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Ecological co-benefits from sea cucumber farming: *Holothuria scabra* increases growth rate of seagrass

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ABSTRACT: Sea cucumber aquaculture is increasing in extent and importance throughout the Indo-Pacific region, supplying a luxury seafood market in Asia. In this context, the grow-out of hatchery-bred juveniles in community-farmed pens is proving to be a viable model, providing increased income security and alternative livelihood options to resource-limited communities. Here, we report a study of the impacts of such sea cucumber farming on the growth of seagrass (a favourable habitat for the animals) at a village-scale aquaculture site in southwest Madagascar. Using experiments, we found that the presence of the hatchery-bred sea cucumber *Holothuria scabra* (sandfish), at stocking densities of 300 g m⁻² (similar to the density used in the farmed pens, but relatively high for natural populations), resulted in a large (~30%), statistically significant increase in the leaf extension rate of the locally dominant seagrass species *Thalassia hemprichii*. However, the other dominant seagrass species, *Cymodocea serrulata*, did not significantly change its leaf extension rate in the presence of *H. scabra*. Since seagrass is a globally important coastal habitat, supporting high biodiversity, carbon sequestration, shoreline stability and nursery grounds for commercial and small-scale fisheries, the positive effect of *H. scabra* farming on the growth rate of at least one dominant seagrass species implies potential important ecological co-benefits. These co-benefits of *H. scabra* farming are likely to be relevant across the tropical Indo-Pacific coastlines, where this species is cultured.

KEY WORDS: *Holothuria scabra* · Sea cucumber aquaculture · Seagrass · *Thalassia hemprichii* · *Cymodocea serrulata* · Madagascar · LMMA · Ecosystem services

1. INTRODUCTION

Holothuroids (sea cucumbers) are benthic organisms belonging to Phylum Echinodermata. They have been harvested for centuries to supply Asian seafood markets, primarily as a luxury dried food item known as bêche-de-mer or trepang (Purcell 2014, Juinio-Meñez et al. 2017). One of the most valuable of these species is *Holothuria scabra* Jaeger,

1833 ('sandfish' or known in local dialect in SW Madagascar as 'zanga fotsy'), which inhabit shallow coastal waters such as seagrass beds across the Indo-Pacific (Mercier et al. 2000, Hamel et al. 2001, Purcell et al. 2012a,b). Rising demand in the 1980s led to the depletion and over-extraction of sea cucumber fisheries and natural stocks (Mercier et al. 1999). In some cases, exploitation became so severe that fisheries governance and regulatory measures alone have

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been incapable of restoring populations (Mercier et al. 1999, Anderson et al. 2011, Friedman et al. 2011, Purcell et al. 2012a, Conand 2018), leading to the development of the sea cucumber aquaculture sector (Eriksson et al. 2012, Purcell et al. 2012b). Typically selling for up to US\$165 kg⁻¹ (for specimens <8 cm) and more than US\$840 kg⁻¹ (for specimens >12 cm) in Hong Kong or Guangzhou, *H. scabra* is now the most extensively cultured tropical species of sea cucumber (Purcell 2014, Juinio-Meñez et al. 2017).

In the southwest region of Madagascar, sea cucumber fishing in shallow coastal lagoons is an integral aspect of the livelihoods of the Vezo people who inhabit this region (Rasolofonirina 2007, Robinson & Pascal 2009). Since 2009, the British-based conservation group Blue Ventures (BV) has been making considerable progress working with communities to develop an innovative sea cucumber aquaculture livelihood model in the village of Tampolove, a small Vezo fishing village situated in the protected waters of the Velondriake locally marine managed area (LMMA) (Cripps & Harris 2009). Here, BV and the Velondriake Association have been working with the village to establish a viable community-led sea cucumber aquaculture business that allows a steady monthly income through the sale of mature adults whilst reducing wild-catch fishing pressure and potentially supporting the recovery of wild sea cucumber populations (Gardner et al. 2020).

