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Coral-macroalgal interactions: Herbivory and substrate type influence growth of the macroalgae *Eucheuma denticulatum* (N.L. Burman) Collins & Hervey, 1917 on a tropical coral reef

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ABSTRACT

Introduced macroalgae becoming invasive may alter ecological functions and habitats in recipient ecosystems. In the Western Indian Ocean (WIO), non-native strains of the native macroalgae *Eucheuma denticulatum* were introduced for farming practices and consequently spread into the surrounding seascape. We investigated potential effects of non-native and native strains of this macroalgae on a branching coral. We conducted a four-factor field experiment where we examined growth and holdfast development of introduced and native *E. denticulatum* on live and dead branches of *Acropora* sp. in the presence and absence of herbivores in Unguja Island, Zanzibar. Moreover, we estimated coral and macroalgae condition by visual examinations, gene expression analyses, and photosynthetic measurements. Macroalgae did not attach to any live coral and coral condition was not impacted by the presence of *E. denticulatum*, regardless of geographical origin. Instead, necrotic tissue on the macroalgae in areas of direct contact with corals indicated damage inflicted by the coral. The biomass of *E. denticulatum* did not differ between the replicates attached to live or dead corals in the experiment, yet biomass was strongly influenced by herbivory and replicates without protection from herbivores had a significantly lower biomass. In the absence of herbivory, introduced *E. denticulatum* had significantly higher growth rates than native algae based on wet weight measurements. These results contribute to an increased understanding of environmental effects by the farming of a non-native strain of algae on corals and stresses the importance to maintain viable populations of macroalgal feeding fishes in such areas.

1. Introduction

Coral reefs play a key role in sustaining critical ecosystem services and ecological functions in tropical marine environments (Moberg and Folke, 1999; Barbier et al., 2011). By creating structurally complex habitats, which host thousands of associated species, coral reefs promote marine biodiversity and support coastal fisheries (Hughes et al., 2007; Graham, 2014). Humans and marine ecosystems are heavily dependent on healthy coral reefs, but increased anthropogenic stressors predict a future of substantial coral loss (Frieler et al., 2013; Darling et al., 2019). Coral reefs are already decreasing globally and there is an urgent need to identify and reduce factors contributing to this decline (Nyström et al., 2000). Phase shifts, i.e., when coral communities are replaced by alternative communities of opportunistic species, usually occur in the aftermath of large-scale coral die-offs (Norström et al., 2009). For example, transitions from coral to macroalgal dominance are reported from various geographical locations (Hughes, 1994; Nyström et al., 2000; Smith et al., 2008; Barott et al., 2012a). Once established, macroalgae can cause further coral mortality, reduce coral growth and induce stress responses in coral colonies by different mechanisms such as shading, abrasion, overgrowth and allelopathic interactions (Jompa and McCook, 2002; Shearer et al., 2012; Rasher et al., 2013). Furthermore, algae may transmit pathogens to corals or release organic carbon which in turn can increase detrimental microbial activities and disrupt

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zooxanthellae functions (Barott et al., 2009; Haas et al., 2016; Haas et al., 2013; Silva et al., 2021; Smith et al., 2006). Several studies have documented reductions in the number of zooxanthellae in corals subjected to different stressors, including algal exposure (da Silva et al., 2017; Quan-Young and Espinoza-Avalos, 2006; Rasher et al., 2011). Substantial loss of zooxanthellae that results in bleached and necrotic coral tissue and subsequently impairment of vital processes will have severe consequences on coral health and may lead to coral mortality (Barott et al., 2012b).

Coral-macroalgal interactions are a continuous interplay in reef environments, but the strength and direction of these interactions might shift depending on species identity and functional traits of corals and algae, and extrinsic factors such as the activity of herbivorous fish (Nugues and Bak, 2006; Barott et al., 2009). Thereby, herbivorous fishes play a key role in balancing benthic communities and preventing macroalgae from becoming dominant on reefs by top-down control (Mumby, 2006; Hughes et al., 2007; Adam et al., 2015). However, the rate of algal removal is not the same for all herbivores and food preferences may vary with species and life stages (Fox and Bellwood, 2007; Hoey and Bellwood, 2009; Smith et al., 2018). Also, native species of algae may be preferred by herbivores over introduced ones (Schaffelke et al., 2006; Stamoulis et al., 2017).

Similarly, there are large differences in the outcome of coral-algal interactions, and a species-specific approach has been suggested to increase the understanding of these (McCook et al., 2001). For example, macroalgae that grow rapidly and have strong allelopathic responses (e.g., *Dictyota* spp.) might induce more harm to corals than slower growing species that are less allelopathic (e.g., *Sargassum* spp. or *Turbinaria* spp.), (Tanner, 1995; McCook et al., 2001; Rasher and Hay, 2010). The growth form of a macroalgae can further affect the interaction; a more compact, massive shaped species (e.g. *Lobophora* spp.) can inhibit coral growth to a larger extent than tall, erect species with only a small adhesive area (Jompa and McCook, 2003). Conversely, corals can suppress macroalgal growth, suggesting that coral-macroalgal interactions are complex and may result in different outcomes (Jompa and McCook, 2002; Nugues et al., 2004). Scleractinian corals can for example use sweeper tentacles (Chornesky, 1983), mesenterial filaments (Nugues et al., 2004) or allelopathy (McCook et al., 2001) when defending themselves against competitive algae. Increases in algal biomass on coral reefs certainly have several underlying causes. One issue that has received limited attention is blooms of non-indigenous algae in tropical areas and how they might affect coral health (but see Conklin and Smith, 2005). Introductions of exotic species are predicted to increase in the future because of globalisation and the expansion of the aquaculture industry, and thus investigating non-native macroalgae and coral interactions is paramount (Schaffelke and Hewitt, 2007; Williams and Smith, 2007).

Intentional introductions of macroalgae for commercial farming purposes have occurred in several tropical locations, both within and outside the species' natural geographical ranges (Bindu and Levine, 2011; Halling et al., 2013). The carragenophytes *Eucheuma denticulatum* (NL Burman) Collins & Hervey 1917, and *Kappaphycus alvarezii* (Doty) Doty ex PC Silva 1996, are some of the most widespread farmed macroalgae in the tropics (Bindu and Levine, 2011; Halling et al., 2013; Kelly et al., 2020). These macroalgae exhibit high growth rates, are relatively large ($\leq$ 0.5 m), coarsely branched with a fleshy corticated thallus, and may display either an erect or a creeping growth form (Mshigeni, 1979). Algae in farms reproduce only vegetatively, and fragments or thallus that are broken off can easily reattach to hard substrate (Halling et al., 2013; Tano et al., 2015). Dispersal by fragments is a successful strategy in the establishment of non-native algae as long as there is substrate that the algae can attach to (Vermeij et al., 2009).

Algal blooms consisting of either *E. denticulatum* or *K. alvarezii*, or both, have been reported to smother coral reefs in Hawai'i, Venezuela and India (Barrios et al., 2007; Chandrasekaran et al., 2008; Conklin and Smith, 2005). Even though this phenomenon is observed over a large geographical range, the algal types that are involved all originate from Southeast Asia (SEA), (Tano et al., 2015; Zuccarello et al., 2006). Because of the low genetic diversity in farmed algae, it is relatively easy to identify and track escaped algae (see e.g., Zuccarello et al., 2006).

