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ORIGINAL PAPER

Different environmental variables predict distribution and cover of the introduced red seaweed *Eucheuma denticulatum* in two geographical locations

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Abstract In this study we examined abiotic and biotic factors that could potentially influence the presence of a non-indigenous seaweed, *Eucheuma denticulatum,* in two locations, one outside (Kane'ohe Bay, Hawai'i, USA) and one within (Mafia Island, Tanzania) its natural geographical range. We hypothesized that the availability of hard substrate and the amount of wave exposure would explain distribution patterns, and that higher abundance of herbivorous fishes in Tanzania would exert stronger top–down control than in Hawai'i. To address these hypotheses, we surveyed *E. denticulatum* in sites subjected to different environmental conditions and used generalized linear mixed models (GLMM) to identify predictors of *E. denticulatum* presence. We also estimated grazing intensity on *E. denticulatum* by surveying the type and the amount of grazing scars. Finally, we used molecular tools to distinguish between indigenous and non-indigenous strains of *E. denticulatum* on Mafia Island. In Kane'ohe Bay, the likelihood of finding *E. denticulatum* increased with wave exposure, whereas on Mafia Island, the likelihood increased with cover of coral rubble, and decreased with distance from areas of introduction (AOI), but this decrease was less pronounced in the presence of coral rubble. Grazing intensity was higher in Kane'ohe Bay than on Mafia Island. However, we still suggest that efforts to reduce non-indigenous *E. denticulatum* should include protection of important herbivores in both sites because of the high levels of grazing close to AOI. Moreover, we recommend that areas with hard substrate and high structural complexity should be avoided when farming non-indigenous strains of *E. denticulatum*.

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Introduction

Invasive species are considered to be a major threat to global marine biodiversity and ecosystem services (Schaffelke and Hewitt 2007; Katsanevakis et al. 2014). Seaweeds (i.e., macroalgae) comprise a large part of non-indigenous species on a global scale (Bax et al. 2003; Schaffelke and Hewitt 2007). Non-indigenous seaweeds can become invasive and influence ecosystem characteristics and functions by altering habitat complexity (Veiga et al. 2014), community composition (Davidson et al. 2015), biodiversity (Casas et al. 2004; Schaffelke and Hewitt 2007) and ecosystem productivity (Sagerman et al. 2014). For example, invasive seaweeds have been reported to induce and/or amplify coral-to-algal phase shifts in tropical reef systems (Schaffelke et al. 2006; Williams and Smith 2007). Once a non-indigenous species has become established in a new area, it can be extremely difficult to eradicate (Critchley et al. 1986; Nyberg and Wallentinus 2005; Bax et al. 2008). Therefore, to better understand potential risks and environmental consequences of introductions of non-indigenous seaweeds, there is not only a need to document occurrence and spread, but also to identify environmental factors predicting their presence and abundance, especially if they become invasive.

The risk that non-indigenous seaweeds becomes invasive depends on a combination of species-specific traits, as well as biotic and abiotic conditions in the new environment (Nyberg and Wallentinus 2005). Environmental conditions known to influence invasions include wave exposure (Levin et al. 2002; D'Amours and Scheibling 2007), habitat complexity (Tamburello et al. 2013), diversity of primary producers (Kimbro et al. 2013), turf and crustose coralline algae cover (Britton-Simmons 2006; Vermeij et al. 2011), seaweed cover (Arenas et al. 2006), herbivory (Vermeij et al. 2009) and substrate availability (e.g., dead or living coral). Substrate availability has a prominent role in massive phase-shifts from coral to macroalgal dominance, a pattern observed in the aftermath of large-scale coral die-offs when substantial areas of hard substrate is made available to settling of algal propagules (McCook et al. 2001). Furthermore, less functionally diverse or reduced algal communities in the recipient system might facilitate establishment of a non-indigenous seaweed through decreased competition (Ceccherelli et al. 2002). Success by an invader might also be attributed to enemy release, i.e. the lack of consumers, or reduced biotic resistance within the recipient ecosystem (Parker et al. 2006; Kimbro et al. 2013).

One example of a deliberately introduced and (in certain locations) invasive species is the red seaweed *Eucheuma denticulatum* (Solieriaceae, Gigartinales, Rhodophyta). This tropical macroalgae grows naturally on hard substrates in Southeast Asia and East Africa and has been introduced to multiple countries for aquaculture purposes, with different environmental consequences (Conklin and Smith 2005; Chandrasekaran et al. 2008; Davidson et al. 2015; Castelar et al. 2015). In the early 1970s, *E. denticulatum* was introduced to Kane'ohe Bay, Hawai'i (USA) for growth studies (Glenn and Doty 1990; Rodgers and Cox 1999; Smith et al. 2002). Although it was believed that *E. denticulatum* would not be able to disperse over deeper waters between reefs (Russell 1983), surveys conducted > 25 years after the introduction have estimated a rate of spread of 250 m year^{-1} (Glenn and Doty 1990; Conklin and Smith 2005). Since then, this seaweed has been patchily distributed throughout the bay and has colonized a number of reefs, potentially overgrowing and shading reef-building corals (Conklin and Smith 2005). Important herbivores such as rabbitfishes (*Siganidae*) are absent on Hawai'i, which in combination with low preference for *E. denticulatum* by indigenous herbivores (Stimson et al. 2001; Stamoulis et al. 2017), could explain the high seaweed cover in locations within the bay (Conklin and Smith 2005; Fox et al. 2009; Hehre and Meeuwig 2015). Nevertheless, it remains unclear how this seaweed is influenced by biotic (e.g., herbivore abundance) and abiotic factors (e.g., wave exposure and substrate availability) in this geographic location. Herbivorous fishes and sea urchins can reduce biomass of *E. denticulatum* (Russell 1983; Neilson et al. 2018), but abundances and hence consumption rates might vary between locations (Stamoulis et al. 2017). Herbivory can be further influenced by seaweed cover (Stamoulis et al. 2017) and wave exposure, which can exclude herbivores with weaker swimming abilities

(Bejarano et al. 2017). Furthermore, water motion (e.g., wave exposure or wind driven swell) might reduce biomass of *E. denticulatum* by the breaking of branches (but potentially facilitating spread), but also increase growth rates by higher rates of water exchange (Russell 1983; Glenn and Doty 1990; Rodgers and Cox 1999). Finally, distance to the source population of the original area of introduction (AOI) could potentially determine distribution patterns of *E. denticulatum* in early stages of an invasion.

Strains of Southeast Asian *E. denticulatum* were introduced for seaweed farming on the island of Zanzibar (Tanzania) in in the late 1980s (Lirasan and Twide 1993), although indigenous strains of *E. denticulatum* were already present along the East African coastline (Mshigeni 1984). Southeast Asian strains were selected for farming due to their faster growth rates (Lirasan and Twide 1993; Tano et al. 2015). With the epicenter on Zanzibar, farming practices using Southeast Asian seeding material have led to a spread of the non-indigenous strains over the East African region (Bryceson 2002; Rönnbäck et al. 2002). Currently, both indigenous and introduced strains are present in wild *E. denticulatum* populations around the island of Zanzibar, and the introduced strains dominate in some locations (Halling et al. 2013; Tano et al. 2015). However, the spread of introduced strains has not yet been confirmed in other areas in Tanzania, and no data exist on how biotic/abiotic factors may influence the presence of *E. denticulatum* in the East African seascape. In fact, there are only a few studies (Vermeij et al. 2009) comparing environmental factors that influence the distribution of non-indigenous seaweeds within and outside their natural biogeographical range.