Although the last 2 decades have seen increased efforts in sea cucumber aquaculture (e.g. Mercier et al. 1999, Lavitra et al. 2010, Purcell 2010, Hair et al. 2016, 2020, Altamirano et al. 2017, Sinsona & Juinio-Meñez 2018), research addressing the basic biology and ecology of hatchery-bred *H. scabra* remains limited. Studies have identified substantial ecological impacts when benthic marine organisms are removed from a particular coastal environment (Solan et al. 2004), and given the importance of sea cucumbers in recycling and remineralising nutrients and organic matter through feeding, excretion and bioturbation activities (Purcell et al. 2016), it is reasonable to assume that both the removal and the introduction of these animals—especially at high densities—could generate considerable ecological impacts on the surrounding coastal ecosystem (Thomson 2017, Ceccarelli et al. 2018, Lee et al. 2018).

Of particular importance is the relationship that *H. scabra* have with seagrass—a favourable habitat for the animals. Sea cucumber larvae rely on seagrass for their settling cues, and the seagrass then provides the juveniles with protection from predation and a suitable substrate on which to grow (Mercier et al.

2000, Hamel et al. 2001, Wolkenhauer et al. 2010, Purcell 2012, Hair et al. 2016, Ceccarelli et al. 2018). Whilst seagrass habitats provide benefits for *H. scabra*, seagrass may also benefit from the presence of holothurians (Wolkenhauer et al. 2010). Through their diel burying cycle, species like *H. scabra* bury into the sediment, potentially having a greater impact on surface and sub-surface sediment displacement and mixing than other holothurians (Yamanouchi 1939, 1956, Mercier et al. 1999, Purcell et al. 2016). This burying has been hypothesised to increase benthic primary production by irrigating and oxygenating deeper sediment layers (Mercier et al. 1999, Purcell et al. 2016), allowing for greater belowground seagrass growth (Wolkenhauer et al. 2010, Rougier et al. 2013). This behaviour may (1) transfer or displace buried sedimentary organic matter to the sediment surface, encouraging aerobic remineralisation and (2) release nutrients trapped in interstitial waters, thereby increasing nutrient efflux to both the water and sediment columns for uptake by seagrass (Massin 1982, Uthicke 1999, Grall & Chauvaud 2002, de Witt 2009). Similarly, the ingestion and excretion of large volumes of sediment by holothurians has been shown to enrich dissolved nutrients in the surrounding sediment (Webb et al. 1977, Conde et al. 1991, Uthicke 2001, Costa et al. 2014), which may also stimulate seagrass growth (Hughes et al. 2004). In support of this hypothesis, a 2 yr experiment carried out by Wolkenhauer et al. (2010) found that when wild *H. scabra* were excluded from experimental pens, seagrass productivity and biomass were diminished in some (but not all) experimental periods.

If this ecological mutualism does exist between *H. scabra* and seagrass, it is likely that under certain circumstances a greater density of *H. scabra* could be positively correlated with greater seagrass growth, as suggested by Rougier et al. (2013), noting that there is a recognised maturity-dependency on sand-fish preference for seagrass (e.g. Ceccarelli et al. 2018). As seagrass meadows are considered highly productive ecosystems (Duarte & Chiscano 1999, Hemminga & Duarte 2000), a positive mutualism could enhance wider ecosystem benefits. Seagrass meadows provide a number of key ecological functions and services, including shoreline stabilisation, coastline protection, nutrient cycling, commercial and small-scale fisheries support, biodiversity enhancement, nursery grounds and habitats for invertebrates, fish and large predators (Hemminga & Duarte 2000, Orth et al. 2006, Heck et al. 2008, Belshe et al. 2017) and livelihood opportunities for

many of the world’s poorest communities (Unsworth et al. 2010). As of yet, no studies have addressed the potentially important role of burying holothurians on seagrass ecosystems in the context of an aquaculture farm, where population densities tend to be higher than in natural local settings.

Here, we report a study of a village-scale, community-led aquaculture site in southwest Madagascar conducted in natural seagrass habitat. The goals were to ascertain whether the presence of hatchery-bred sandfish affected growth of the dominant seagrass species in the study area, adjacent to a community *H. scabra* farming operation. We hypothesised that the addition of *H. scabra* would increase seagrass growth through increased bioturbating and burying activities, improving sediment oxygenation and enhancing organic matter remineralisation, thereby increasing primary productivity.