In Tanzania, East Africa (EA), which is one of the top-ten producers globally of SEA *E. denticulatum* (Hayashi et al., 2010, 2017), there are observations of macroalgae spreading from farms into surrounding ecosystems (Eggertsen et al., 2020; Tano et al., 2015). Information on how this may affect the shallow ecosystems is lacking (Eggertsen and Halling, 2020). East Africa harbours native populations of both *E. denticulatum* and *K. alvarezii* (Zuccarello et al., 2006; Tano et al., 2015), which makes introductions of SEA haplotypes difficult to detect, and hence the ecological effects caused by these introductions are not fully understood. Farms are commonly placed in shallow areas close to shore (Hedberg et al., 2018), and because closeness to farms is an important predictor of presence in SEA *E. denticulatum* (Eggertsen et al., 2020), the shallow seascape will potentially be the most impacted area by this algae compared to other coastal areas.

There is mainly one SEA haplotype (E13) that is currently (2020) farmed in Tanzania (Eggertsen et al., 2020; Halling et al., 2013; Tano et al., 2015). Native *E. denticulatum* was found to be unsuitable for farming, and was thus abandoned for the more resistant and fast growing SEA algae (Lirasan and Twide, 1993; Tano et al., 2015). However, high growth rates and high tolerance to environmental conditions may increase the risk that a non-native species would establish itself in the recipient ecosystem (Schaffelke et al., 2006). Moreover, the farmed haplotype E13 is genetically similar to E32, the haplotype which has formed detrimental blooms in Hawai'i, with subsequently devastating effects for scleractinian corals (Conklin and Smith, 2005; Rodgers and Cox, 1999; Russell, 1983). How the E13 haplotype may affect corals in the shallow seascape of EA is, however, currently not known.

The structurally complex Acroporidae corals are key species of shallow coral communities as they constitute and create a large part of the three-dimensional reef matrix, critical for the survival of numerous reef organisms (Dixson and Hay, 2012). They are among the most abundant reef building corals in the EA region (Hamilton and Brakel, 1984; van der Ven et al., 2016) and dominate the shallow coral reef systems along the Tanzanian coast (Mbije et al., 2002; McClanahan et al., 2011). In 2002, Zanzibari reefs had an estimated cover of 60% live coral of which Porites was the most abundant genus, followed by Acropora (Mbije et al., 2002). However, acroporids are highly susceptible to bleaching events (McClanahan et al., 2007; Darling et al., 2019), which are predicted to increase in the near future (Hoegh-Guldberg, 1999; Veron et al., 2009; Frieler et al., 2013). Coral communities of Zanzibar, and especially acroporids, were badly hit by the coral bleaching event in 2016, reducing cover of this genera with as much as 85% in some sites (Ussi et al., 2019). Loss of coral cover and consequently of structural complexity is a strong negative driver of reef fish abundances (Wilson et al., 2008; Berkström et al., 2012; Graham and Nash, 2013; Darling et al., 2017), which in turn could have negative effects on ecosystem functioning and small-scale coastal fisheries (Pratchett et al., 2014; Graham, 2014). Moreover, acroporids have been shown in experimental studies to be more sensitive to algal interactions than other genera of corals (Smith et al., 2006; Rasher et al., 2011), but there is also contradictory evidence that this genus can be highly competitive against macroalgae (Diaz-Pulido et al., 2009). Information on species-specific interactions are therefore needed to improve our understanding of coral-algal interactions. There is evidence from several geographical locations that the *Eucheuma/Kappaphycus*-complex is impacting coral communities in a detrimental way (Rodgers and Cox, 1999; Conklin and Smith, 2005; Barrios et al., 2007; Chandrasekaran et al., 2008). However, extrapolating environmental impacts by an introduced species based upon evidence from other geographical locations to a new introduction site is not reliable, given that there might be large variations in conditions among different recipient ecosystems (Grosholz, 1996; Schaffelke and Hewitt, 2007). Therefore, site-specific studies are needed to accurately identify potential effects by the

introduction of non-native strains of macroalgae in coral reef environments.

In this context, the overall aims of the present study were to investigate (1) if there is a difference in how introduced (SEA) and native (EA) haplotypes of *E. denticulatum* affect growth and condition of branching *Acropora* sp., and (2) how substrate (dead or live coral) and herbivory may affect growth rates of introduced (SEA) and native (EA) *E. denticulatum.* This was accomplished by conducting a four-week field experiment where growth rates and interaction effects of different strains of *E. denticulatum* were studied on live and dead branches of *Acropora* sp. in the presence and absence of herbivores. Coral condition was visually estimated and also measured as photosynthetic activity by corals, potential differences in zooxanthellae composition and gene expression. RNA-based methods, such as gene expression analysis, have been shown to be a useful tool when studying effects of stressors in corals (Kenkel et al., 2011; Louis et al., 2017; Shearer et al., 2012). Such methods will enable the detection of stress responses in a coral even if no visible signs are distinguishable (Shearer et al., 2014). Furthermore, we aimed to survey an *E. denticulatum*-dominated reef to estimate cover area and biomass of introduced algae and investigate if results from the field experiment could explain some of the macroalgal-coral growth patterns observed *in situ*. In doing so, we aimed to gather information that could be useful for the management of the coastal zone in the WIO area.

2. Methods

2.1. Study sites

The study was conducted in southern Zanzibar, Tanzania, in Menai Bay, Sume Island (6° 18′50.2“S 39° 19’03.4”E) (field case study), Komonda Island (6° 21′02.5“S 39° 18’24.1”E) (collection of algal material) and Jambiani (6° 18′11.2“S 39° 33’27.0”E) (experiment) during October–November 2018 (Fig. 1). The study coincided with the north-east monsoon (October–March), which is relatively sunny with few heavy rains. (McClanahan, 1988; McClanahan et al., 2007). During this monsoon, nitrogen concentrations, chlorophyll *a* and phytoplankton abundances are peaking compared to the rest of the year (McClanahan, 1988; Ussi et al., 2019).

Sume and Komonda Islands are located in a shallow embayment (< 15 m dept) with 6 small islets (Berkström et al., 2013). The bay harbours a mosaic of patch and fringing coral reefs, seagrass meadows, reef flats, mangroves and macroalgal habitats (Berkström et al., 2013). The reef flats adjacent to land are dominated by algae such as *Halimeda* and *Sargassum* spp. and small seagrass species, whereas deeper areas harbour extensive seagrass meadows, mainly consisting of *Thalassodendron ciliatum,* and patch reefs (Berkström et al., 2013; Tano et al., 2016). Algal dominated reef flats are mainly composed of hard substrate (~70%) with slightly higher coral cover than that found in seagrass meadows (~13 versus 3%, respectively) (Tano et al., 2017). Large, monospecific stands of *Acropora* spp. were common at depths of 2–4 m, but were severely affected by the bleaching event in 2016, and is currently transformed into extensive coral rubble areas (Mbije et al., 2002; Ussi et al., 2019; M. Eggertsen, pers. obs.).

Jambiani is characterised by a large and sandy shallow lagoon (< 5 m depth) with a distinct fringing reef bordering the open ocean (Dorenbosch et al., 2006). The experimental site was located in a tidal channel at 4–6 m depth (depending on the tide), subjected to strong tidal currents, especially during spring tides. Water temperatures at the experimental site ranged between 25 °C - 28 °C. Tides in the area are semi-diurnal with amplitudes up to 4 m (Berkström et al., 2013).

2.2. Fish census

To collect information on the presence and abundance of macroalgae-consuming fish species, a standardized point count census method according to Berkström et al. (2013) was performed at each field site ($n_{Sume} = 37$, $n_{Jambiani} = 20$).