Against this background, the objective of the present study was to identify biotic and abiotic factors influencing the distribution of *E. denticulatum* introduced in two contrasting geographical locations: Kane'ohe Bay (Hawai'i, USA) and Mafia Island (Tanzania). We hypothesized that (1) certain environmental variables would be more important in one geographical location than the other depending on site characteristics (e.g., habitat availability such as coral rubble) and history of introduction and (2) *E. denticulatum* is subjected to stronger top-down control by herbivorous communities in East Africa than in Hawai'i due to enemy release (i.e. the absence of certain consumers and low preference for *E. denticulatum* by native herbivores). Furthermore, we investigated if non-indigenous strains of *E. denticulatum* have spread from AOIs on Mafia Island.

Materials and methods

Description of study sites

Kane'ohe Bay, Hawai'i, USA

Kane'ohe Bay (21°28′N; 157°48′W) is a semi-enclosed, 46-km^2 bay located on the east coast of the island of Oahu, Hawai'i (Bahr et al. 2015a, b; Stimson et al. 2001; Fig. 1a). Fringing reefs border the coastline and a 5-km barrier reef/sand bar protects the bay against the open ocean in the eastward direction (Stimson et al. 2001). Approximately 70 patch reefs composed of coral rubble and live coral (mainly *Montipora capitata* and *Porites compressa*) are scattered throughout the bay, of which most rise to less than 1 m below the surface (Bahr et al. 2015a; Stimson et al. 2001). Between the patch reefs, water depth ranges between 10 and 15 m and substrate consists of rubble, coral, mud, and sand (Bahr et al. 2015a). Corals and seaweeds are restricted to the shallower areas, most likely due to the high turbidity within the bay (Stimson et al. 2001). Tides are semi-diurnal with a mean amplitude of 0.7 m (Ringuet and Mackenzie 2005).

During the twentieth century, Kane'ohe Bay was subjected to several major disturbance events such as dredging/removal of reefs, freshwater inflows, coral bleaching, substantial sewage discharges, and introduction of non-indigenous seaweed species (Jokiel et al. 1993; Smith et al. 2002; Bahr et al. 2015a, b). Currently, four introduced seaweeds are abundant throughout the bay: *Acanthophora spicifera, E. denticulatum, Gracilaria salicornia* and *Kappaphycus alvarezii* (Stamoulis et al. 2017). Populations of *E. denticulatum* in Kane'ohe Bay consist of haplotype E32, which is of Southeast Asian origin (Zuccarello et al. 2006; Conklin et al. 2009). No commercial farming of *E. denticulatum* has been conducted on Oahu, and growth trials were abandoned in 1977 (Glenn and Doty 1990; Conklin and Smith 2005). Since then, no new introductions have been made and all *E. denticulatum* in Kane'ohe Bay therefore originate from the experiments conducted in the 1970s.

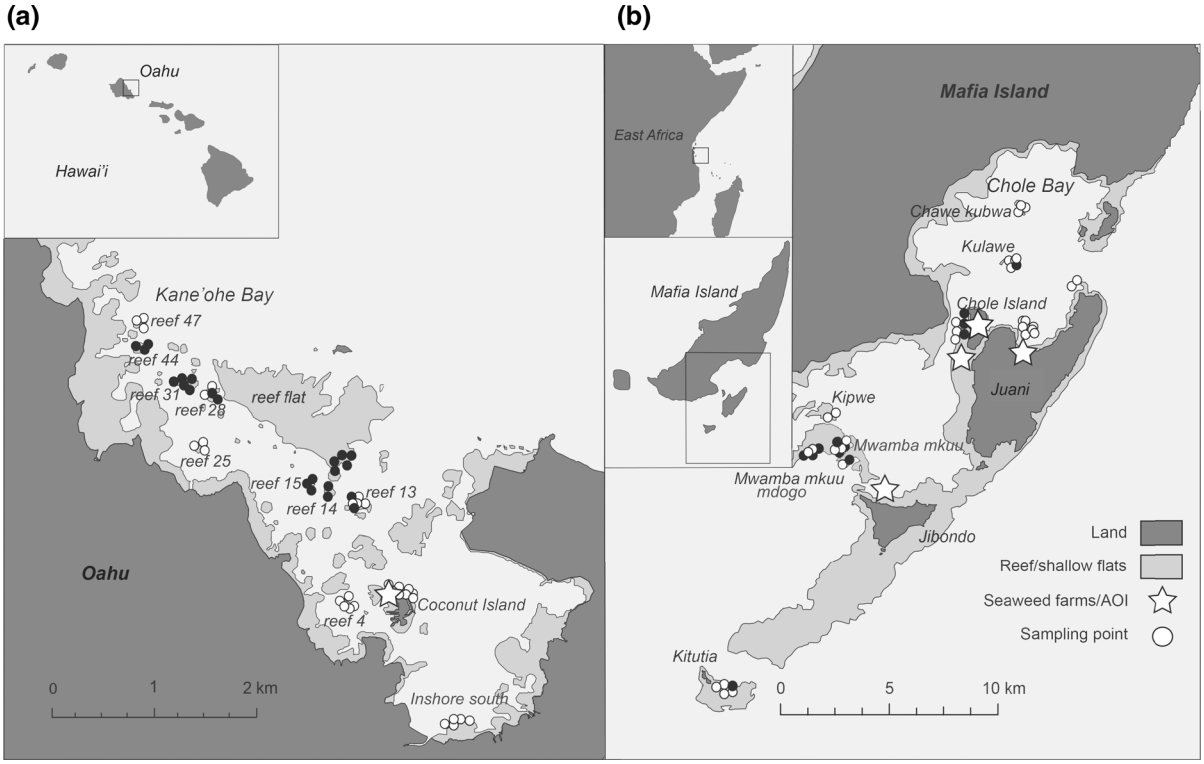

Fig. 1 Study area in **a** Kane'ohe Bay and **b** Mafia archipelago. Small maps show location of study area on **a** Oahu and **b** Mafia Island. Black and white circles show the location of sampling points where *Eucheuma denticulatum* was present or absent, respectively

Substantial efforts have been made to decrease the abundance of *E. denticulatum* and *K. alvarezii* in Kane'ohe Bay, including manual removal and the use of a biocontrol agent, the sea urchin *Tripneustes gratilla* (Neilson et al. 2018).

Mafia Island, Tanzania

Mafia Island (7°40′S; 39°41′E) is the main island in a small archipelago situated 20 km from the Tanzanian mainland, south of the island of Zanzibar (Fig. 1b; McClanahan et al. 2008). The southeastern part of the island is included in a large (822 km^2) marine protected area, the Mafia Island Marine Park (MIMP). MIMP was established in 1995 (Garpe and Öhman 2003; Gaspare et al. 2015) and prohibits the use of destructive fishing methods, but artisanal fisheries by local communities are allowed in certain zones in the outer part of the protected area (McClanahan et al. 2008).

Mafia Island is subjected to the East African Coastal Current (EACC) and semidiurnal tides with a mean amplitude of 3.3 m (Garpe and Öhman 2003). The eastern side, where this study was conducted, is protected by fringing reefs, but tides and monsoonal patterns create strong and complex currents that can reach up to 6 knots (Garpe and Öhman 2003; Berkström et al. 2013; Gaspare et al. 2015). The study area consists of a diverse and pristine patchwork of seagrass meadows, patch reefs, sandy areas, and seaweed beds, and is characterized by high biodiversity of scleractinian corals and fish (Horrill et al. 1996; Garpe and Öhman 2003; Berkström et al. 2013). Small-scale farming of Southeast Asian strains of *E. denticulatum* in the archipelago was initiated in the beginning of the twenty-first century (Torre-Castro et al. 2012; Msuya et al. 2014) and now occurs on Mafia Island, Chole Island, Juani Island and Jibondo Island (I. Bryceson, pers. comm.).