2. MATERIALS AND METHODS

2.1. Study site

Tampolove is a small village (population ~500 people) situated on the southern shore of the Bay of

Assassins; a broad and shallow bay located ~150 km north of Toliara in southwest Madagascar (22° 13.3' S, 43° 16.0' E; Fig. 1). The bay is well-flushed, with a water depth ranging to ~10 m in the central area, a tidal range of ~2.9 m during spring tides and ~1.5 m during neap tides and no major freshwater inputs. On average, this region has a hot, semi-arid climate, with open water sea surface temperature (SST) typically ranging from about 24.1°C in August to 29.1°C in February (mean monthly SST 1982–2019, IGOS-nmc; Reynolds et al. 2002). The 4 ha farm is located ~750 m offshore from the village (Fig. 1) and operates as a no-take zone (with the exception of the principal sandfish predator, the blue swimming crab *Thalassidroma crenata*, which are removed when encountered). The boundaries are delineated by a grid of 41 farmed pens (30 × 30 m; Fig. 2), and are used to grow out hatchery-supplied juvenile *Holothuria scabra* until they reach marketable size. The farm has an average water depth of 0.5 m relative to low water spring tide level and sits atop a thin veneer of sediment, ranging in thickness from 0.01–1.12 m. The seabed at the site is mostly covered with seagrass with some bare sandy patches and is dominated by poorly–very poorly sorted fine sand with an average carbonate content of around 45–50%. In total, 7 spe-

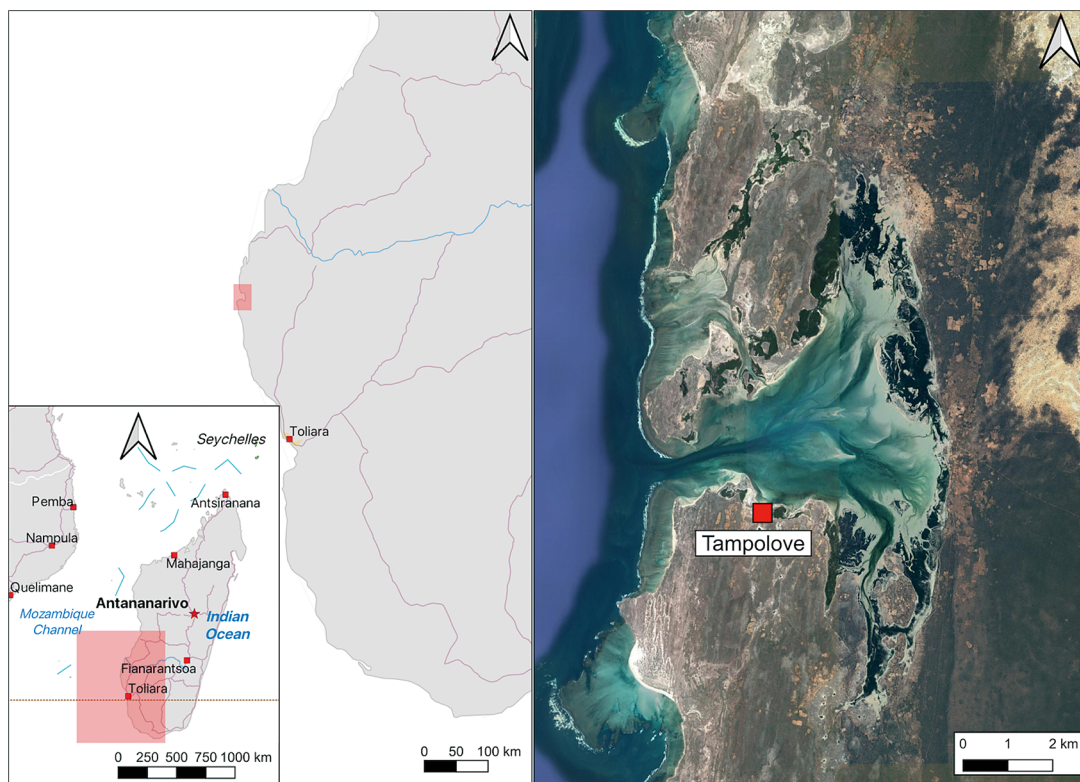


Fig. 1. Location of Tampolove within the Bay of Assassins in southwest Madagascar