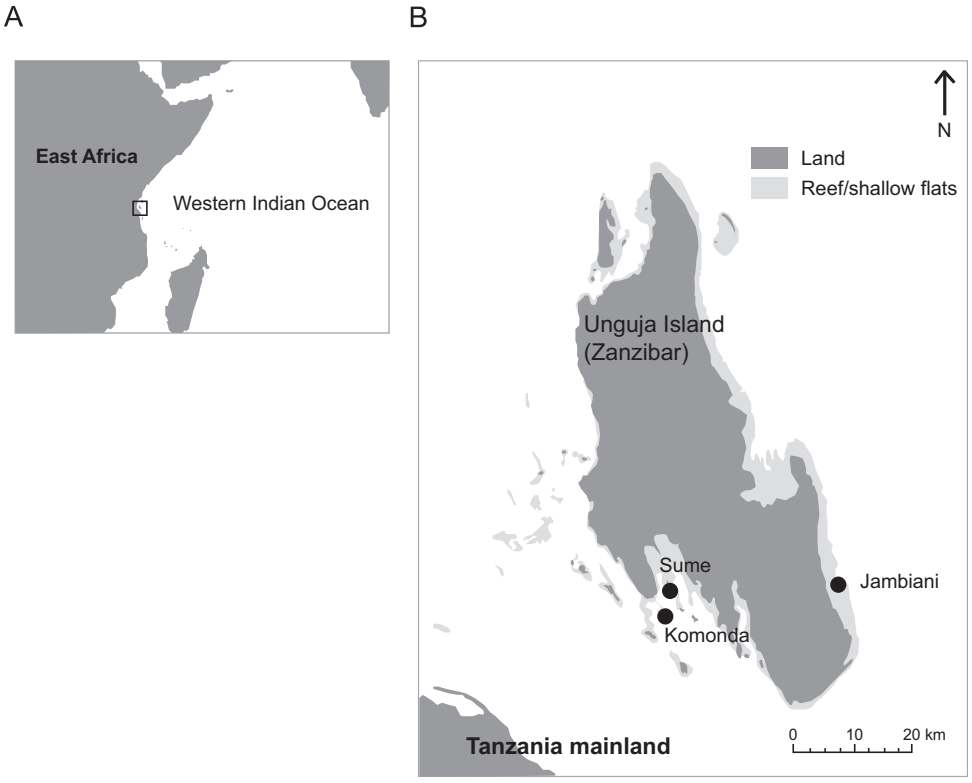

Fig. 1. Map of study sites *A)* location of Zanzibar (Unguja Island) on the East African coast *B)* overview of the study sites around Zanzibar.

2.3. *Eucheuma denticulatum* field case study

The SEA *Eucheuma denticulatum* strain E13 (hereafter 'haplotype') is currently the dominating non-native euchemoid identified in Tanzanian shallow waters (Tano et al., 2015). The other farmed species, *Kappaphycus alvarezii,* is not common which is probably due to small farming volumes as a consequence of repeated harvest failures (Msuya, 2011). Therefore, the present study only includes *E. denticulatum.*

To estimate the extent of dense blooms of SEA *E. denticulatum* on a local scale, Sume Island was chosen as a case study site because of previous observations of patches of high cover of SEA *E. denticulatum* around the island (pers. obs. M. Eggertsen). Native and non-native *E. denticulatum* have slightly morphological differences; EA *E. denticulatum* tend to have a spinier appearance compared to the SEA haplotype and a more creeping growth form, which makes it possible to distinguish between the two haplotypes in the field.

Eucheuma denticulatum can form extremely dense mats on top of reef structures, creating distinct patches with clearly defined edges. In the present study, patches were recorded based upon the criteria that *E. denticulatum* cover should dominate the reef benthos (> 50%). To estimate the area of the reef where *E. denticulatum* constituted the dominating species, GPS coordinates were collected by a snorkeler equipped with a GPS (Garmin etrex 10) placed in a waterproof bag and set on tracking mode, measuring position every 5th second. A snorkeler surveyed the reef area around Sume island systematically and when an *E. denticulatum* patch was encountered, the snorkeller swam around the contours of the patch keeping the GPS bag on the surface as close as possible to herself. Area measurements were then performed in ArcMap 10.5 based on the GPX files of the contours of macroalgal patches using the polygon function.

To estimate the amount of biomass of *E. denticulatum* on the coral reefs, a quadrat of 0.2 × 0.2 m was placed on patches of 100% macroalgal cover. All *E. denticulatum* were carefully removed and stored in ziplock bags (n = 10). Squares were photographed before and after algal removal, and the amount of dead/bleached/live coral was estimated (Fig. S1). The amount of grazing was estimated and binned into five categories (100, 75, 50, 25 and 0%) with 100% denoted as all tips bitten off, and 0% as no grazing. Attachment substrate was noted (dead or live coral). Algal samples were cleaned from mobile invertebrates and epiphytic algae and dried in 60 °C for 72 h (or until completely dry) and dry weight was measured. Remaining salt may have added a small increase in weight to the algal samples, but as we always used the same method, we consider any error this introduced to our measurements to be consistent and therefore not interfering significantly with our results. Wet weight of *E. denticulatum* derived from the literature were roughly converted to dry weight (divided by a factor of ten) (Foscarini and Prakash, 1990).

To investigate the current attachment substrate of SEA *E. denticulatum,* a randomized sample was taken when swimming over any overgrown reef, where a thallus of *E. denticulatum* was carefully removed (n = 43) and the attachment substrate was noted (dead or live coral). Geographic origin of algae was visually determined, and in case of uncertainties, tissue samples were collected for DNA analysis (~1.5 cm of a tip of a branch) (n = 8). Samples were dried and stored in 2 ml Eppendorf tubes with silica gel until analysis.

2.4. Field experiment set-up: Coral-macroalgal interactions

To evaluate potential effects on *Acropora* sp. by introduced and native strains of *E. denticulatum,* a field experiment was conducted using a four-factor design. The field experiment was conducted in Jambiani, Zanzibar (Fig. 1b) using coral nubbins of the same*Acropora* species obtained from a coral nursery (marinecultures.org). All coral samples originated from surrounding reefs and had been kept in the nursery ~1 year. Live and dead *Acropora* sp. (Fig. 2) of the same size (6.68 ± 0.13 cm from base to top) were attached to concrete pegs and fixed on a 'table' (a steel mesh mounted on 4 legs), approximately 0.5 m above the bottom at 4–6.5 m depth, depending on tide (Fig. 2). Coral samples were placed >0.15 m apart, secured to the mesh with strong rubber bands and marked with tags. Coral height was measured to the nearest mm.

Macroalgae (EA and SEA algae) were collected from southern Zanzibar, on a reef flat surrounding Komonda Island (Fig. 1b). To verify haplotype origin of the macroalgae a small sample (~1.5 cm of a tip of a branch) were taken from each individual for genetic identification and stored in 2 ml Eppendorf tubes with silica gel until analysis. The sampled macroalgae were kept in aerated seawater over night. Prior to transplantation, they were shaken 20 times to get rid of excess water and weighted (1.2–6.8 g).