Field survey

The field survey was conducted in 2016 during July (Kane'ohe Bay, Hawai'i) and September to November

(Mafia Island, Tanzania). The survey in Kane'ohe Bay coincided with the warmer season (May–September) with mean sea surface temperature ~ 27° C (Jokiel 1991) and the survey on Mafia Island with the cooler season (June–October), mean sea surface temperatures of ~ 26° C (McClanahan et al. 2007). While the fieldwork occurred during different seasons, the sea surface temperature was similar in the two locations. The field surveys consisted of belt transects (25 m × 2 m) in which we estimated benthic habitat characteristics, algal abundance, herbivore abundance and grazing on *E. denticulatum* fronds. A total of 100 transects were conducted: 52 in Kane'ohe Bay and 48 on Mafia Island (Table 1).

Habitat and *Eucheuma denticulatum* surveys

Within the belt transects habitat characteristics and seaweed cover were estimated by a snorkeler (M. Eggertsen). All transects were conducted in depths 0.5–3.5 m, as *E. denticulatum* is rarely found deeper (Russell 1983). Transects were placed at least 10 m apart, and locations were selected to encompass variation in environmental conditions, including benthic substrate composition, rugosity, wave exposure, depth and distance to areas of introductions (AOI) or seaweed farms. The location of the AOI of *E. denticulatum* in Kane'ohe Bay (i.e., the area where growth experiments were conducted) was derived from literature (Russell 1983). Reefs in Kane'ohe Bay that had been subjected to sea urchin transplantations or manual removal of *E. denticulatum* were also identified from the literature (Neilson et al. 2014, 2018). Two of these reefs (# 14 and 15) were surveyed in the present study. On Mafia Island, AOIs were defined as locations where seaweed farming was active, or where farming had ceased during the previous year, but farms and pieces of loose seaweeds still remained (visual observations by M. Eggertsen and D.H. Chacin). Information of locations where farming activities had previously been conducted was not available.

Benthic variables were visually estimated in 2 × 2 m sections along the transect line. Substrate composition (percent cover), *E. denticulatum* (percent cover), and the type of substrate where *E. denticulatum* was attached was identified. Bottom rugosity was visually estimated on a 1–5 scale following Gratwicke

Table 1 Environmental variables (transect^{-1}) at the two different study locations, $N_{Kane'ohe\ Bay}$ = 52 and $N_{Mafia\ Island}$ = 48. Values are mean values ± SE. AOI denote area of introduction, and each transect is 50 m^2

Variables	Kane'ohe Bay	Mafia Island
Eucheuma denticulatum cover (%)	3.29 ± 0.76	0.98 ± 0.33
Biomass herbivorous fish (g)	50.94 ± 7.76	66.20 ± 13.94
Abundance herbivorous fish (50 m^2)	16.8 ± 2.48	13.0 ± 2.15
Abundance sea urchins (50 m^2)	1.27 ± 0.61	3.02 ± 1.29
Total abundance of herbivores (herbivorous fish + sea urchins; 50 m^2)	18.10 ± 2.48	16.02 ± 2.49
Number of other seaweed species (50 m^2)	1.92 ± 0.19	8.13 ± 0.44
Cover of other seaweed species (%)	7.55 ± 1.24	29.05 ± 2.61
Turf cover (%)	15.17 ± 1.22	11.79 ± 1.18
CCA cover (%)	13.45 ± 1.37	4.42 ± 0.93
Live coral cover (%)	45.81 ± 2.84	5.19 ± 1.89
Rugosity (1–5)	3.23 ± 0.11	2.14 ± 0.10
Weighted fetch (fetch = 10 km)	5.37 ± 0.44	5.82 ± 0.29
Depth (m)	1.58 ± 0.07	1.89 ± 0.11
Visibility (m)	6.18 ± 0.41	8.04 ± 0.43
Amount of soft substrate (%)	17.10 ± 3.12	51.37 ± 4.22
Amount of dead coral rubble (%)	36.14 ± 2.56	32.46 ± 3.36
Distance to AOI (m)	3105 ± 305.6	3033 ± 419.5

and Speight (2005) where 1 is completely flat and 5 denoting very high structural complexity. The percent cover of other fleshy macroalgae (as potential competitors), crustose coralline algae (CCA), algal turf and live corals was also documented. At both ends of each transect, GPS coordinates were recorded allowing for geographical positioning (± 5 m). All distances were measured in ArcMap 10.5 and measured as linear distance. Depth was measured at both ends of the transect with a dive computer (Suunto Vyper), and a mean value was calculated.

Grazing estimations

Grazing intensity on *E. denticulatum* found in transects was estimated using a 7-grade percent scale (1, 5, 10, 25, 50, 75, 100). Grazing was defined as 100% when all tips of branches within a patch of *E. denticulatum* had been removed, 50% when half of all tips had been removed and so on. It was also noted whether the grazing scars were caused by fish, urchins, or smaller invertebrates. Fish inflict straight bite marks, urchins cause irregular bites on the thallus with jagged edges, and invertebrates leave small cavities on the thallus (Hay 1981).

Estimations of relative wave exposure

Wave exposure is a major structuring force in marine communities (Harrold et al. 1988; Friedlander et al. 2003; Chollett and Mumby 2012). Here, relative wind fetch was calculated and used as a proxy for wave exposure (Burrows 2012). First, a shapefile was created in ArcGIS (ArcGIS 10.5), in which the locations of transects were projected and all land areas defined with polygons. Shallow reef areas exposed during low tide were also identified as land (objects reducing waves). Wave fetch was then calculated in R version 3.3.1 using the "fetchR" package (Seers 2017). To be able to detect both large- and fine-scale variation in relative wave/wind exposure, the fetch was set to a maximum of 10 km. The number of wind directions per measuring point was set to 36. Finally, a weighted mean fetch (depending on the frequency of different wind directions) was calculated in Excel, using wind data from Iowa Environmental Mesonet (Iowa State University; https://mesonet.agron.iastate.edu/request/download.phtml) for each respective month (July for Kane'ohe Bay and September–November for Mafia Island) and location (station Kaneohe_MCAS/OAHU and Dar es Salaam AR, respectively). A mean value for the start and end point of each transect was used in the calculations.

