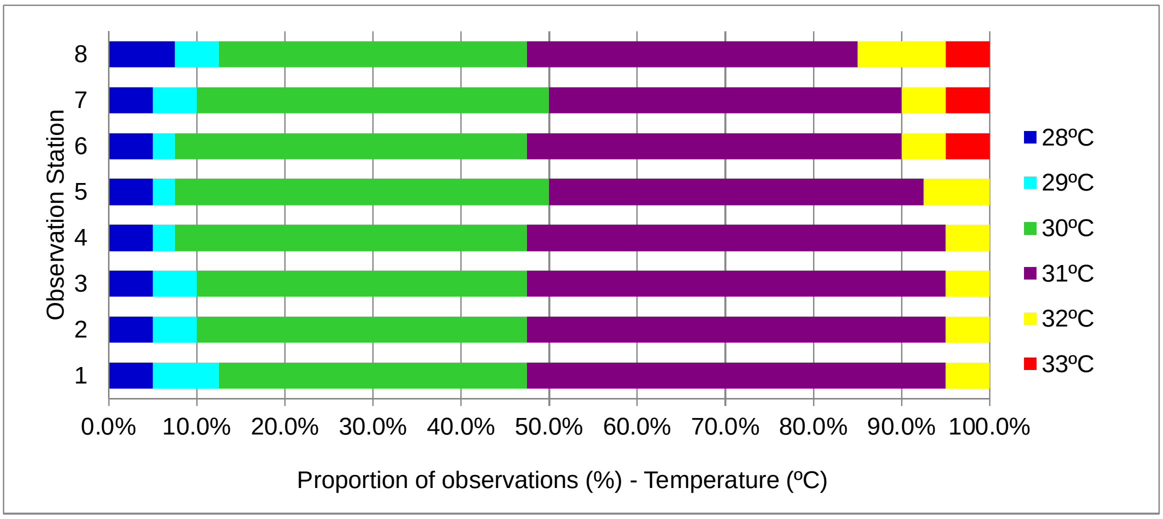


Figure 7. Water temperature in °C at 0.5 m depth by station.