Pieces of *E. denticulatum* (20 EA and 20 SEA) were tied to 20 dead and 20 live corals, one macroalgal piece per colony by 'tie-tie' strings. This type of string is a plastic twine which is extensively used within seaweed farming activities in Zanzibar, because it lasts long in seawater and does not cut into the thallus of algae (Lirasan and Twide, 1993). Neither the corals in the field experiment, nor the *E. denticulatum* were observed to

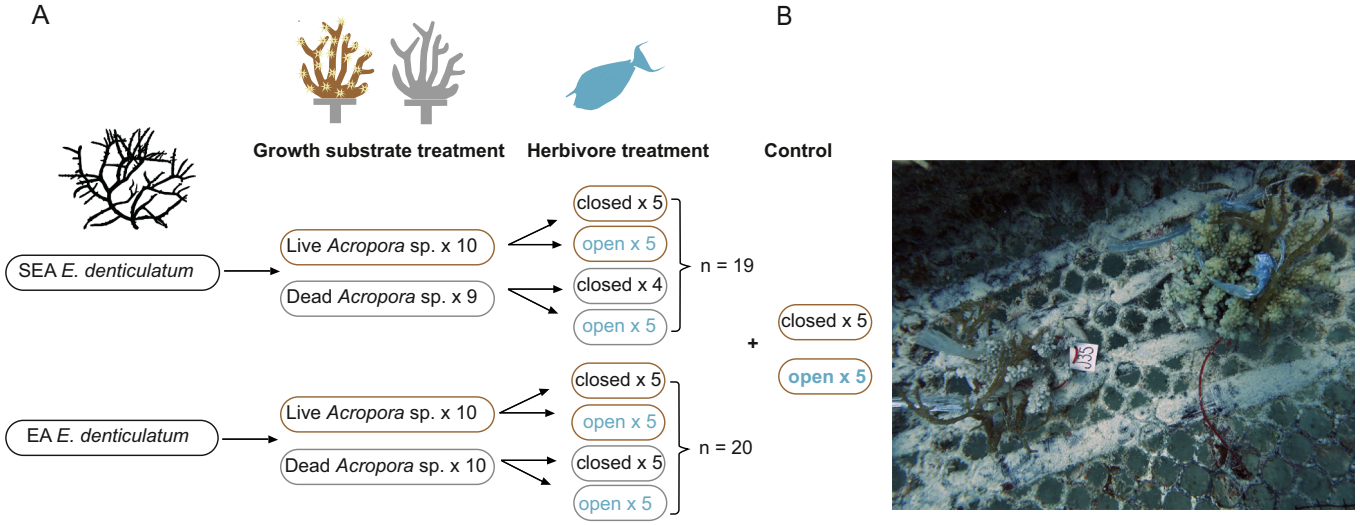

Fig. 2. *A)* Schematic illustration of the field experimental design. Controls are coral samples without any algae attached. "Closed" and "open" denote absence or presence of herbivore (fish and sea urchins) exclusion cages, *B)* dead and live *Acropora* sp. with pieces of *E. denticulatum* tied to colonies at the initiation of the experiment.

be negatively affected by the plastic twine; corals overgrew the tie-ties very quickly with soft tissue.

To test the effect of potential herbivory by fishes and urchins, 20 of the samples (10 dead and 10 live corals) were covered with herbivore exclusion cages made of plastic mesh (0.02 × 0.02 m grid), cylindrical, ~0.25 m high and with a diameter of 0.2 m. This mesh size was chosen because it was small enough to exclude herbivorous fishes and sea urchins, but large enough to not affect organisms inside the cages by e.g., shading effects (Russ, 2003; Tootell and Steele, 2016). Sea urchins were not common at the experimental site and none made it up onto the experimental table.

To control for handling, macroalgal or cage effects, 10 live coral samples were left without macroalgae, and 5 of these were covered with herbivore exclusion cages (Fig. 2). The experiment was run for 1 month (28 days), and cages were thoroughly cleaned from filamentous algae twice a week. During each cleaning occasion, algal and coral samples were visually inspected for signs of bleaching and grazing damage (algae) and algae were secured with new tie-ties if needed. A number of algae in open treatments were heavily grazed during the experiment period and were completely gone (or remains were so small so they were not possible to weigh) at the termination of the experiment ($n = 13$).

2.5. PAM fluorometry measurements

To measure possible effects on coral condition inflicted by *E. denticulatum,* measurements were made in situ with an underwater pulse amplitude modulated fluorometer (Diving-PAM, Heinz Walz GmbH). Measurements were conducted at the start of the experiment and then once a week until termination (in the case of losing samples or if severe damage/mortality would occur). However, because this was not the case, only the values obtained from the last sampling occasion (at the termination of the experiment) were used in the statistical analysis.

The light sensor of the Diving-PAM was calibrated prior to measurements in the field by following a standardized protocol (WALZ manual 1998). To ensure that all measurements were made on a standardized distance (3 mm) and with the accurate angle from the sample, specific leaf clips ('Dark Leaf Clips Diving LC', WALZ, Germany) were used. F_v/fm was measured in dark adapted samples as an indication of the maximum quantum yield of photosystem II (PSII). Minimum fluorescence (F_0) and maximal fluorescence (F_m) are values obtained by the PAM fluorometer. F_v (variable fluorescence) is calculated as:

$$F_v = F_m - F_0$$

Dark adaptation was obtained by carefully transferring the coral samples to a light impermeable dive bag (60 l) for 15 min. This period of time is considered sufficient for opening of all PSII reaction centres, hence ensuring maximum quantum yield of photosynthesis (Beer et al., 2014). Reduction of photosystem II (PSII), for example due to bleaching, should result in values <0.5, (Fitt et al., 2000), which we used as a proxy for severe stress. All measurements were conducted between 09:00–14:00. Coral samples were measured in random order. The Dark Leaf Clips were attached to the coral samples as close as possible to the algae attachment site (although with some variations due to difficulties to apply the Dark Leaf Clips correctly because of the corals' structural form). Any visually detectable effects on the coral colony (e.g., bleaching, discoloration of tissue) were noted.

To collect information on how dense mats of *E. denticulatum* may reduce light intensities on infested reefs, we measured ambient light above and underneath 100% cover of *E. denticulatum* in situ on the overgrown reefs around Sume Island. This was done by using a photosynthetic active radiative (PAR) light sensor connected to the diving-PAM ($n_{above} = 6$, $n_{underneath} = 3$).

2.6. Field experiment termination

At the termination of the experiment samples for subsequent DNA and RNA analyses were taken. The tip of a branch of a coral (~ 0.5 cm) was cut and placed in 2 ml Eppendorf tubes with 95% EtOH (DNA samples) and RNALater® (5 x sample size, SigmaAldrich) (RNA samples). All samples were kept in −20 °C until analysis. Macroalgae were carefully removed from coral samples and location of attachment (on live coral, coral peg or dead coral) and status of attachment (not attached/attached) was noted. Corals were measured (height) to the nearest mm, photographed and any visible bleaching effects or scars were noted. Extra care was taken to visually inspect the area where coral and macroalgae had been in direct contact. Coral and macroalgae health status were visually estimated and appointed to one of five categories ranging from 1 = no visual effects of discoloration, 2 = some visual effects, e.g., a slight alteration in colour and/or outer layer beginning to disintegrate, 3 = apparent visual effects with tissues beginning to disintegrate, and parts of branches gone (algae), 4 = severe effects with bleached tissue (corals) and red tissue/large parts of branches gone (algae), 5 = completely bleached with necrotic tissue. All estimations were conducted by the same observer (C. Åkerlund), to ensure that any potential bias would be consistent. Macroalgae were transported to the lab in closed zip-lock bags, shaken 20 times to get rid of excess water, weighted and photographed. Corals were relocated to the nursery.

2.7. Molecular analysis - Eucheuma denticulatum

Molecular analyses were performed to separate introduced (SEA origin) from native individuals (EA origin) of *E. denticulatum* and verify visual identification of geographic origin. Total genomic DNA was isolated using a modified CTAB extraction (Zuccarello and Lokhorst, 2005) (detailed description in Table S3).

For identification of different haplotypes, the mitochondrial cox2–3 spacer was used, with forward primer (cox2-for) 5'-GTACCWTCTTTDRGRRK-DAAATGTGATGC-3′ and reverse primer (cox3-rev) 5'-GGATCTACWAGAT-GRAAWGGATGTC-3′, following methods described in (Zuccarello et al., 2006) and in Table S4.