Abundance and biomass of herbivores

Herbivores were surveyed by counting fish and sea urchins along each transect. Herbivorous fish were identified to the lowest taxonomical level (usually species or genus), and body size was estimated to the closest 1 cm, following Tano et al. (2017). To minimize potential disturbance to fishes, surveys were conducted 5 min after the transect line was placed. A snorkeler swam twice along the transect at ~ 0.1 m s^{-1}, first documenting all easily visible fish species, and second, all cryptic species. To facilitate species identification, each snorkeler was equipped with a camera (Canon Powershot G7x Mark II and Canon WP-DC54 underwater housing) used to record unfamiliar species. To avoid potential bias regarding length estimations, size trial estimations were done prior to the study so that all snorkelers were calibrated with each other and any possible biases were consistent. All transect surveys were performed during high tides between 09:30–16:00. Literature was used to define fishes as herbivores (e.g., Froese and Pauly 2017), and in cases where it was not possible to identify a fish to species level, the trophic group for the family in question was used (e.g., juvenile scarine labrids). Although not all herbivorous fishes remove fleshy seaweeds intentionally (e.g., fishes targeting epiphytes can also remove parts of seaweeds), the overall effect of herbivory suppresses algal biomass and promotes coral cover (Bellwood et al. 2004; Mumby 2006, 2016), and thus analyses were performed on the total herbivorous fish assemblage. Herbivorous fish biomass was calculated using species-specific length–weight relationships for total length (TL) of each individual. If the species could not be determined or if species-specific values were lacking, relationships for the same subfamily were used instead. To describe the herbivorous fish assemblage, fishes were classified into juveniles, subadults and adults based on length estimations using the 1/3 and 2/3 cutoff method (Nagelkerken and Van der Velde 2002; Tano et al. 2017). If information on length at maturity (L_m) was available for a particular species,

these values were used instead of the 1/3 method (see Tano et al. 2017). L_m values were extracted from FishBase (www.fishbase.org) and literature (DeMartini et al. 2005; Mangi and Roberts 2006; Taylor and Choat 2014).

Genetic sampling and analysis

Molecular analysis was used to determine which *E. denticulatum* strains that were dominant in Kane'ohe Bay and to be able to identify introduced (Southeast Asian origin) versus indigenous individuals (East African origin) on Mafia Island. An algal patch of *E. denticulatum* was considered as one individual and one frond was collected from each such algal patch along transects (N_{total} = 167). This sampling method was used because *E. denticulatum* (especially when grazed intensely) is rarely identifiable as individuals, but rather grows as dense patches which can cover a large area. The fronds were then dried and stored individually in sampling containers with silica gel. In the lab, total genomic DNA was isolated using a modified CTAB extraction, based on the protocol by Zuccarello and Lokhorst (2005). In short, a small piece of tissue was soaked in 500 µl CTAB buffer (Karolinska University Laboratory) for 2 h and homogenized using glass, metal, and ceramic beads in FastPrep MP24 (Nordic Biolabs) at a speed of 6.0, time for 40 s, which was repeated 5 times. The homogenized tissue was incubated overnight at 56 °C in 5 µl RNAse A (1000 mg ml^{-1}, Thermo Scientific) and 10 µl proteinase K (20 mg ml^{-1}, Thermo Scientific), and then extracted with chloroform:isoamyl alcohol (24:1, 500 µl) and centrifuged for 10 min (14,000 rpm). DNA suspended in the aqueous phase was carefully separated from the interphase (300–450 µl) and re-extracted in chloroform:isoamyl alcohol (24:1). DNA was precipitated using ice-cold isopropanol (100%) and incubated in –20° C for 30 min and centrifuged for 20 min in 14,000 rpm to retain a DNA pellet. The pellet was washed with 70% ethanol with subsequent centrifugation of (10 min, 14,000 rpm), air-dried and dissolved in 100 µl 0.1 × TE buffer. DNA yield and quality were estimated on agarose gel (stained with SYBRSafe; 5 µl 100 ml^{-1}, for 30 min, Life technologies) and Nanodrop 2000 spectrophotometer. DNA was then stored in −80 °C freezer.

For identification of different haplotypes, the mitochondrial *cox2-3* spacer was used, as described by Zuccarello et al. (1999). PCR purification and Sanger sequencing (forward and reverse) were carried out by Macrogen Europe Inc., using an ABI3730XL sequencer. Quality evaluation and alignment of sequences was conducted using MEGA 6.0. Haplotypes were aligned manually and identified using reference sequences (Zuccarello et al. 2006; Halling et al. 2013; Tano et al. 2015). A haplotype was considered new if there were ≥ 1 single nucleotide polymorphism (SNP) difference between the haplotype in question and reference haplotypes. All new haplotypes were carefully checked using chromatograms, reassuring that differences in SNPs were not due to insufficient quality of sequences. Ambiguous sequences/haplotypes were corrected using the chromatograms.

Statistical analyses

To explore which abiotic and biotic factors that influence the presence of *E. denticulatum,* a mean value for each variable was calculated for each transect. Data from Kane'ohe Bay and Mafia Island were analyzed separately, as the two sites have different environmental conditions and the same factors might not have the same impact at the different geographical locations.

There was high incidence of zero-values in the cover of of *E. denticulatum* (> 60% of transects) but preliminary analyses using zero-inflated poisson models (ZIPs) showed a poor model fit to assumptions. Moreover, % cover in transects where *E. denticulatum* was present was generally low (≤ 24%), average cover of *E. denticulatum* per transect in Kane'ohe Bay was 3.3% and on Mafia Island 1%, and in transects where *E. denticulatum* was found 7.8% and 3.5%, respectively. Consequently, we converted all *E. denticulatum* cover data into presence (1) or absence (0), and then tested the influence of environmental variables using mixed logistic regression. Variables influencing presence/absence of *E. denticulatum* in Kane'ohe Bay were tested with binomial generalized mixed effects models (GLMMs), using the R packages "lme4" (Bates et al. 2015), "glmmADMB" (Fournier et al. 2012; Skaug et al. 2016). Because at least two transects were sampled in each same patch reef or area in both Kane'ohe Bay and Mafia Island (Fig. 1), "reef" was initially included in all models as a random factor. Furthermore, because the variable "reef

treatment" ("manual removal/sea urchin transplantations" or "none") was non-normality distributed and not possible to transform satisfactorily, this variable was excluded. Hence, the random factor "reef" includes both potential variation caused by reef treatment and spatial grouping of reefs. Because no variation was added to the Mafia Island data set depending on "reef", generalized linear models (GLMs) from package "stats" (R Core Team 2017) were used. Predictor variables [biomass of herbivorous fishes, total herbivore abundance (ind. transect^{-1}), abundance of sea urchins (ind. transect^{-1}), number of other seaweed species, cover of other seaweed species, turf cover, CCA cover, live coral cover, rugosity, relative wave exposure, depth, amount of soft substrate, amount of dead coral rubble and distance to AOI] were checked for multicollinearity by pairwise comparison using the Spearman rank test and by evaluating variation inflation factor (VIF) values (Zuur et al. 2010). Predictor variables with VIF-values ≥ 2 were removed from the same model. Model selection was performed by starting with the full model (including all predictors). Non-significant variables were then removed one by one until the most parsimonious model remained, based on Akaike's Information Criterion corrected for small sample sizes (AICc) (Johnson and Omland 2004). If ΔAICc ≥ 2, the model with the lowest AICc value was considered the most parsimonious one. Each model was then tested for interaction effects against all environmental variables (allowed in the same model based upon Spearman rank and VIF tests). Prior to model fitting, normal distributions of predictor variables were visually examined by basic diagnostic plots, and if needed, transformation log(x + 1) and rescaling to size range were performed. All final models were tested with influence measures, Cessie van Houwelingen test and Pearsons x^2 test for assumptions for binomial GLM and GLMM.

Differences in grazing intensity between Kane'ohe Bay and Mafia Island were analyzed by Kruskal-Wallis rank sum test. The same type of test was used to compare the level of grazing scars on *E. denticulatum* among different patch reefs in Kane'ohe Bay. A two-way ANOVA was used to test for differences in grazing among sampling sites on Mafia Island and if this was dependent on distance to AOIs. Transects were classified as "close" if they were located at distances < 1 km from an AOI or "far" if > 1 km. To test for an effect of distance from AIOs on the proportion of non-indigenous and indigenous strains of *E. denticulatum* on Mafia Island, all *E. denticulatum* individuals found in transects were used. Proportion values were calculated for each sampling area (Chole Channel, Jibondo, Juani, Kitutia, Kulawe, Mwamba mkuu, Mwamba mkuu mdogo), and these were classified as "close" if they were located at distances < 1 km from an AOI or "far" if > 1 km. Origin of seaweeds were obtained from the DNA analyses and the proportion of non-indigenous and indigenous strains of *E. denticulatum* was analyzed with a Pearson chi square test. All statistical analyses were performed in R version 3.3.1 (R Core Team 2017).