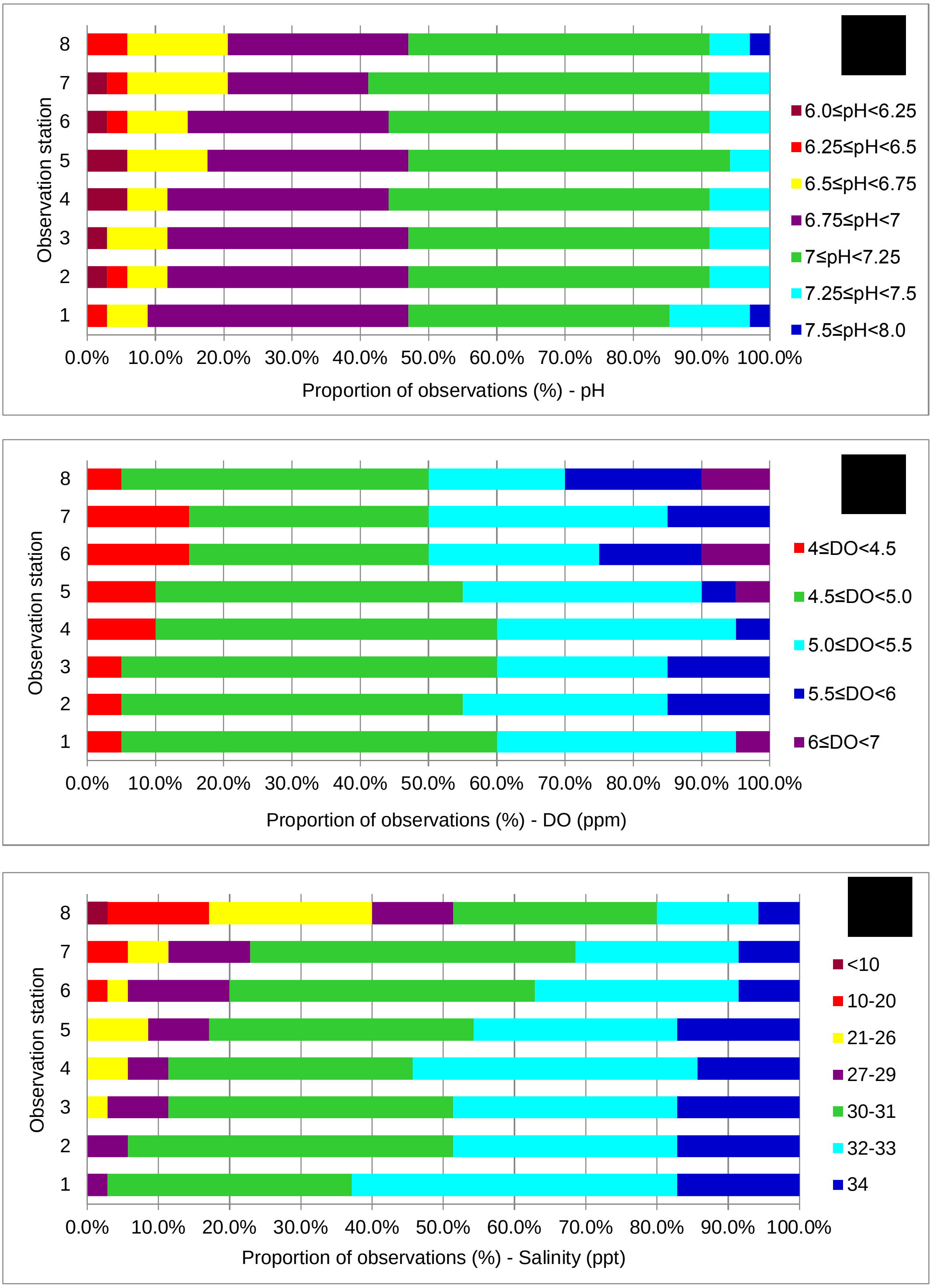
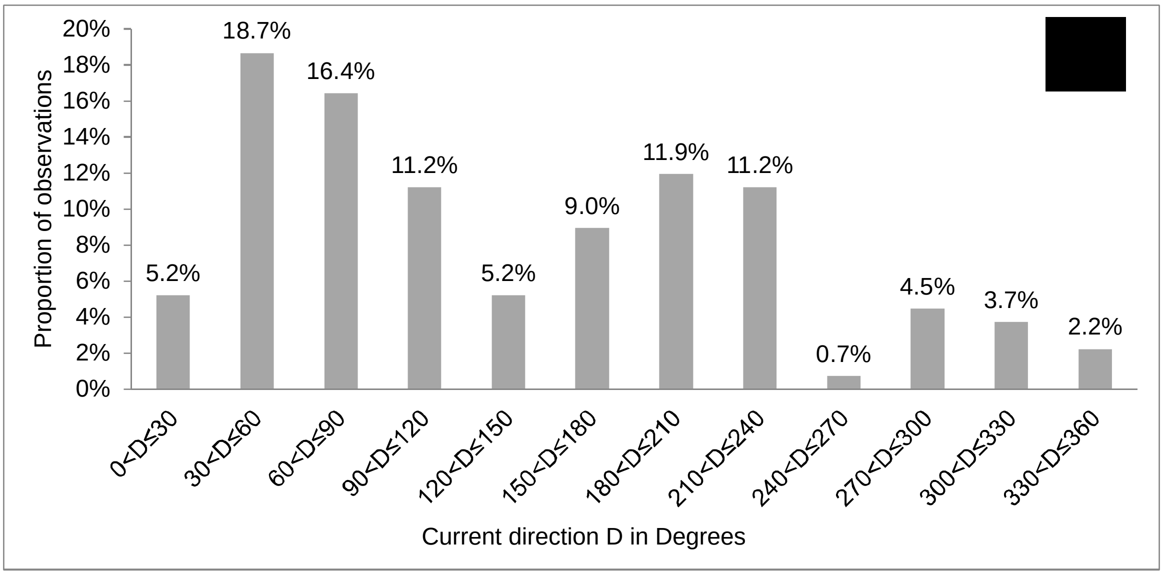


Figure 8. Water quality parameter values at 0.5 m depth by station. a. pH; b. dissolved oxygen (DO, ppm); c. salinity (ppt).