2.8. Molecular analysis - Symbiodinium spp. Ribosomal Internal Transcribed Spacer (ITS)

Given the importance of the zooxanthellae to coral survival and health we also aimed to study variation among the zooxanthellae *Symbiodinium* in our experimental corals. This knowledge is relevant to understand the ability of corals to cope with stressors (Buddemeier and Fautin, 1993), and may enable detection of stress responses not distinguished by visual inspection. Total genomic DNA of symbionts was isolated from coral tissue using the same CTAB extraction as for *E. denticulatum*, with modifications including the use of only glass and metal beads in FastPrep MP24 (Nordic Biolabs), speed: 4.0, time: 40 s, repeated 2 times and an extended extraction phase of 60 min in −20 °C.

The symbionts were genotyped using the *Symbionidium* ITS2 region amplified by the ITSIntFor2 Primer 5'-GAATTGCAGAACTCCGTG-3′ and the ITS-reverse primer 5'-GGGATCCATATGCTTAAGTTCAGCGGGT-3′ (LaJeunesse, 2002). PCR amplifications were performed following a 'touch-down' protocol modified from (LaJeunesse, 2002) (Table S3). PCR purification and Sanger sequencing (forward and reverse) were carried out by Macrogen Europe Inc., using an ABI3730XL sequencer.

2.9. Analysis of genetic markers

Quality evaluation and alignment of all sequences were conducted using MEGA 6.0 (Tamura et al., 2013). For haplotype identification of *E. denticulatum* the sequences were aligned manually and identified using reference sequences (Zuccarello et al., 2006; Halling et al., 2013; Tano et al., 2015). Ambiguous sequences/haplotypes were corrected

using the chromatograms and heterozygote single nucleotide polymorphism (SNP) were denoted with their corresponding SNP code. A haplotype was considered new if there were > 1 single SNP difference between the haplotype in question and reference haplotypes. For identification of *Symbionidium* spp. haplotypes the sequences were aligned manually using MEGA 6.0 (Tamura et al., 2013), consensus sequences were created using forward and reverse sequences and trimmed to 281 bp. All sequences were identified using BLAST with default settings. To evaluate differences in the composition of *Symbiodinium* spp. in coral colonies prior and post exposure to *E. denticulatum,* pairs of samples prior and post exposure were compared and sequences were visually investigated using a maximum likelihood tree with clade A as root in MEGA 6.0 (Tamura et al., 2013).

2.10. Quantitative real-time PCR (rt-qPCR)

To analyse the potential negative effects of algal growth on corals, the relative expression of five genes previously identified to be connected to stress responses (Császár et al., 2009; Kenkel et al., 2011; Shearer et al., 2012) were analysed using rt-qPCR in coral tissue from each individual sampled at the termination of the experiment. GSP2 was used as a reference gene (internal control), reported to be stable during both long and short term stress in *Acropora millepora* (Kenkel et al., 2011). For more details of rt-qPCR methods, see supplementary material.

2.11. Statistical analyses

Differences in abundances of herbivorous fishes between the two sites Jambiani and Sume were analysed using Kruskal Wallis rank sum test. Differences in percent of macroalgal biomass (pre- and post-experiment) among growth substrate (dead or live coral), herbivory (cage or no cage), and geographic origin of algae (EA or SEA) were tested by a three-way ANOVA. Pairwise comparison between different treatment levels for significant two-way interactions were analysed using Bonferroni adjustments to a family wide significance level of $\alpha = 0.05$. The pooled error sum of squares and degrees of freedom (DF) were obtained from the three-way ANOVA model using package rstatix (Kassambara, 2021). Potential differences in coral growth and the photosynthetic activity of corals related to algal treatment (no algae, EA algae or SEA algae) or caging effects were conducted using two-way ANOVAs. All ANOVAs were conducted by the Anova() function in the package 'car' (Fox and Weisberg, 2011).

Differences in coral condition (visually estimated) in corals exposed to *E. denticulatum* were analysed using Kruskal-Wallis rank sum test. Differences in visually estimated stress responses in algae depending on growth substrate (dead or live coral) were analysed using non-parametric Kruskal-Wallis rank sum tests because criteria for normality was not fulfilled.

Differences in gene expressions between corals exposed to *E. denticulatum* and controls were analysed using generalised linear models (GLM) included in the package 'stats'.

Normal distributions were checked by visual examination using diagnostic plots and differences were considered significant at $p \leq 0.05$. All data were analysed in the statistical program R version 3.5.3, 2019 (R Core Team, 2019).

3. Results

3.1. Field case study

Inventory studies of fish assemblages showed that macroalgal feeding species (such as *Siganus* spp. and *Naso brevirostris*) were present in both Jambiani and Sume (Fig. 3). However, there was a significant difference in the abundance of herbivores between the sites, in Jambiani there were 0.10 ± 0,02 ind. Per m^2 (mean ± SE) and in Sume 0.16 ± 0.04 ind. Per m^2 (Kruskal Wallis rank sum test, chi square = 6.53, df = 1, p = 0.011). There was also a slight difference in herbivorous species composition between the two sites; *Calotomus carolinus* and *N. brevirostris* were found in Jambiani but not in Sume, whereas *Leptoscarus vaigiensis* was only found in Sume.

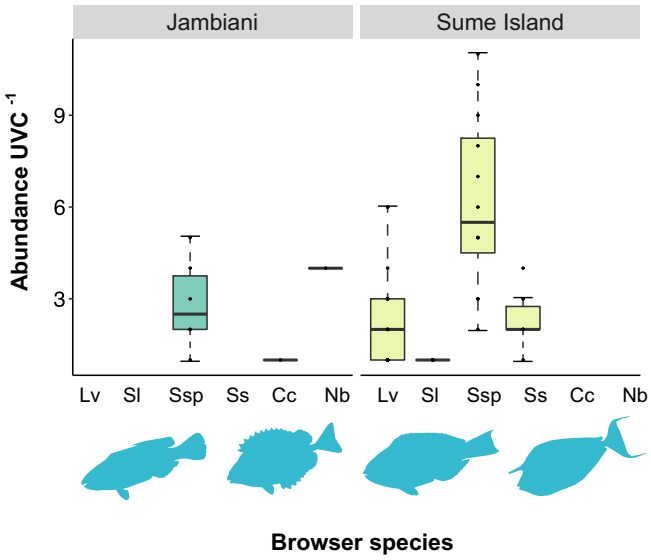

Fig. 3. Abundances of macroalgal feeding fishes in the two sites (Jambiani and Sume Island) per UVC (19.6 m^2). Each point in the figure denotes a sample (1 UVC) and error bars are 95% confidence intervals ($n_{Jambiani} = 20$, $n_{Sume} = 37$). Each box shows median (black line) and 25th and 75th percentile. Lv = *Leptoscarus vaigiensis*, Sl = *Siganus luridus*, Ssp = Siganus sp., Ss = S. sutor, Cc = *Calotomus carolinus*, Nb = *Naso brevirostris*.

Field observations around Sume Island in southern Zanzibar confirmed that *Eucheuma denticulatum* is growing on *Acropora* spp. reefs. Macroalgal patches covered an area of ~1300 m^2 (Fig. S2). Cover of 100% of *E. denticulatum* corresponded to a mean value of 831 ± 72.9 g^{-1} m^{-2} dry weight.

Algal branches were 100% grazed ($n = 10$, mean = 100 ± 0 SE), and all *E. denticulatum* that were sampled were attached to dead parts of coral colonies or coral rubble (Fig. S2 b,c). Necrotic tissue was observed on some macroalgae branches that were in direct contact with live coral tissue. All *E. denticulatum* growing on the reefs were confirmed by the molecular analyses to be of SEA origin (haplotype E13). Ambient light above 100% *E. denticulatum* cover ($n = 6$) had a mean value of ± SE of 204.3 ± 85.04 μmol photons m^{-2} s^{-1} whereas underneath ambient light ($n = 3$) was 5.0 ± 0.58 μmol photons m^{-2} s^{-1}.