Results

Factors influencing the presence of *Eucheuma denticulatum*

Several environmental characteristics differed between Kane'ohe Bay and Mafia Island (Table 1). *E. denticulatum* and live coral cover were higher in Kane'ohe Bay whereas cover and number of other seaweed species, biomass of herbivorous fish and amount of soft substrate were higher on Mafia Island (Table 1). However, the abundance of herbivorous fish and distances to AOIs were similar between the two locations.

Kane'ohe Bay

The likelihood of finding *E. denticulatum* increased with wave exposure ($p < 0.05$, Table 2; Fig. 2a) and was dependent on site ("reef"). *E. denticulatum* was only found in 23 of the 52 transects sampled, mainly in the northern and central part of Kane'ohe Bay (Fig. 1). At the AOI at Coconut Island, *E. denticulatum* was not found, and it was also absent from the southern inshore areas. Cover of *E. denticulatum* was generally low, ranging from 1.2—24.2% among transects where it was present. The distribution was patchy, with cover reaching up to 50% at heavily colonized subsections within transects. The substrate to which *E. denticulatum* was attached consisted almost exclusively of coral (living coral or coral rubble) with a high degree of structural complexity, mainly *P. compressa.*

Table 2 Results of binomial generalized mixed linear model (GLMM) displaying environmental variables tested against presence of *Eucheuma denticulatum* in Kane'ohe Bay. Significant values are indicated in bold. AOI denotes the area of introduction

Predictor variables	Response variable	
	Presence *E. denticulatum*	
	z-value	p-value
Biomass herbivorous fish (g m^{-2})	0.04	0.968
Abundance herbivorous fish (50 m^2)	−0.310	0.757
Abundance sea urchins (50 m^2)	0.728	0.467
Number of other seaweed species (50 m^2)	1.488	0.137
Cover of other seaweed species (%)	1.757	0.079
Turf cover (%)	1.436	0.151
CCA cover (%)	1.803	0.071
Live coral coral (%)	−0.667	0.505
Rugosity (1–5)	−0.964	0.335
Relative wave fetch/exposure (fetch = 10 km)	2.272	**0.0231**
Depth (m)	−1.393	0.164
Amount of soft substrate (%)	−1.436	0.151
Amount of dead coral rubble (%)	1.210	0.226
Distance to AOI (m)	1.371	0.170

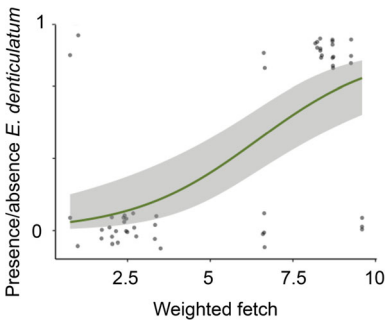

Fig. 2 Presence of *Eucheuma denticulatum* as a function of wave exposure (measured as weighted fetch) in Kane'ohe Bay, results from binomial generalized linear mixed model (GLMM)

Scarine labrids were the most abundant herbivores, and the majority consisted of juveniles or subadults. Few fish exceeded 15 cm, although larger individuals were observed on the barrier reef flat outside the transects. Adult *Zebrasoma flavescens* and *Z. veliferum* were frequently observed grazing on *E. denticulatum,* but these species were not abundant within the transects.

Mafia Island

The likelihood of finding *E. denticulatum* decreased with distance from AOIs (p = 0.009, Table 3) and increased with cover of dead coral rubble (p = 0.006, Table 3). There was also a significant interaction between the two variables (p = 0.02, Fig. 3), where occurrence of *E. denticulatum* decreased less with distance from AOIs in the presence of dead coral rubble. There was also a (weak) interactive effect of distance from AOIs and live coral (p = 0.042, Table 3), but not from live coral cover only (p = 0.527, Table 3).

On Mafia Island, *E. denticulatum* cover was considerably lower (0.1–11% in transects where it was encountered) than in Kane'ohe Bay. Average cover per transect was 1% (all transects), and 3.4% in transects where *E. denticulatum* was encountered. The distribution of *E. denticulatum* was very patchy. Larger patches (up to 4 m^2) with high cover of *E. denticulatum* (> 40%) were only found within 50 m of AOIs. Further away only solitary individuals were found. Coral rubble (usually remnants from branching corals such as *Acropora* spp.) was the most common substrate for attachment, followed by sponges and small rocks. No *E. denticulatum* was found in transects with high live coral cover.

Herbivorous fish assemblages were dominated by scarine labrids, consisting mainly of juveniles and subadults. Larger (adult) acanthurids, kyphosids and siganids were observed within the study area, but rarely in the transects.

Table 3 Results of binomial generalized linear model (GLM) displaying environmental variables tested against presence of *Eucheuma denticulatum* on Mafia Island. Significant variables are indicated in bold. Only the significant interactions were included in the table although all variables were tested for interactions

Predictor variables	Response variable	
	Presence *E. denticulatum*	
	z-value	p-value
Biomass herbivorous fish (g m^{-2})	−0.410	0.682
Abundance herbivorous fish (50 m^2)	−0.198	0.843
Abundance sea urchins (50 m^2)	−1.063	0.288
Number of other seaweed species (50 m^2)	0.642	0.521
Cover of other seaweed species (%)	−0.946	0.344
Turf cover (%)	−0.382	0.703
CCA cover (%)	−0.696	0.486
Live coral coral (%)	0.632	0.527
Rugosity (1–5)	0.415	0.678
Relative wave fetch/exposure (fetch = 10 km)	−0.199	0.842
Depth (m)	0.226	0.821
Amount of soft substrate (%)	0.339	0.735
Amount of dead coral rubble (%)	2.744	**0.006**
Distance to AOI (m)	−2.595	**0.009**
Interaction (distance to AOI × dead coral rubble)	−2.325	**0.020**
Interaction (distance to AOI × live coral cover)	−2.900	**0.042**

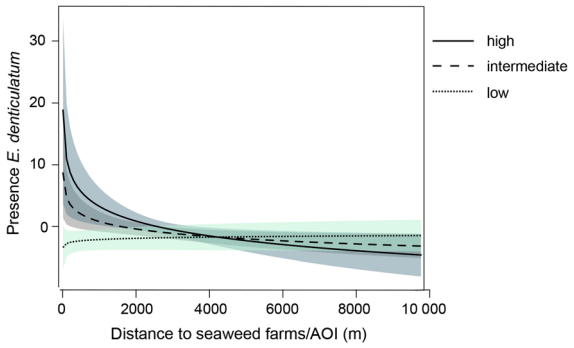

Fig. 3 Interaction plot of the generalized linear model (GLM) displaying fit of model with the interaction between distance to area of introduction (AOI) and cover of dead coral rubble (black and dashed lines) for presence of *Eucheuma denticulatum* (log odds) on Mafia Island. Shaded areas denote partial residuals. "High" (black line) denotes cover of dead coral rubble in an interval of 92.5–61.7%, "intermediate" (dashed line) cover of 61.7–30.8% and "low" (dotted line) cover of 30.8–0%

Grazing intensity

In Kane'ohe Bay, *E. denticulatum* was estimated to be grazed 100% by fish (all fronds cropped). There were no significant differences in abundance of herbivorous fishes among sites (ANOVA, f = 3. 9, df = 6, $p > 0.05$). Almost all *E. denticulatum* observed in the study were cropped below the level of coral branches (Fig. 6a).