Table 5

Values of the water quality parameters measured at 0.5 m depth over the 45 day trial period by station (mean ± standard deviation)

Parameter	*Unit*	*Range per station*							
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Temperature	°C	30.39 ±0.87	30.43 ±0.87	30.43 ±0.87	30.45 ±0.85	30.45 ±0.87	30.51 ±0.98	30.49 ±1.03	30.50 ±1.16
pH	-	6.99 ±0.28	6.98 ±0.24	6.98 ±0.23	6.97 ±0.26	6.97 ±0.24	6.97 ±0.26	6.98 ±0.24	6.97 ±0.30
DO	ppm	5.00 ±0.41	5.02 ±0.47	5.03 ±0.40	4.95 ±0.35	5.03 ±0.49	5.07 ±0.63	5.04 ±0.58	5.16 ±0.60
Salinity	ppt	32.06 ±1.47	31.66 ±1.64	31.43 ±1.96	31.23 ±2.17	30.91 ±2.69	30.51 ±2.74	29.89 ±3.65	26.77 ±6.30
Current speed	cm s^{-1}	4.23 ±2.36	4.52 ±2.32	3.91 ±1.90	4.10 ±4.39	3.88 ±2.61	3.39 ±2.77	3.39 ±2.77	3.39 ±2.77



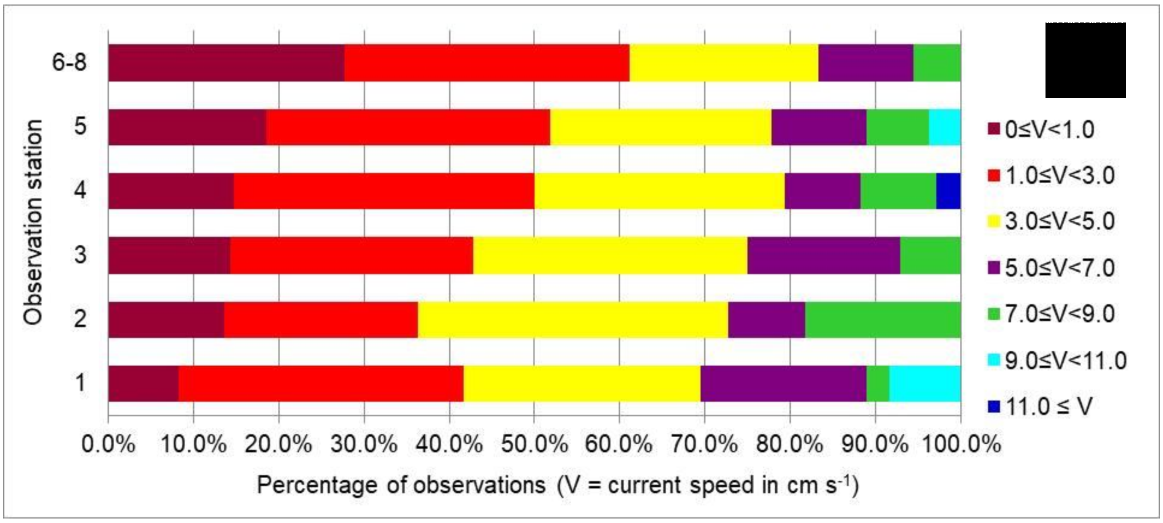


Figure 9. Current speed (a) and direction (b) by station measured over the study period.

Discussion

Influence of environmental parameters. The findings of this study indicate that under the conditions experienced *E. denticulatum* (*spinosum*) grew well and gave a considerably higher yield than *K. alvarezii* (*cottonii*). The poor performance of *K. alvarezii* is similar to that obtained in 2008 during a trial on the south coast of Tomini Bay in Ampana Tete Sub-District, Tojo Unauna District (A. M. Moore & S. Ndobe unpublished data). The data from the 2008 study show a strong negative correlation between seawater temperature and seaweed growth at day 45 (6 weeks after planting) with R^2 = 0.762, indicating that approximately 87% of the variation could be explained by mean water temperature over the period. While grazing was a problem at all stations, negative growth due to the ice-ice disease was a major problem at three stations which experienced temperatures above 30ºC for more than 3 weeks (i.e. over half of the planting to harvest cycle).