3.2. Field experiment

Haplotype origin of algae determined by molecular analysis confirmed that visual identifications of algae used in the experiment were 100% accurate.

There was a significant interaction effect between herbivory and growth substrate (live or dead coral) (Table 1, Fig. 4). There was also a significant effect between herbivory and the geographical origin of algae (EA or SEA); SEA algae displayed higher growth rates on dead coral substrate compared to live coral in samples closed to herbivory (Table 1, Fig. 4). Growth substrate (dead or live coral) had an effect on algal growth rates in samples closed to herbivory but not in samples open to herbivory (Table 1, Fig. 4). In samples open to herbivory, there were no differences in growth rates between EA and SEA *E. denticulatum* or between substrate type (Table 1, Fig. 4).

The stress response (visually estimated) was significantly higher in *E. denticulatum* exposed to live than dead coral (Kruskal-Wallis rank sum test, chi-square = 16.43, df = 1, $p < 0.001$) (Fig. 5) and no difference

Table 1
Results from the field experiment analysed with a 3-way ANOVA testing the difference in growth rates (percent) of introduced and native *Eucheuma denticulatum* subjected to different growth substrate and herbivory. Significant *p*-values are indicated in bold.

Treatment	Sum sq	Df	F-value	p-value
Growth substrate (live or dead coral)	95,291	1	12.807	**0.001**
Herbivory (closed or open)	807,234	1	108.494	**< 0.001**
Algal origin (EA or SEA origin)	30,583	1	4.110	0.051
Growth substrate x Herbivory	93,851	1	12.614	**0.001**
Growth substrate x Algal origin	6300	1	0.847	0.365
Herbivory x Algal origin	46,571	1	6.269	**0.018**
Growth substrate x Herbivory x Algal origin	12,556	1	1.688	0.204
Residuals	230,652	31		

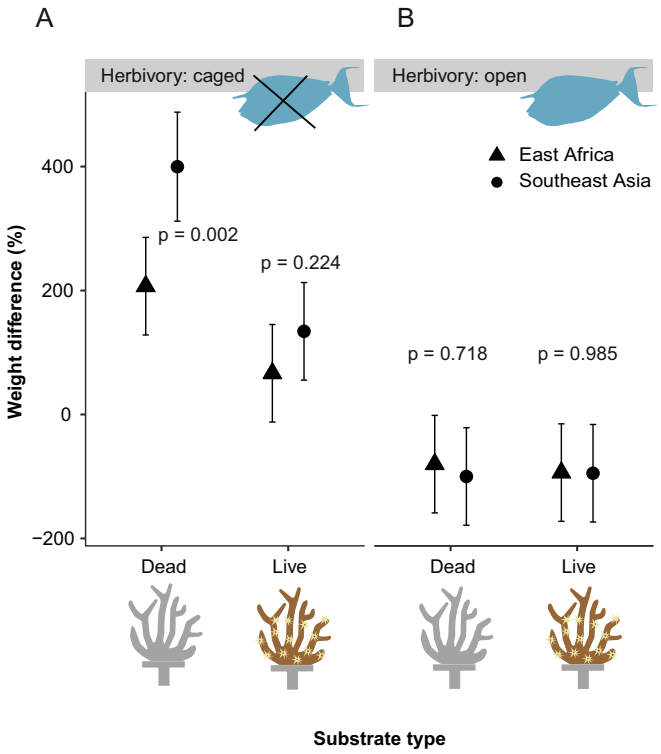

Fig. 4. Results from the field experiment (three-way ANOVA) showing biomass change (in percent) of *E. denticulatum* on different types of substrate (live and dead coral) between start and end of the experiment in *A)* caged treatments and *B)* treatments open to herbivory. Significant *p*-values are $p \leq 0.05$.

between algae with SEA and EA origin were found. Algae were not able to attach to living coral, but attached to dead coral and coral mounting pegs.

Coral samples in cages ($n = 15$, mean value and SE 0.05 ± 0.01 mm) had significant higher growth rates compared to corals without herbivore exclusion cages (n = 15, 0.01 ± 0.009 mm, two-way ANOVA; $F = 12.8$, df = 24, $p = 0.002$), but there were no differences between algal exposures (EA algae, SEA algae or controls). No significant effects were found on the condition of *Acropora* sp. inflicted by algal exposure when visually estimated (ANOVA; $F = 1.81$, df = 2, $p > 0.05$). Furthermore, no significant effects on maximum quantum yield of *Acropora* sp. could be found between algal treatments (no algae, EA algae or SEA algae) or caging effects (two-way ANOVA, df = 24, $p > 0.05$, Table S1). Relative mRNA expression was not significantly altered in 4 of the 5 genes of interest, although one gene, Manganese Superoxide dismutase (MnSOD), was significantly down regulated in corals exposed to *E. denticulatum* compared to controls (Table S2), irrespective of algae haplotype origin. All zooxanthellae were identified to clade C3 with 99% identity and E values <0.001 (Table S3). No differences in zooxanthellae composition were detected in coral colonies prior-and post exposure to *E. denticulatum* (Fig. S3).

4. Discussion

The present study is, to our knowledge, the first to test the effects of *Eucheuma denticulatum* on *Acropora* sp. and compare potential effects between a native and a non-native haplotype of the same algal species. Our results show that *E. denticulatum* of SEA origin has spread and established itself on Zanzibari coral reefs, in similar densities that are documented in other geographical locations (Smith et al., 2002; Neilson et al., 2018). Biomass comparisons of introduced *E. denticulatum* covering coral reefs in other geographical locations were only possible to conduct between Hawai'i and Zanzibar (Russell, 1983; Conklin and Smith, 2005; Neilson et al., 2018). Our results align with algal biomass records from the most recent study (Neilson et al., 2018) conducted on Hawai'i, were estimated dry weight of *E. denticulatum* ranged between mean values of 622–810 g^{-1} m^{-2} on coral reefs.

Even though *E. denticulatum* (SEA origin) was found in patches of high densities the alga was only attached to dead coral surfaces and never to live coral. However, this does not imply that *E. denticulatum* initially settled on dead coral substrate. We found that algae could not develop holdfasts on live specimens of the one *Acropora* species used in our experiments, but it is not unlikely that *E. denticulatum* may be able to do so on other species of corals (in addition to potential other negative effects). Drifting pieces of *E. denticulatum* originating from farms could have been entangled in the branches of live corals, and subsequently overgrew and smothered these. Dead coral structures in the field site may therefore be either a result of the current *E. denticulatum* bloom, or a prerequisite for its initiation. It is beyond the scope of this study to investigate smothering effects by mat-forming *E. denticulatum*, and also species-specific effects on several species of corals, but these are valid questions related to potential negative effects of algae on corals and should be addressed in future studies.

Algae did not inflict any damage or stress on corals that we could detect, even when in direct contact. On the contrary, the algae showed signs of stress when in direct contact with live corals, even though the overall growth rates of algae were not affected (and there were no difference between algae of EA or SEA origin).