Compared to Kane'ohe Bay, a lower grazing pressure of *E. denticulatum* was found on Mafia Island (average 50%) (Kruskal-Wallis rank sum test, chi-square = 20.031, df = 1, $p < 0.001$; Fig. 4). Even though sea urchins (*Diadema savignyi, D. setosum, Echinometra mathaei* and *Echinothrix diadema*) were more abundant on Mafia Island than in Kane'ohe Bay, fish were still the most common grazers on *E. denticulatum* based on the type of grazing scars observed. The amount of grazing scars decreased with distance from AOI (ANOVA, f = 5.33, df = 1, $p < 0.05$).

Genetic composition

All identified *E. denticulatum* from Hawai'i (N = 21) belonged to a single haplotype (E32), the Southeast Asian haplotype previously described by Zuccarello et al. (2006). Seaweeds from Mafia Island consisted of a mix of seven haplotypes: one Southeast Asian and commonly farmed haplotype (E13, N = 30), three East African haplotypes [E60, KOM3, PAC5 (Zuccarello et al. 2006; Halling et al. 2013; Tano et al. 2015); N = 15, 1, and 13, respectively], and three newly identified haplotypes [MAF2 (MH115464),

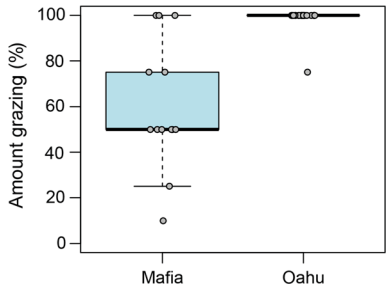

Fig. 4 Amount of grazing measured as % of grazing scars on individual *Eucheuma denticulatum* fronds found in transects on Mafia Island (N = 12) and in Kane'ohe Bay, Oahu (N = 22). Fronds on Mafia Island were on average grazed 60.3% and in Kane'ohe Bay 98.9%. Horizontal lines denote median values, boxes 25th and 75th percentiles, and error bars 95% confidential intervals. Filled circles denote outliers

MAF4 (MH115465) and MAF6 (MH115466); N = 1, 3, and 4, respectively]. All new identified strains were single nucleotide polymorphisms (SNPs) of haplotype E60 (Fig. 5). Seaweeds sampled close to farms ($\leq$ 50 m) consisted solely of introduced haplotypes (Fig. 5), while transects further away from AOIs had higher proportions of indigenous strains (chi-squared = 151.7, df = 1, $p < 0.001$). At the most remote location (Kitutia) only one individual of *E. denticulatum* was found, which belonged to the indigenous haplotype KOM3.

Discussion

This study shows that different factors predicted the presence of *E. denticulatum* in the two geographic locations. Relative wave exposure increased the presence of *E. denticulatum* in Hawai'i, but had no effect on Mafia Island. Furthermore, *E. denticulatum* was more grazed in Kane'ohe Bay than on Mafia Island, which refutes our hypothesis that presence of *E. denticulatum* is regulated by herbivory to a higher degree on Mafia Island than in Kane'ohe Bay. On Mafia Island, however, the amount of hard substrate (dead coral rubble and live coral cover) close to areas of introductions (AOIs) was the main factor predicting the presence of *E. denticulatum* but not in Kane'ohe Bay.

Studies have identified water movement and water exchange as important factors influencing productivity among seaweeds, because a high degree of water movement (to a certain extent) enhances CO_2 concentration in the water and thus increases nutrient and gas exchange between the macroalgae and the surrounding water (Hurd 2000). In Kane'ohe Bay, water movement is mainly generated through wave and wind exposure, whereas within the Mafia seascape, water movement is also driven by large tidal differences, potentially explaining why wave exposure is not as important on Mafia Island. However, water movement might have various and ambiguous impacts on algal assemblages, e.g., reducing biomass by dislodging thalli or branches due to mechanical stress (and thus possibly facilitating spread; Jackelman and Bolton 1990; Rodgers and Cox 1999), or a positive impact by decreasing herbivory because of exclusion of fishes with weaker swimming abilities (Bejarano et al. 2017). Water movement probably has an important role in the dispersal of *E. denticulatum* (Russell 1983), which is similar to other non-indigenous seaweeds with vegetative reproduction, such as *Hypnea musciformis* (Vermeij et al. 2009).

The survey of grazing scars and the restriction of *E. denticulatum* to protected microhabitats (i.e., in high complexity habitats) suggests that populations in Kane'ohe Bay are intensely grazed by herbivorous fish, although this was not supported by fish biomass and abundance data obtained from the field study. Biomass of herbivorous fishes was considerably lower than in other studies on the Hawai'ian islands (e.g., Kauai $\sim$ 12 g m^{-2}, Maui $\sim$ 20 g m^{-2}, this study $\sim$ 1 g m^{-2}) and Oahu as a whole ($\sim$ 10 g m^{-2}; Helyer and Samhouri 2017; Gorospe et al. 2018). Avoidance behavior of fish towards observers is a potential risk when conducting underwater visual census (Kulbicki 1998; Edgar et al. 2004) and might explain why fish biomass was not a predictor of *E. denticulatum* in our study. Adult herbivores displayed a stronger avoidance behavior than juvenile and subadult individuals, of which the latter two were dominant in our surveys and thus resulting in low biomass estimates. Future studies should explore whether the use of sampling methods that reduce the observer effect, e.g., remote underwater video (RUV), can better resolve the potential relationship between non-indigenous seaweed densities and herbivorous fishes. According to our grazing scar inventory, native herbivores in Kane'ohe Bay might have the ability to control *E. denticulatum* biomass, given the low seaweed cover observed