The relationship between seaweed growth and temperature has been studied for a range of species, including the two species (*E. denticulatum* and *K. alvarezii*) in this study. In general, the form of the relationship is a positive up to a given temperature where it remains fairly constant until a physiological tolerance limit is reached and mortality occurs (Neish 2008). In particular, the balance between photosynthesis and respiration breaks down above the temperature at which photosynthesis peaks and then declines sharply until lethal temperature is reached. A study on photosynthesis and respiration in *E. denticulatum* and *Kappaphycus striatus* (previously *Eucheuma striatum*) Tambalang and Elkhorn varieties (Glenn & Doty 1981) found similar maximum photosynthesis peaks (30-32°C depending on treatment); however, *E denticulatum* had a much slower decline in photosynthesis above this peak than the *Kappaphycus* varieties. This indicates that *E. denticulatum* should be more likely to be able to sustain respiration and other metabolic functions at higher temperatures. Similarly, Borlongan et al (2017) found differences in temperature tolerance between *E. denticulatum* (19-33ºC), a brown strain of *K. alvarezii* (20-29ºC) and a green strain of *K. alvarezii* (17-32ºC). In our study, although qualitative data were not collected, there was no apparent difference between the performance of brown and green *K. alvarezii* thalli.

While there is no doubt that, at the global scale, seawater temperatures are rising, at a finer scale the seawater temperature can be highly variable both temporally and spatially (Liu et al 2014). In addition to the underlying upwards trend in mean temperatures, there is also an upwards trend in the occurrence and severity of so-called "marine heatwaves" (Fordyce et al 2019; Oliver et al 2019). These have been defined as a period of at least 5 consecutive days with seawater temperature above the 90th percentile of historically observed values for that location for that time of year, and can have a wide range of negative consequences on marine organisms and ecosystems (Hobday et al 2018).

The relatively high seawater temperatures in Tables 3 and 4 and Figure 7 may well have been related to the thermal anomaly in Tomini Bay in 2010. This anomaly was detected by the US National Oceanographic and Atmospheric Agency (NOAA) Coral Reef Watch (CRW) program (Strong et al 2011) during the 2010 mass coral bleaching event (JWRC and GCRMN 2010). The CRW methodology (Strong et al 2011) uses the widely recognised Degree Heating Week (DHW) unit (Kayanne 2017), a measure of heat stress combining the effects of magnitude and duration of sea surface temperature (SST) that exceeds the expected summertime conditions accumulated across a rolling 12-week period (Fordyce et al 2019). Data from the NOAA CRW website (Figure 10) shows that in 2010 Tomini Bay experienced an extended temperature anomaly of at least 16 DHW, the highest category on the scale used. This thermal anomaly appears to qualify as a marine heatwave, and resulted in significant coral bleaching in Tomini Bay, including both Parigi Moutong and Tojo Unauna Districts (Muslihuddin et al 2012).