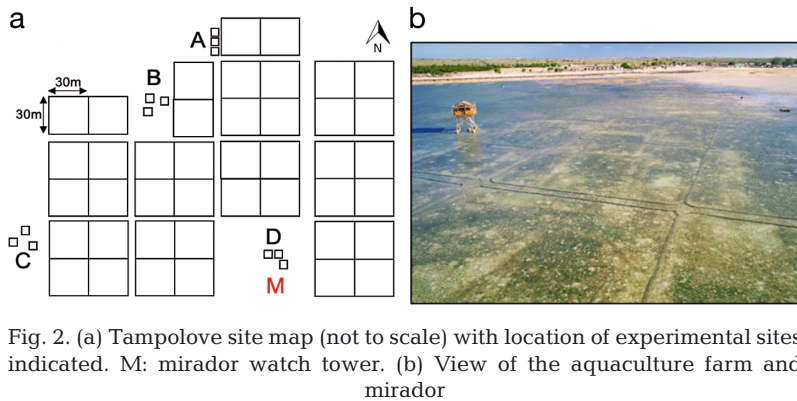


Fig. 2. (a) Tampolove site map (not to scale) with location of experimental sites indicated. M: mirador watch tower. (b) View of the aquaculture farm and mirador

cies of seagrass have been identified and are listed here in order of decreasing prevalence across the site: *Thalassia hemprichii*, *Cymodocea serrulata*, *Halodule uninervis*, *Thalassodendron ciliatum*, *Halophila ovalis*, *H. decipiens* and *C. rotundata*.

2.2. Experimental design

The experiment was conducted over 2 tidal cycles during July and August 2019 and was designed to identify any differences in seagrass growth rates associated with the presence of *H. scabra*. Due to the nature of the site and experiment, all sampling occurred on foot during spring low tides. The experiment was undertaken in 4 m² pens that were constructed (see Text S1 in the Supplement at www.int-res.com/articles/suppl/q013p301_supp.pdf for detail) in seagrass beds at 4 (unfarmed) sites (3 pens site⁻¹) on the periphery of the farm (n = 12) in areas void of wild sea cucumber populations. Site location (and pen positions therein) were chosen to ensure comparable seagrass coverage, and the position of each treatment pen was haphazardly chosen within each site. All 4 sites (identified A–D; Fig. 2) were densely covered with mixed beds of either *T. hemprichii* and *H. uninervis* (dominating Sites A and B), or *C. serrulata* and *H. uninervis* (dominating Sites C and D). At each site, 3 different treatments were applied: control pens, void of *H. scabra*; medium-density pens, where pens were stocked with *H. scabra* at a density of 150 g m⁻²; and high-density pens, where pens were stocked with *H. scabra* at a density of 300 g m⁻². The high-density treatment was based on the farm's optimal stocking density, which is determined by the critical biomass value of the sediment (Lavitra et al. 2010, Plotieau et al. 2013). Animals used to stock the experimental pens weighed between 30 and 150 g and were supplied by the hatchery used to stock the commercial pens. Whilst these sandfish were representative of the

current stock intake, the experiment did not attempt to simulate the natural variability in the size of the animals usually found in the commercially farmed pens, which range from <15 g to >500 g. Furthermore, as the experiment was based on biomass (g m⁻²) rather than ind. m⁻², the number of animals per pen varied between and within the treatments, although care was taken to ensure the size and number of *H. scabra* was roughly consistent between pens (Table S1).

2.3. Pen characterisation

Prior to the experiment, data were collected for several descriptor variables for each experimental pen through visual surveys. Seagrass cover (%) and species composition (%) were calculated using standardized estimates from Seagrass Watch (McKenzie et al. 2001) to visually estimate seagrass cover on a scale of 1–100%. Sediment thickness (m) and sea- and rockbed elevation were calculated by measuring sediment and water depth and then calibrating against a local tidal datum (spring low tide level observed during the experiment). The number and type of holothurian and thalassinidean shrimp sediment mounds (species unknown and both of which may have an impact on sediment oxygenation) present within each pen was recorded. Sediment samples were collected from the top 5 cm of sediment prior to the experiment for subsequent analysis of sediment grain size and sediment organic carbon content (C_{org} %).