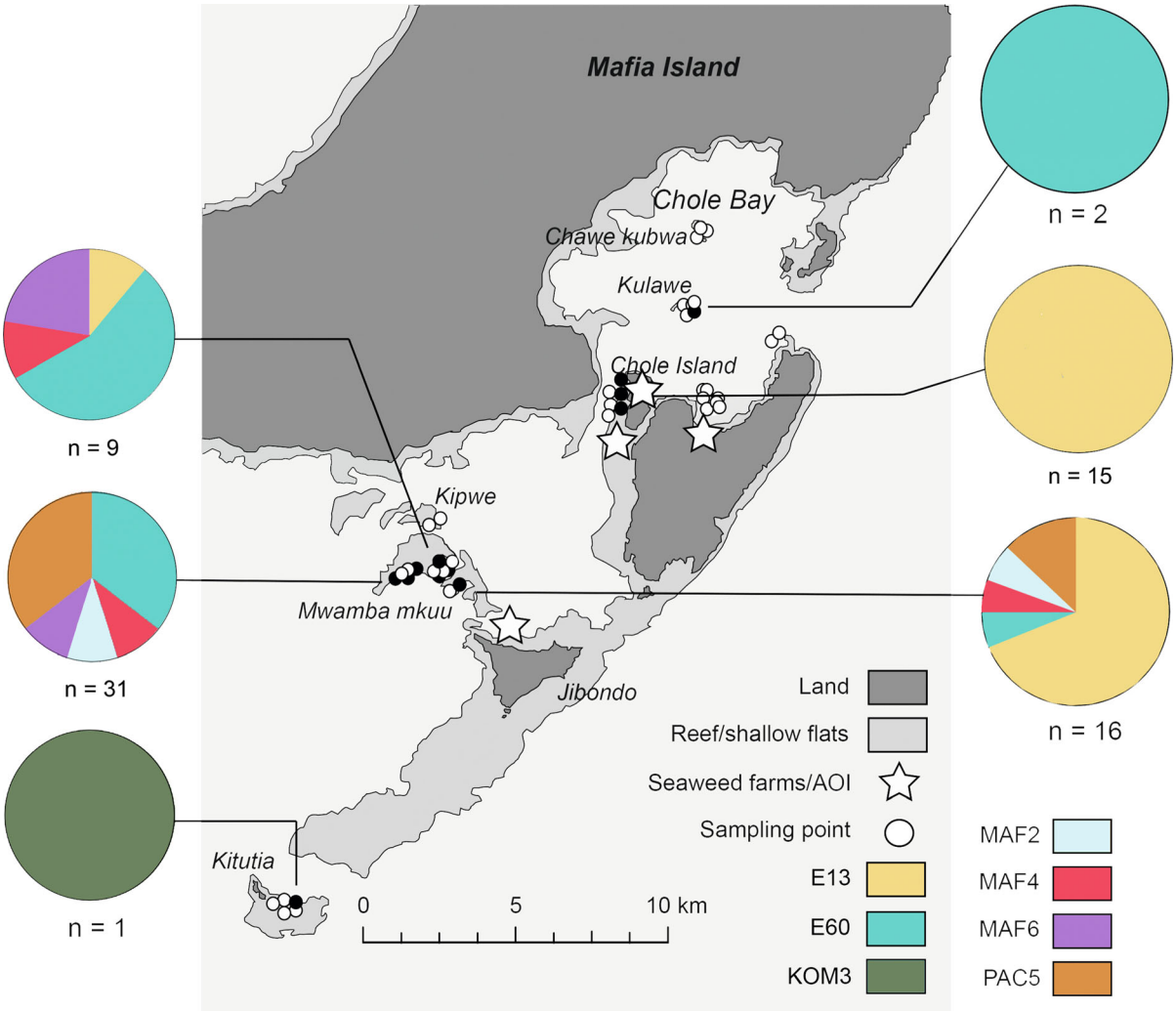

Fig. 5 Overview of identified haplotypes of *Eucheuma denticulatum* and geographical location within the study area. Pie charts display composition of *E. denticulatum* haplotypes at sampling locations. Haplotype E13 is of Southeast Asian origin, and all the others are native to East Africa. Due to patchy seaweed distribution, sample size differs between locations. Filled (black) circles denote sampling points where *E. denticulatum* was found

during the survey year (2016). Additionally, the substrate on which this seaweed is usually found (dead coral rubble) hampers predation as many herbivorous fish species forage on less structurally complex surfaces (Brandl and Bellwood 2014). Such microhabitat topography has been shown to be an important factor in structuring tropical seaweed assemblages by creating grazing refuges in high-complexity reefscapes (Poray and Carpenter 2014).

On Mafia Island, *E. denticulatum* was also grazed but not to the same extent as in Kane'ohe Bay. According to the degree of grazing scars, seaweeds growing close to AOIs were grazed much more than seaweeds growing further away. Similarly, the likelihood of finding *E. denticulatum* was also higher close to the AOIs. These observations may be explained by several mechanisms. Seaweeds in farms were generally also heavily grazed (D.H. Chacin, pers. obs.), and seaweed farms are known to attract siganids (Eklöf et al. 2006), which are efficient browsers and croppers of seaweeds (Bennett and Bellwood 2011; Hoey et al. 2013). This observation is in line with findings from Kenya and Southeast Asia, where there is a positive relationship between farming of eucheumoid

seaweeds and siganid fisheries (Hehre and Meeuwig 2016; Anyango et al. 2017). Few siganids were encountered in the transects, but many were spotted in the surveyed areas. It is possible that the presence of active seaweed farms on Mafia Island, by attracting and concentrating herbivorous fishes, reduces grazing intensity on seaweeds outside farms. In support of this idea, a previous study from Kane'ohe Bay showed that fish preference for non-indigenous seaweeds reduced grazing on other algae (Stimson et al. 2001). Moreover, *E. denticulatum* located further away from farms grew mainly as solitary plants instead of in large patches, and fronds also grew more cryptically (under ledges, in cracks) at the more remote sites than closer to farms (Fig. 6b, c). These growth patterns might have made fronds at remote sites more difficult to detect by herbivorous fishes.

On Mafia Island, distance to AOI was a significant factor for predicting the presence of *E. denticulatum,* because the likelihood of finding *E. denticulatum* was much higher closer to AOIs. This pattern was not observed in Kane'ohe Bay, but because the original AOI were the growth trial took place 40 years ago (and no new introductions have been made since) did not contain any *E. denticulatum* at the time of our study, reefs with higher cover might act as new "seeding points/AOIs" and mask this effect by constituting "stepping stones" for spread of the species throughout the bay. Although not investigated in the present study, the number of years a non-indigenous species has been present in the recipient ecosystem might be an important factor influencing which environmental variables that predict presence and spread of an invader.

The other main factor predicting presence of *E. denticulatum* on Mafia was the amount of dead coral rubble and live coral cover close to seaweed farms. Coral rubble originating from branching corals (e.g., acroporids) provides a three-dimensional structure, which may favor colonization by *E. denticulatum* if pieces of thallus can get intercepted and entangled in branches long enough for holdfasts to develop. Sexual reproduction is not common for this species, so dispersal is limited to thallus fragmentation and water movement (Rodgers and Cox 1999; Conklin and Smith 2005). The ability of *E. denticulatum* to regrow and form attachments from small thallus fragments (Conklin and Smith 2005) in combination with the high percentage of introduced seaweed haplotypes found on rubble close to farms (100% of Southeast Asian origin), suggests that algal fragments from farms have dispersed and reattached to hard substrate in adjacent areas. If no or little suitable habitat was present, cover of introduced haplotypes was very low, which in theory should also reduce the risk of spread. Considering that seaweed farms were first introduced to Mafia Island around the year 2000, these results imply a slightly slower spread than documented for Kane'ohe Bay (Conklin and Smith 2005), which might depend on the availability of suitable substrate.

Different patterns of genetic structure of *E. denticulatum* populations were found between the two geographical locations, with only one haplotype (E32 from Southeast Asia) present in Kane'ohe Bay, but seven haplotypes on Mafia Island, of which only one was from Southeast Asia (E13). On Mafia Island, six native haplotypes of *E. denticulatum* were present in low quantities and exhibited a sparse coverage, and a higher proportion of Southeast Asian haplotypes were found closer to AOIs (Fig. 5). Furthermore, the Southeast Asian haplotype generally had a high cover (Fig. 6b), likely due to new propagules from farms (see above), in combination with higher growth rates (Tano 2016). These results confirm that non-indigenous strains of *E. denticulatum* have spread to Tanzanian reefs, similar to patterns observed on Zanzibar (Halling et al. 2013; Tano et al. 2015). Earlier studies have shown that native haplotypes of *E. denticulatum* exhibit lower growth rates than introduced haplotypes (Lirasan and Twide 1993; Mtolera et al. 1995), indicating that East African haplotypes are less competitive and may therefore not dominate reef communities in a detrimental way.