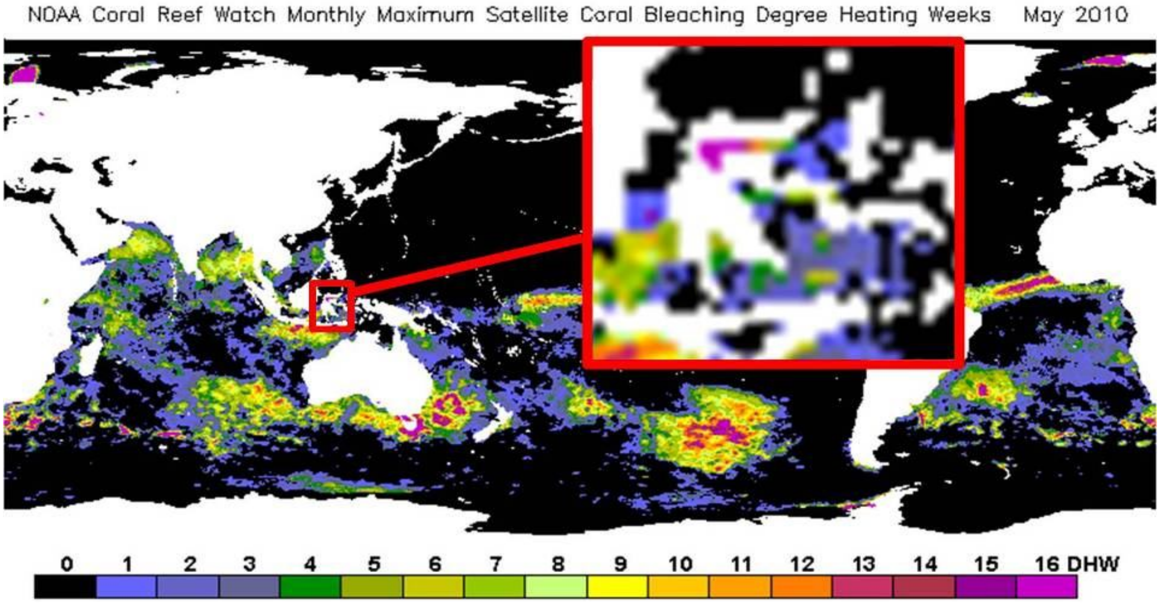


Figure 10. The global thermal anomaly of 2010 - degree heating weeks (DHW) to May 2010. Insert: central Indonesia, including Sulawesi with inset showing 16 DHW in western Tomini Bay (Source: https://coralreefwatch.noaa.gov/).

The authors directly experienced the results of heating when diving at several sites around Tomini Bay during and after the anomaly. Seawater temperatures were unusually (at times uncomfortably) warm down to depths of 10 metres or more; there was little or no change with depth. This is in contrast to the period 1999-2009 where the ambient temperature was noticeably lower at deeper depths, and abrupt thermoclines generally occurred at depths between 2 and 5 m.

Pests and diseases. In this study, although some damage from herbivory was observed, the main apparent causes of seaweed morbidity and mortality/tissue loss in *K. alvarezii* were the ice-ice disease and epiphytic algae. At the time of the trial, the cause of the condition called "*bulubabi*" (pig bristles) by local seaweed farmers (Figure 6c) was unknown. However, the symptoms are very similar or identical to those reported from infestations of parasitic red seaweeds belonging to the genus *Polysiphonia* in Chile (Leonardi et al 2006), Madagascar (Tsiresy et al 2016), the Philippines (Largo 2002; Hurtado et al 2006) and/or the genus *Neosiphonia* in the Philippines, Indonesia, Malaysia, Tanzania and China (Vairappan et al 2008; Tsiresy et al 2016). Largo (2002) describes small, slightly elevated pores on the surface of the thalli around the epiphytes as "goosebumps", while the "hairy" appearance giving rise to the name "*bulubabi*" is described in several studies (Critchley et al 2004; Tsiresy et al 2016). Excrescences observed in thalli affected by "*bulubabi*" seem to be similar to the "galls" described by Critchley et al (2004) as being produced where the epiphytes attached to *K. alvarezii* thalli in the Philippines. Vairappan et al (2008) describe the appearance of black spots prior to the "hairy" phase, as was observed at the Silampayang site in our study.

In *Gracilaria*, Leonardi et al (2006) report that *Polysiphonia harveyi* penetrated between the cells and deep into the host seaweed; cellular compression as well as partial digestion of the cell wall and the cytoplasm were observed in the host seaweed when its cells came contact with the rhizoid of the epiphyte. Despite the extensive damage which could be caused by these mechanisms, Leonardi et al (2006) still classed *Polysiphonia harveyi* as an epiphyte rather than a parasite, as "intercellular connections, like those reported for parasitic red algae and their hosts [...], were not detected". Describing the results of *Polysiphonia* infestation, Critchley et al (2004) report that the *Kappaphycus* thalli rotted, fragmented and fell off the cultivation lines. They furthermore state that the epiphyte attack resulted in economic and environmental problems, with farmers giving up and, in some cases, returning to destructive fishing practices (dynamite and or cyanide fishing). Similar symptoms are reported for infestation by *Neosiphonia apiculata*

(Vairappan et al 2008). In addition, Vairappan et al (2008) found evidence that these infestations can alter the bacterial communities present on host thalli and promote the proliferation of pathogenic bacteria and secondary bacterial infections.

It is not clear which of these two genera caused the infestation in Tomini Bay, however it seems likely that several (possibly all) reported *Polysiphonia* infestations in the Indo-Pacific region may in fact have been *Neosiphonia* infestations (Neish 2008; Vairappan et al 2008). Such a confusion would explain the similar (or even identical) symptoms reported for these two genera. Furthermore, Tsiresy et al (2016) report that epiphyte infestations in Tanzania could be comprised of up to 8 species, identified as belonging to the two genera *Polysiphonia* and *Neosiphonia* based on morphological characters. When analysed using molecular biology (DNA) methods (sequences from a 253-bp portion of the rbcL gene), these species formed a monophyletic clade, indicating a need for further investigation and possible revision of the taxonomy of these epiphytes.