Smothering and overgrowth of *Acropora* spp. colonies by *E. denticulatum* in the WIO might not be prevented by defence mechanisms of corals alone, due to their limited ability to obstruct algal growth. Instead, top-down control by herbivores may constitute a critical mechanism contributing to coral reef health in Zanzibar as shown both in our field experiment and in the field case study. Extensive herbivory was observed in Menai Bay; all algae were heavily cropped resulting in little shading of coral colonies by macroalgae. Growth rates of algae was significantly higher when herbivores were excluded. Herbivores did not seem to distinguish between haplotypes of different geographical origin (EA or SEA), because the rate of herbivory was identical between the haplotypes. Non-native macroalgal species have been reported to escape grazing intensity elsewhere because many herbivores prefer native species (Gollan and Wright, 2006; Williams and Smith, 2007). However, our results did not show such preferences. Important macroalgal feeding fish species such as *Naso brevirostris* and *Siganus* spp. are common in the WIO region and were frequently observed in our fish surveys. Herbivorous fish are considered a key player within coral-macroalgal competition by controlling macroalgal growth (Hughes et al., 2007; Bonaldo and Hay, 2014; Adam et al., 2015). Our results support previous findings and further highlight the importance of preserving key ecological functions within marine ecosystems by avoiding overexploitation of ecologically important species, such as herbivores.

All sampled *E. denticulatum* from the Sume reef consisted of SEA

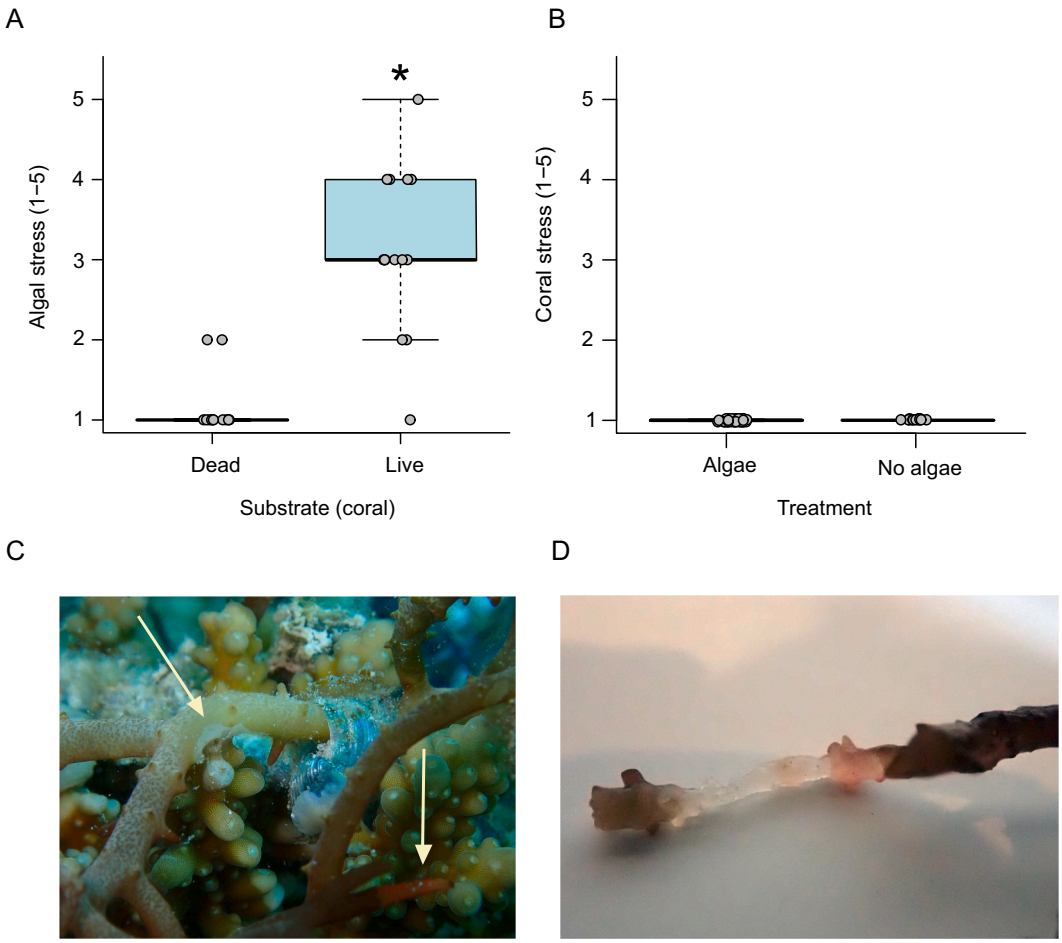

Fig. 5. "Stress response" of transplanted *E. denticulatum* individuals that have been subjected to direct contact with *Acropora* sp. corals *A)* boxplot showing visually estimated stress of algae after 4 weeks exposure to *Acropora* sp. colonies (live and dead colonies). Each point in the figure denotes a sample and error bars are 95% confidence intervals. Boxes show median (black line) and 25th and 75th percentile ($n_{\text{dead coral}} = 19$, $n_{\text{live coral}} = 20$) *B)* visually estimated stress of coral colonies after 4 weeks exposure to *E. denticulatum* ($n_{\text{algae}} = 20$, $n_{\text{no algae}} = 10$) *C)* arrows indicate areas on *E. denticulatum* where algae and corals have been in direct contact which has resulted in damaged tissue (white and red areas on branches) *D)* necrotic tissue on branch of *E. denticulatum* exposed to *Acropora* sp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

haplotypes (E13). Sexual reproduction is infrequent in *E. denticulatum* and has not yet been observed for eucheumoids outside their geographical range (Conklin and Smith, 2005; Tano et al., 2015). Spread of SEA haplotypes in Zanzibar is most likely due to vegetative reproduction; i.e., through loose pieces of algae drifting in the water column. Shallow coral reefs within this area might be exposed to SEA algae more frequently than to EA algae due to several reasons. First, there is an overall higher abundance of the SEA haplotype compared to EA *E. denticulatum* in this area (Tano et al., 2015) and continuous input of drift macroalgae from farms contributes to high concentrations of SEA *E. denticulatum*, thus enhancing encounter rates between algae and coral reefs. Second, EA *E. denticulatum* has a more cryptic, creeping growth form than SEA haplotypes which displays a more pronounced erect growth form, possibly leading to the latter being more susceptible to break-offs by currents and waves (Eggertsen et al., 2020). Third, the SEA *E. denticulatum* is more tolerant to desiccation and sun radiation than the EA variant (pers. obs. M. Eggertsen) which might enable it to exploit new niches in substrate that gets exposed during spring low tide. However, this remains to be further investigated.

Higher growth rates were one of the reasons why SEA *E. denticulatum* was initially chosen as farming material over EA algae in Zanzibar (Halling et al., 2013; Tano et al., 2015). In closed treatments, SEA *E. denticulatum* had significantly higher growth rates than EA algae, but only for algae growing on dead coral substrate. These findings stress the importance of herbivory, and especially so in locations where coral mortality is widespread and coral-algal competition is reduced. Algae that have the ability to rapidly take advantage of previously unavailable substrate may create extensive blooms and further increase coral loss by overgrowing damaged or bleached tissues (Diaz-Pulido et al., 2009). Impairment of top-down control caused by e.g., overfishing of herbivores in combination with coral mortality may therefore have larger consequences for reef health and algal dynamics in areas where SEA *E. denticulatum* is present than in areas where only the EA haplotype occurs.

Moreover, due to the ability of loose pieces of *E. denticulatum* to develop new holdfasts on dead reef substrate, the higher amount of SEA haplotypes on Zanzibari reefs may be partly explained by the larger densities of non-native haplotypes originating from macroalgal farms. When SEA *E. denticulatum* is established on reefs, it may supress recruitment or growth of other macroalgae and corals by the formation of extremely dense mats which occupy settling substrate and efficiently exclude sunlight, as demonstrated in our PAR measurements.