2.4. Seagrass growth

Seagrass growth was measured by determining the vertical growth in seagrass blades over the course of 3 spring tides. Growth was measured in *T. hemprichii* blades at Sites A and B, and in *C. serrulata* blades at Sites C and D (even where *T. hemprichii* dominated cover in pens C1, C2 and D1; see Table 1). Following the 'hole-punch' method detailed by Zieman (1974), seagrass blades were stapled at the base of the leaf, left to grow and harvested after 14 d. The distance from the base of the leaf to the staple was measured wet (cm), allowing for leaf extension rates to be expressed as cm shoot⁻¹ d⁻¹.

To account for any between- or within-site variation in environmental conditions, seagrass extension rates were first calculated without the presence of *H. scabra* over the first tidal cycle (pre-stocking). In each experimental pen, a small area of 20 cm² was haphazardly marked (ensuring sufficient coverage of the corresponding seagrass species at the respective sites) using a quadrat and small metal rods. Within these 20 cm² areas, a minimum of 25 seagrass blades were marked individually with a staple and their number recorded, although due to the heterogeneity in seagrass cover, this number varied between pens; 14 d later, all stapled blades were harvested and stored in water for subsequent measurement. Pens were then stocked with the sea cucumbers (at the respective densities) and the process was repeated for another 20 cm² area within the pens over the next tidal cycle (post-stocking). The dynamic coastal setting meant that the blades naturally suffered varying degrees of loss (e.g. through grazing or disturbance), meaning not all blades that were stapled survived the experiment. The average number of stapled blades retrieved at the end of the experiment was 25 but ranged from 16–32 among pens.

2.5. Elemental and sediment grain size analysis

Sediment samples were analysed for total C_{org} (%) content using an organic elemental analyser (Carlo Erba NA 2500, Eager 300 software). Sediment grain size was measured using a Beckman-Coulter LS 230 laser particle size analyser equipped with a fluid module (see Text S2).

2.6. Statistical analyses

All descriptive statistics are presented as means ± SE unless stated otherwise. Given non-normality of data and small sample sizes, non-parametric Mann-Whitney *U*-tests were used to identify any significant within-site and between-site differences for pre-stocking data as well as any significant differences between pre-stocking and post-stocking control data. Linear regression was used to determine relationships between pen characteristics and seagrass leaf growth rates. To assess the impact of stocking density, we constructed mixed effects models with the growth of individual grass blades (cm shoot⁻¹ d⁻¹) as the response variable, holothurian density as a fixed effect (control, medium and high) and site as a random effect (A, B, C and D). Model residuals were

checked for normality and homoscedasticity with respect to fitted values and explanatory variables. To evaluate the importance of holothurian density, we compared the values of Akaike's information criterion corrected for small sample size (AIC_C) of a model with holothurian density as a fixed effect versus a null model without. A difference in AIC_C values greater than 2 can be taken as evidence that there is a statistically detectable effect (Burnham & Anderson 2004). We conducted additional tests on the pairs of sites with similar dominating seagrass species (i.e. just Sites A and B, and just Sites C and D). Finally, to assess if any significant effects of holothurian density were present at medium densities or just at high densities, we constructed similar models but grouped the control with medium-density plots and alternatively grouped the medium-density and high-density plots. The AIC_C values of these models were compared to the model with 3 separate density categories. Significance was accepted at $p \leq 0.05$, and analyses were conducted in R v.4.0.2.

3. RESULTS

3.1. Pen characterisation

Environmental conditions were similar among pens within the same site, though there were some noteworthy between-site differences. Site A was most anomalous, with considerably lower seagrass cover and a thinner sediment layer than the other 3 sites. Sites A and B had greater average water depth (lower seabed elevations) than Sites C and D. Seagrass species composition within Sites C and D were also considerably more varied than those from Sites A and B (Table 1), with pens C1, C2 and D1 dominated by *Thalassia hemprichii*. Despite these differences, linear regression analyses indicated no significant relationships between pen characteristics and seagrass leaf extension rates.