Infestations of "*bulubabi*" were most severe in the areas of our study site where fluctuations in salinity, pH and temperature were most extreme and current velocity was generally low. This is consonant with the results of studies on infestations of *Polysiphonia* and/or *Neosiphonia*, both of which appear to be more prevalent where there are "drastic" fluctuations in water quality parameters such as salinity, temperature and nutrient levels (Vairappan et al 2008), low water motion and high light levels (Neish 2008; Hurtado et al 2006) and elevated water temperatures, especially when combined with any other potential stressors (Israel et al 2010).

Unlike "*bulubabi*", green algal epiphytes (*Ulva* sp. and other) were more prominent in the areas further offshore where there was less fluctuation in water quality and more water movement due to waves and currents. These epiphytes were observed on *E. denticulatum* as well as on *K. alvarezii*. While on the former they appeared to be mainly a nuisance from the point of view of harvesting and processing, on the latter their presence was often associated with that of the ice-ice disease. It is not known whether there was a causal link between green algal epiphyte cover and disease, as seems likely to be the case for infestation by the red algal epiphytes described above. However, in this trial the prevalence of both red and green algal epiphytes was (positively) correlated with temperature. This indicates possible interactions between epiphytes and the ice-ice disease and/or possible shared causal factors (e.g. seawater temperature).

Potential of E. denticulatum for GCC mitigation and adaptation. In this trial, *E. denticulatum* exhibited fast growth and resistance to disease of under sub-optimal conditions. The thalli remained healthy and grew rapidly and the thalli retained a healthy appearance even when infested with epiphytes (mostly green algae, dominated by *Ulva* sp.), i.e. condition GY. The currently more valuable and favoured *K. alvarezii* performed poorly under the same conditions. The most challenging environmental conditions during the trial, in terms of parameters such as water temperature, pH and DO, can be considered similar to those predicted to become more widespread under anthropogenic climate change (Doney 2010; Gattuso et al 2015). The trial results indicate the potential for expanding culture of *E. denticulatum* in areas already or likely to become unsuitable for *K. alvarezii* cultivation, particularly in equatorial regions. Furthermore, as an application of the "Blue Carbon" concept, farming climate tolerant seaweed could contribute to climate change mitigation through carbon absorption and sequestration (Lovelock & Duarte 2019).

An expansion of *E. denticulatum* culture could be considered as part of a GCC adaptation strategy in terms of maintaining production volume. However, the *E. denticulatum* produced would need to be absorbed by the market at prices which could maintain production value and economically viable livelihoods. These considerations imply that developments in agronomy need to be accompanied by downstream research and development, in order to expand the demand and for this seaweed in terms of both diversity and volume. This was highlighted by Hurtado et al (2019) who considered that an initial wave of research and development on eucheumatoid seaweed products (focused largely on carrageenan) had been followed by a period of stagnation with "a paucity of innovation leading to new applications and markets for at least two to three decades".

There are signs of renewed interest in research on products from seaweeds, including *E. denticulatum*. Some promising avenues include the use of *E. denticulatum* as a source of biomass for biofuels and bioethanol (Sondak et al 2016; Neish & Suryanarayan 2017; Alfonsín et al 2019); commercial liquid fertilisers or biostimulants (Eswaran et al 2005), and the development of zero-effluent seaweed processing with a wide array of potential products (Neish & Suryanarayan 2017). There is also potential for expanding the use of *E. denticulatum* for human consumption and health; for example as a sea vegetable (Hurtado et al 2019), as a food ingredient (Faris et al 2019), as an edible film (Farhan & Hani 2017), and as a source of anti-oxidants, anti-inflammatory agents and other bioactive compounds (Balasubramaniam et al 2015; Podungge et al 2018).

Conclusions. This study found that, under a localised marine heatwave scenario, *Eucheuma denticulation* was able to thrive and performed significantly better than *Kappaphycus alvarezii* in terms of both growth and health. The fast growth and resistance to disease of *E. denticulatum* under conditions similar to those predicted to become more widespread due to global climate change (GCC) indicates potential for expanding culture of this species, particularly in equatorial regions. Such an expansion, accompanied by downstream research and development, could be considered as part of a GCC adaptation strategy.

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