No direct effects of *E. denticulatum* on coral condition could be detected in the present study. Coral growth was not affected by the presence of algae, but there was a caging effect which positively influenced growth, which could depend on lower predation pressure on coral colonies, caused by the exclusion of corallivorous fishes.

In addition, only one of the five genes connected to stress was

differentially expressed by the interaction with the macroalgae, further confirming that the corals did not seem to be negatively affected by the presence of macroalgae. The MnSOD gene was downregulated in the corals exposed to algae compared to corals in the control group (no macroalgae exposure). MnSOD is a gene involved in restoring cellular homeostasis during oxidative stress and has previously been shown to be upregulated during thermal stress (Császár et al., 2009; Souter et al., 2011) and upregulation has also been connected to bleaching of corals (Louis et al., 2017). Previous studies have shown a large variation in the direction and amplitude of expressed genes related to a stress response with differences both within and between coral colonies (Császár et al., 2009; Seneca et al., 2010). MnSOD was found to be consistently upregulated in *A. millepora* under thermal stress in laboratory conditions, but superoxid dismutase (SOD) and thioredoxin (Txn) were upregulated in 80% of the colonies and downregulated in 20% of the colonies (Souter et al., 2011). It has also been suggested that the corals response to oxidative stress is transient (Császár et al., 2009) and that higher levels of antioxidant gene expression such as MnSOD, Txn and SOD in the onset of the study may have been missed. However, previous studies on coral responses to different species of macroalgae show that the interactions between corals and macroalgae are complex and unique to the specific coral-macroalgae pairing. These diverse responses by the corals may enable some corals to tolerate macroalgae competitors better than others (Shearer et al., 2012, 2014).

Even though *Acropora* spp. are found to be more affected by allelopathic macroalgae compared to other corals (Rasher et al., 2011; Bonaldo and Hay, 2014), *E. denticulatum* did not affect *Acropora* sp. negatively in this study. However, all coral samples in our field experiment were healthy colonies without any initial evidence of bleaching (visually estimated or measured by PAM fluorometry). Adult corals may have a competitive advantage over macroalgae, but macroalgae are probably more successful competitors if coral health is already reduced (McCook et al., 2001; Kuffner et al., 2006). Moreover, pieces of transplanted algae in our study were relatively small compared to the coral samples at the initiation of the field experiment, which may have made potential impacts less pronounced and more difficult to measure by PAM fluorometry (e.g., difficulties to measure the impacted area accurately because of the small sizes of areas). Damage to coral tissues induced by algal allelochemicals should however have been visible at surfaces in direct contact, even if algal samples were rather small, and this was not the case.

A limitation of the present study is that coral replicates in the field experiment were obtained from a nursery, and it was not possible to control for the potential risk that some of the coral samples were clones. Variations in responses to macroalgae may occur on an individual level, which in this case could lead to an underestimation of negative effects on *Acropora* sp. induced by *E. denticulatum*. Visual inspections of acroporid corals overgrown by *E. denticulatum* in the field (Sume Island) did not reveal any signs of bleaching on surfaces being in close/direct contact. However, these were not the same species as the corals used in the experiment. Also, the present study excludes potential long-term effects of coral-macroalgal exposure, as the experiment was only conducted for 28 days. Previous studies investigating negative effects of macroalgae on coral health detected effects on corals within the same time frame (Smith et al., 2006; Rasher and Hay, 2010; Shearer et al., 2014), although further studies spanning over longer time periods and also different seasons are recommended to disentangle interaction effects of *E. denticulatum* on shallow water corals more accurately.

Future studies are also recommended to incorporate several response variables that were beyond the scope of the present study and monitor these over years and seasons. The complexity of coral-macroalgal interactions in reef environments may not be possible to detect until after several months (Brown et al., 2020). For example, both algae and corals release dissolved organic carbon (DOC) which affects microbial communities and productivity on reefs differently (Haas et al., 2013, 2016). Also, algae and corals create strong gradients in oxygen concentrations on spatial scales of only a few millimetres which may further affect microbial communities and coral health (Haas et al., 2013). Competition of macroalgae and corals is also linked to seasonality by e.g., temperature dependent differences in growth rates and production of allelochemicals of algae (Brown et al., 2020). Furthermore, increased sea temperatures and ocean acidification rates may shift algal-coral competition in the favour of algae (Diaz-Pulido et al., 2011; Rölfer et al., 2021; Roth et al., 2021), which is an issue that could be addressed in future studies, possibly by running aquaria experiments.

Reef recovery is dependent on successful recruitment (Kuffner and Paul, 2004). The macroalgae in this study may supress recruitment rather than damage adult corals. Drifting pieces of SEA *E. denticulatum* are capable of rapidly attaching to dead coral rubble surfaces and grow to extremely dense patches (Conklin and Smith, 2005; Eggertsen et al., 2020), which constitute a potential disturbance of coral recruitment. By pre-empting space, *E. denticulatum* can reduce coral recovery by making substrate unavailable for settling coral larvae. In fact, there is an inverse relationship between macroalgal biomass and coral recruitment (Kuffner and Paul, 2004). Some macroalgae have the ability to suppress coral settlement by inducing avoidance behaviour (Elmer et al., 2018; Evensen et al., 2019) reducing fitness or even by killing coral larvae (Kuffner and Paul, 2004). Similar studies have not yet been performed for *E. denticulatum*, but are needed in areas where introductions of SEA haplotypes are occurring and in areas with extensive farming, especially in the face of climate change and increased frequencies of coral bleaching events.

The success of non-native algal haplotypes and the consequences it may have for coral reef communities can be complex due to the interplay among different factors. In this study we demonstrated that bottom-up mechanisms such as available growth substrate and top-down control such as the browsing of macroalgae (herbivory) are key components in this interplay (Jompa and McCook, 2003; Titlyanov and Titlyanova, 2008; Greff et al., 2017; Johns et al., 2018; Eggertsen et al., 2020). However, the factor "available growth substrate" in natural reef environments is much more complex than the bivariate experimental design in the present study (live and dead corals), and may be further impacted by e.g., nutrient concentrations (Lapointe, 1997), presence of other algae (Nieder et al., 2019) and microtopography (Brandl and Bellwood, 2016; Davis, 2018; Poray and Carpenter, 2014). Moreover, the mechanisms that shape these patterns may vary with dominating species, prevailing environmental conditions and geographical location, highlighting the need of further studies (Bonaldo and Hay, 2014). We have the ability to mitigate negative effects by maintaining communities of ecologically relevant functional groups of fishes, which are able to buffer algal proliferation and hence preserve reef health. Current densities of herbivorous fishes seem to control growth of SEA *E. denticulatum* on the shallow coral reefs despite high fishing intensity around Zanzibar. However, this should be continuously monitored, since macroalgal top-down control can be severely impaired by the removal of herbivores, with negative consequences on reef health (Bonaldo and Hay, 2014).

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Author contributions

ME planned, designed and conducted the fieldwork and experiments, collected samples, contributed to molecular DNA/RNA analysis, conducted statistical analyses and wrote the manuscript. JL conducted fieldwork and experiments, collected samples, conducted molecular DNA analysis, and wrote the manuscript. TP conducted fieldwork and experiments, collected samples, performed qPCR and wrote the manuscript. CÅ conducted fieldwork and experiments, collected samples and

reviewed drafts of the paper. DHC conducted fieldwork and experiments, collected samples and reviewed drafts of the paper. CB conducted fieldwork and experiments, collected samples and reviewed drafts of the paper. NJ contributed with local knowledge as well as important contacts and facilities and reviewed drafts of the manuscripts. NK contributed with conceptual discussions and constructive feedback and reviewed the drafts of the manuscript. CH held main responsibility for the project from planning to the final manuscript. All authors read and approved the final manuscript for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151606.

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