3.2. Seagrass growth

Due to the physiological differences in the seagrass species, analyses were carried out separately for the 2 pairs of sites (A–B and C–D), allowing differences in growth rates between species to be measured. During pre-stocking, no statistically significant differences were detected between pens within a single site. When control-pen data were compared between the pre- and post-stocking growing phases (thus

Table 1. Descriptor variables characterising the environmental conditions of each individual aquaculture pen. C_{org} : organic carbon. *Th*: *Thalassia hemprichii*; *Cs*: *Cymodocea serrulata*; *Hu*: *Halodule uninervis*; *S*: shrimp mound; *H*: holothurian mound. Seabed and rock elevation data are relative to low water spring tide of 0.35 m (17 May 2018 at 14:15 h)

Pen	Seagrass cover (%)	Species composition (%)	Number of mounds	Total C_{org} (%)	Sediment grain size (median value; μm)	Sediment depth (m; mean \pm SE, n = 3)	Seabed elevation (m)	Rock elevation (m)
A1	78	94:6 (<i>Th</i> : <i>Hu</i>)	1 (<i>S</i>)	0.5	131	0.17 \pm 0.003	0.08	-0.05
A2	75	95:5 (<i>Th</i> : <i>Hu</i>)	1 (<i>H</i>)	0.6	155	0.14 \pm 0.003		
A3	65	92:8 (<i>Th</i> : <i>Hu</i>)	0	0.7	144	0.11 \pm 0.002		
B1	95	95:5 (<i>Th</i> : <i>Hu</i>)	2 (<i>S</i>)	0.7	132	0.35 \pm 0.006	0.05	-0.14
B2	94	90:10 (<i>Th</i> : <i>Hu</i>)	0	0.8	125	0.28 \pm 0.004		
B3	94	92:8 (<i>Th</i> : <i>Hu</i>)	1 (<i>H</i>)	0.7	124	0.31 \pm 0.002		
C1	93	85:10:5 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	2 (<i>S</i>)	0.9	131	0.30 \pm 0.003	0.25	-0.10
C2	80	70:20:10 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	1 (<i>S</i>)	1.0	113	0.23 \pm 0.003		
C3	95	35:50:15 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	1 (<i>H</i>)	0.9	121	0.20 \pm 0.003		
D1	92	65:5:30 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	0	0.8	131	0.27 \pm 0.002	0.23	0.01
D2	75	10:65:25 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	2 (<i>S</i>)	0.7	115	0.29 \pm 0.003		
D3	95	20:75:5 (<i>Th</i> : <i>Cs</i> : <i>Hu</i>)	0	0.8	106	0.22 \pm 0.003		

accounting for external factors that may have influenced growth rates between the 2 sampling periods), there were no statistically significant differences in seagrass growth rates between the 2 growing phases for either species (*T. hemprichii*: $U = 1467$, $p = 0.670$, $n = 111$; *Cymodocea serrulata*: $U = 924.5$, $p = 0.295$, $n = 92$). These observations improve confidence in attributing any observed between-treatment differences in seagrass growth rate within sites during the

post-stocking phase to the addition of sea cucumbers. During post-stocking, in both the medium- and high-density pens, leaf extension rates increased for *T. hemprichii* but not *C. serrulata* (Fig. 3). The high-density pens displayed the highest growth rates for *T. hemprichii* ($0.307 \pm 0.023 \text{ cm shoot}^{-1} \text{ d}^{-1}$), which was ~33% faster on average than that observed in the controls ($0.231 \pm 0.021 \text{ cm shoot}^{-1} \text{ d}^{-1}$). The addition of *Holothuria scabra*, irrespective of density, pro-