Establishment of Southeast Asian haplotypes outside farms may result in a shift from indigenous to introduced *E. denticulatum* within the Tanzanian seascape, with considerably lower genetic diversity as a consequence (Tano et al. 2015). However, baseline data on densities, cover, and settling substrate of wild eucheumoid populations prior to seaweed farming is lacking. Also, further research is needed to examine if the introduced haplotypes have a negative effect on corals in Tanzania similar to that documented in Kane'ohe Bay (Conklin and Smith 2005; Neilson et al. 2018). To minimize further spread of non-indigenous haplotypes in Tanzania, we suggest avoiding placing seaweed farms close to areas with hard substrate with a high degree of three-dimensional

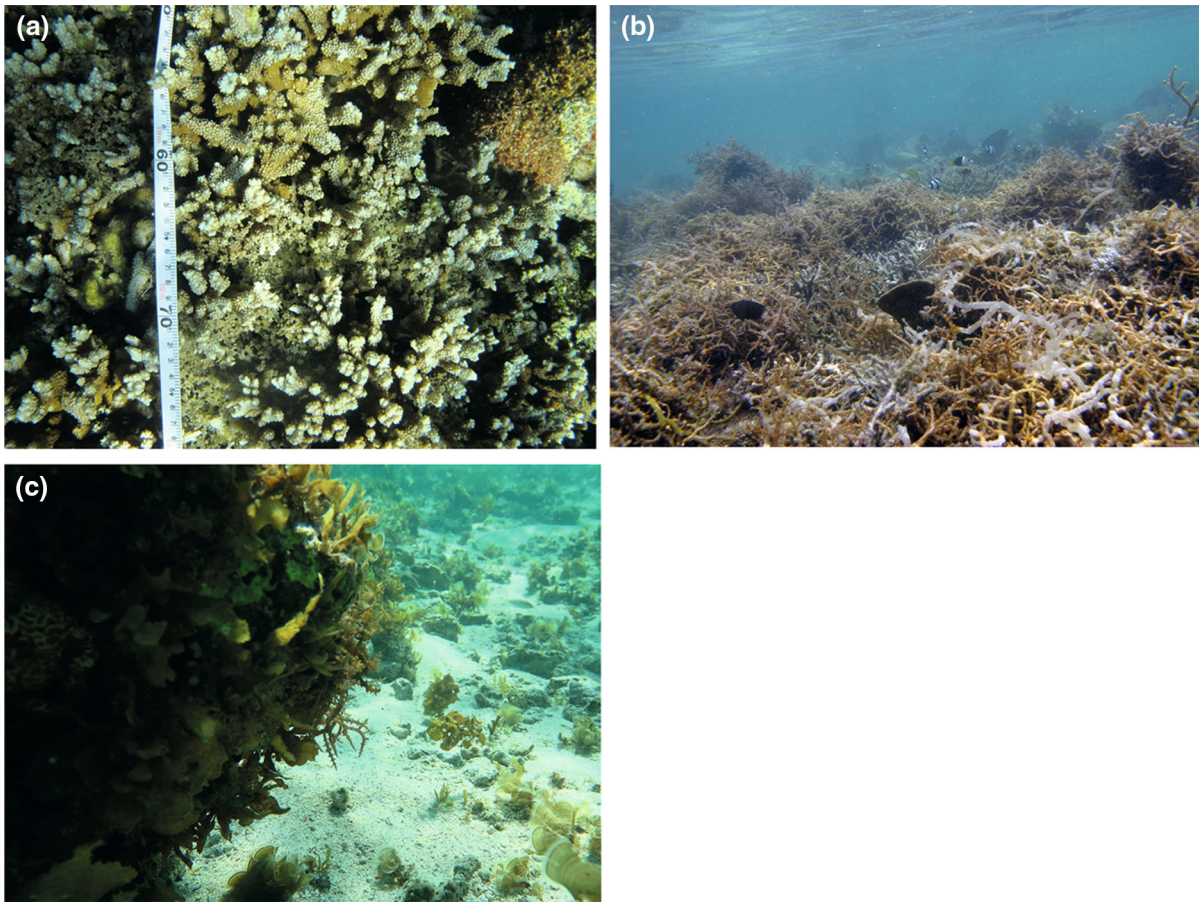

Fig. 6 Photos of *Eucheuma denticulatum* at different sampling sites; **a** *E. denticulatum* in Kane'ohe Bay, Hawai'i. Seaweeds are heavily grazed and cropped below branches of scleractinian corals. **b** Southeast Asian (E13) *E. denticulatum* growing on a patch of coral rubble on Mafia Island. **c** An East African *E. denticulatum* (haplotype KOM3) growing under a rock at Kitutia, Mafia Island

complexity. Threshold values may vary with geographical location and need to be adjusted depending on currents, tides, and herbivorous communities.

Compared to previous studies of *E. denticulatum* in Kane'ohe Bay, we found considerably lower cover which also consisted of smaller and heavily grazed seaweeds (Conklin and Smith 2005; Neilson et al. 2018). We can only speculate about the scarcity found in the present study. First, in the attempt to capture a wide range of environmental conditions (including different substrates) our study did not specifically target areas which were already colonized by *E. denticulatum*. Likely, this choice increased the number of transects where *E. denticulatum* was not observed (i.e., "absent"). Second, there might be seasonal or annual fluctuations in cover that were beyond the scope of this study.

Different factors predict the presence of *E. denticulatum* in the two studied locations, and this result supports previous suggestions that intrinsic characteristics of the recipient ecosystem are crucial for influencing species introductions that result in invasions (Bulleri et al. 2008). Furthermore, we cannot rule out the possibility that since our surveys occurred during different seasons, *E. denticulatum* phenology could have played a role in the patterns observed. We therefore recommend studies that investigate seasonality of macroalgal abundance across geographic locations. To understand and predict consequences of introductions of non-indigenous species or haplotypes, such factors need to be identified. Risk

assessments that combine data on species traits with local environmental conditions (e.g., wave exposure, herbivore abundances or high cover of suitable substrate) might be a useful approach. However, as illustrated here, depending on the characteristics of the study sites direct comparisons may be difficult. There are large differences in both temporal and spatial scale, as Kane'ohe Bay is considerably smaller than the study area on Mafia Island, and the introductions occurred much earlier (1970s vs. 2000s). Also, Kane'ohe Bay has been subjected to multiple disturbances resulting in loss of live hard coral cover, while the Mafia Island seascape is relatively pristine. However, overfishing of herbivores, combined with disturbances causing coral die-offs that increase the amount of advantageous substrate for *E. denticulatum*, might result in increases in seaweed biomass also on Mafia Island.

Conclusions

Here we show that the presence of the introduced *E. denticulatum* in Kane'ohe Bay and on Mafia Island are predicted by different factors. Moreover, the introduction of *E. denticulatum* might not have inferred similar detrimental effects on Mafia Island that have been observed in Kane'ohe Bay. On Mafia Island, suitable substrate (dead coral rubble) and distance to AOI constrains the establishment of introduced haplotypes. We therefore recommend that *E. denticulatum* biomass should be continuously monitored in Mafia Island and farm locations carefully planned to avoid placement near areas with abundant hard substrate, i.e. habitat patches with a high degree of complexity that may act as stepping stones for spread of introduced haplotypes. In Kane'ohe Bay the abundance of herbivores (sea urchins and fish) likely have the ability to reduce biomass of *E. denticulatum*, making it desirable to maintain high densities of these consumers to reduce the risk for further spread and invasions.

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Compliance with ethical standards

Conflict of interest. The authors have no potential conflict of interest concerning the present study.

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