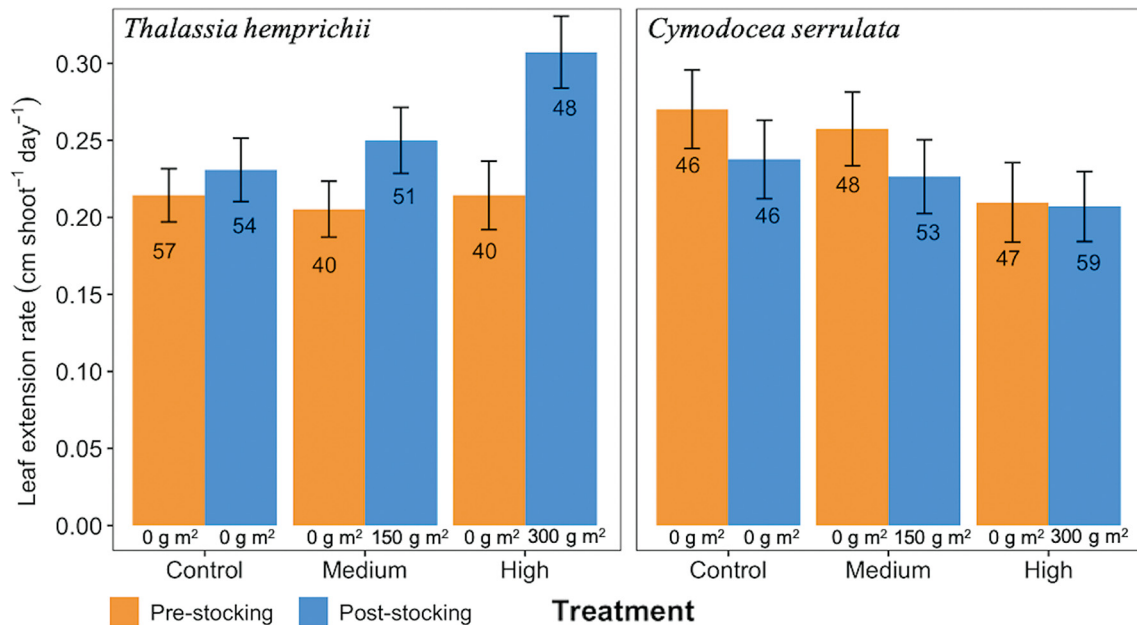


Fig. 3. Mean (\pm SE) seagrass leaf extension rates for the 2 most dominant seagrass species. Stocking densities ($\text{g Holothuria scabra m}^{-2}$) used in the 3 treatments are shown below each bar for the 2 growing phases: pre-stocking and post-stocking. Each bar represents the mean growth rate of all individual seagrass blades from Sites A and B for *Thalassia hemprichii* and from Sites C and D for *Cymodocea serrulata* for each treatment (number of observations are shown underneath error bars)

duced a negligible effect on growth rates for *C. serrulata*, with the high-density pens producing somewhat (but not statistically significantly) lower growth rates than both the control and medium pens.

Our mixed effects statistical models indicate that holothurian stocking density did have a statistically detectable effect on the growth of *T. hemprichii* (Table 2; ΔAIC_C of 2.5 between null model and full model), but not *C. serrulata*. This effect seems to be driven by higher seagrass growth in the high-density plots since grouping the medium-density plots with the control plots into a single category improved the model (i.e. lowered the AIC_C values; Table 2). Conversely, when we conducted analyses across all 4 groups of pens (i.e. pens dominated by *T. hemprichii* and those dominated other seagrass species), we did not detect any statistical effect of holothurian density (null model had a lower AIC_C value by 0.7 units). To emphasise this result, when the analysis was restricted to just *C. serrulata* growth, the null model outperformed the full model by 4.1 AIC_C units.

4. DISCUSSION

The experimental data indicate that *Holothuria scabra* have a net overall positive effect on seagrass leaf growth but that this effect is conditional on 2 considerations. Firstly, the data suggest that there is some threshold effect of *H. scabra* density on seagrass growth as only the high-density pens experienced a large (~30%) and statistically significant increase in growth rates of *Thalassia hemprichii*. This may imply that only at certain density will *H. scabra* make a notable difference on the local environment. Secondly, it suggests that this relationship may only hold true for certain species of seagrass. This may be due to differing functional traits of the 2 species,

which may have led to different growth rate responses that were not fully captured within this study. As there are many different aspects to plant expansion and maturation, it is difficult to capture a holistic picture of whole plant growth with just one method. Future experiments would benefit from measuring belowground biomass growth through rhizome marking and plastochrone interval. Ranges in seagrass growth observed through the experimental period correspond reasonably well with maximum growth rates found in other studies for *T. hemprichii* (e.g. Ogden & Ogden 1982, Duarte 1991, Erftemeijer & Herman 1994, Lin & Shao 1998), but for *Cymodocea serrulata*, our growth ranges were more variable compared to other studies (e.g. Udy & Denison 1997, Kamal et al. 1999, de Boer 2000, Yamada et al. 2018).

Bioturbators are a natural component of seagrass ecosystems, providing essential services within seagrass meadows, without which they would struggle to exist (Kristensen et al. 2012, Thomson 2017). Whilst the role of sea cucumbers as bioturbators is less well understood, these results indicate that some species like *H. scabra* could have greater ecosystem value than previously thought through their alteration of sediment biology, geochemistry and physical structure. For seagrasses, sustained functioning of roots and rhizomes depends on an adequate supply of oxygen (Duarte et al. 1998). Therefore, it is likely that burying activities carried out by *H. scabra* destabilise the stratified sediment causing increased aeration, thus increasing sediment oxygen supply and contributing to plant growth. These actions may also potentially release organic material and nutrients trapped in sediment porewaters back into the water column (Massin 1982, Uthicke 1999), thereby providing additional nutrients for seagrass. Likewise, the ingestion of large volumes of organic compounds contained within subsurface sediments and subsequent excretion of this material on the seabed results in the recycling of nutrients (particularly ammonium; cf. Uthicke 2001 for *Holothuria atra*) back into the water column and sediments (Webb et al. 1977, Massin 1982, Wainright 1990, Conde et al. 1991, Uthicke 2001), thereby stimulating seagrass growth (Hughes et al. 2004, de Witt 2009, Costa et al. 2014).

To more fully constrain and understand the impact of farmed *H. scabra* on seagrass growth and productivity, future studies would benefit from considering 3 additional factors that were beyond the scope of the current study. Firstly, estimation of changes in root and rhizome biomass and production to give a more complete picture of the impacts of total seagrass pro-

Table 2. Model performance for mixed effect models to evaluate the effect of holothurian stocking density on seagrass growth for Sites A and B only (*Thalassia hemprichii*). Differences in Akaike’s information criterion corrected for small sample size (ΔAIC_C) values are given relative to the best-performing model, which itself has a ΔAIC_C value of 0 ($p < 0.05$). C: control (no *Holothuria scabra*); M: medium stocking density; H: high stocking density

Model	AIC_C	ΔAIC_C
Null model (only random effects)	-1128.0	3.7
Model with C, M and H separate	-1130.5	1.2
Model grouping M and H vs. C	-1129.9	1.8
Model grouping C and M vs. H	-1131.7	0

ductivity. Secondly, undertaking multi-year experiments to assess long-term impacts. And, finally, greater replication (including more experimental pens) to increase statistical confidence and help rule out the possibility of 'non-demonic' intrusion (sensu Hurlbert 1984) influencing the interpretation of observed differences in growth rates.

5. CONCLUSIONS

This study found that *Holothuria scabra*, stocked at the relatively high population density used in aquaculture pens, significantly increased the growth rate of a common seagrass species. Since seagrass ecosystems are considered to be amongst the most productive and diverse on earth (Belshe et al. 2017, Unsworth et al. 2010) but are also threatened globally by human activities (Wylie et al. 2016), the positive impact of *H. scabra* aquaculture on growth rates raises the possibility of important ecological co-benefits. The sea cucumber farm at Tampolove operates under a strict 'no-take-zone' policy and can be viewed as 'non-invasive' (i.e. the farm requires no inputs such as feed and uses a native and endangered species that were previously highly abundant in this area). Therefore, not only is the farm offering an alternative livelihood, but the high density of farmed *H. scabra* may simultaneously protect, conserve and even 'boost' the seagrass habitat, with potential knock-on effects to recovery of local fish stocks and wild sandfish populations. This finding has relevance to sandfish farming across many regions of the tropical Indo-Pacific.

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