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Extensive spread of farmed seaweeds causes a shift from native to non-native haplotypes in natural seaweed beds

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Abstract Seaweed farming has been the cause of introductions of non-indigenous seaweed species and genotypes throughout the world. In Zanzibar, Tanzania, foreign genotypes of *Eucheuma denticulatum* were introduced for farming purposes in 1989, and in recent years a spread of non-indigenous haplotypes has been reported. The current study aimed to investigate the presence and extent of introduced and native haplotypes of *E. denticulatum* as well as their relative frequencies, to obtain the severity of the spread of cultivated seaweed and the current state of the native populations. The results show that all investigated sites are dominated by the introduced South-east Asian haplotypes, even where seaweed farming has never occurred. As the frequencies of East African haplotypes are remarkably low, this shows a shift from native to introduced *E. denticulatum*. This shift may, at least in part, be caused by earlier overharvest of natural seaweed populations, and indicates a cryptic invasion of the introduced haplotypes at the potential cost of the recovery of the native haplotype populations.

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Introduction

Eucheumoid seaweeds, such as *Kappaphycus alvarezii* and *Eucheuma denticulatum*, are the globally most produced seaweeds within aquaculture (FAO 2014). Cultivation of eucheumoids was initiated in the Philippines during the 1970s, compensating production loss as the natural populations had declined due to overharvest (Parker 1974). Since then, introductions of both the South-east Asian farming technique and the farmed seaweeds have been made to areas outside of the species natural range (e.g. Hawaii: Glenn and Doty 1981; Brazil: Bulboa and de Paula 2005; Mexico: Muñoz et al. 2004; India: Mairh et al. 1995), as well as within it, where native strains of the seaweeds already exist (Tanzania: Lirasan and Twide 1993, Ask and Azanza 2002; Madagascar: Mollion and Braud 1993, Ask et al. 2003; Kenya: Yarish and Wamukoya 1990).

Although seaweed farming generally is considered relatively harmless from an environmental perspective (Zemke-White and Smith 2006), it is important to consider the potential consequences of introducing foreign species. Today there is a rising awareness that introductions of non-indigenous seaweed species may lead to unwanted and sometimes severe ecological effects (Ferrer et al. 1997; Williams and Smith 2007; Klein and Verlaque 2008). Introduced macroalgal species have been shown to impact their new environments in several ways, for instance reducing the cover, productivity and diversity of native seaweeds (Britton-Simmons 2004; Ferrer et al. 1997; Piazzi et al. 2001). In the case of introduced eucheumoids, spread from farm areas have been confirmed in Hawaii (Rodgers and Cox 1999), India (Chandrasekaran et al. 2008), Venezuela (Barrios et al. 2007) and Tanzania (Halling et al. 2013), but in most areas of introduction investigations of potential

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spread have not been made (Ask et al. 2003). In studies from Hawaii and India, it has been shown that introduced eucheumoids have the possibility to not only spread but also to become nuisances in their new environment, where they can overgrow live coral, eventually killing it (Woo et al. 1999; Conklin and Smith 2005; Chandrasekaran et al. 2008; Kamalakannan et al. 2010).

In Tanzania, several native eucheumoids existed in large populations in the 1970s (Mshigeni 1973), with the most common species, *E. denticulatum,* having an average cover of 22 % in areas where it was predominant (Mshigeni 1984). In Zanzibar, hundreds of tonnes dry weight were collected and exported annually between the 1950s and the end of the 1970s, when eucheumoid resources declined (Pettersson-Löfquist 1995). Due to the continuously increasing demand for carrageenan (FAO 2010), and as native East African *E. denticulatum* appeared unsuitable for farming purposes (Lirasan and Twide 1993; Pettersson-Löfquist 1995), highly productive *E. denticulatum* and *K. alvarezii* were introduced from South-east Asia in 1989 (Lirasan and Twide 1993). Today the introduced *E. denticulatum* is farmed widely around Zanzibar, whereas *K. alvarezii* only to a lesser degree due to problems with die-offs (Msuya 2011). East Africa is unique in the sense of eucheumoid introductions, as the region already harbours native haplotypes that are now known to be genetically well separated from the haplotypes introduced from South-east Asia (Zuccarello et al. 2006). It has recently been confirmed that *E. denticulatum* with South-east Asian origin have spread and can be found growing outside of farms (Halling et al. 2013), alongside their native counterparts. Due to the morphological plasticity that occurs within as well as between eucheumoid species (Zuccarello et al. 2006), it is, presently, only possible to distinguish between native East African haplotypes and their South-east Asian counterparts through molecular methods, meaning that there is a risk of a cryptic invasion taking place. There has been many reports of productivity problems such as 'ice-ice', where parts of the algal tissue become bleached and necrotic (Largo et al. 1995), and epiphyte infestations in eucheumoid aquaculture (e.g. Hurtado et al. 2006; Vairappan et al. 2008; Tisera and Naguit 2009), which may partly be caused by the limited amount of seaweed material used in cultivation and its vegetative propagation (Hurtado et al. 2014). This points out the importance of preserving wild populations as future sources of seed stock, and also raises the question of the extent of the spread of South-east Asian haplotypes and the state of native populations of *E. denticulatum* in the recipient ecosystem.

In the present study, we investigate *E. denticulatum* cover and density coupled with genetic analysis, to determine the presence and extent of wild-growing non-indigenous and native haplotypes in intertidal areas around Zanzibar. We also examine the presence of reproductive structures in order to evaluate the potential for hybridisation between haplotypes. In addition to this, we survey what haplotypes are currently used in seaweed farms, as well as the broad-scale occurrence of wild-growing introduced haplotypes in farming areas.

Materials and methods

Description of the study area and species

The study was carried out at Zanzibar Islands, Tanzania. Zanzibar consists of two main islands, Pemba and Unguja, and is separated from mainland Tanzania by the Zanzibar Channel. The study area is located in tropical East Africa in the Western Indian Ocean (WIO) region, which is highly influenced by tides, with tidal amplitudes of approximately 4 m. The study was conducted during the South East monsoon (SEM), which is characterised by low temperatures and solar insolation, with strong currents and high wave action (McClanahan 1988). The sampling period was chosen to coincide with the higher abundances of *E. denticulatum* that can be found during the colder period (pers. obs.), which is also indicated by higher growth rates of eucheumoids in East Africa coinciding with the cold season (Wakibia et al. 2006, 2011). All investigations reported in the present study were carried out during two periods: October to November in 2011 and July to October in 2012.

E. denticulatum (Solieriaceae, Gigartinales, Rhodophyta) is the most commonly farmed eucheumoid species in Zanzibar. It is a cartilaginous species with large plasticity, which in the wild grows mainly on hard substrate with sufficient water movement, and can tolerate tidal areas that are exposed to air during parts of the day (Mshigeni 1979). The species has a triphasic life cycle, but in the commercial strains of *E. denticulatum*, reproductive structures appear to be rare (Doty and Santos 1978) and *Eucheuma* farmed in shallow water is commonly sterile (Doty 1987).

Seaweed farms in the area mainly use the shallow water off-bottom technique, where seaweed fronds are tied to ropes which are then attached to wooden pegs driven into the sediment (Msuya and Salum 2011). The propagation of plants is vegetative, and re-seeding of farms is done by using cuttings from the last harvest. The farms are commonly located in sandy areas of high tidal influence.

Study of farmed *E. denticulatum*

In order to determine the haplotypes of *E. denticulatum* currently farmed in Zanzibar, and the genetic origin of attached *E. denticulatum* fronds found outside but in close vicinity (<200 m) of seaweed farms, samples were

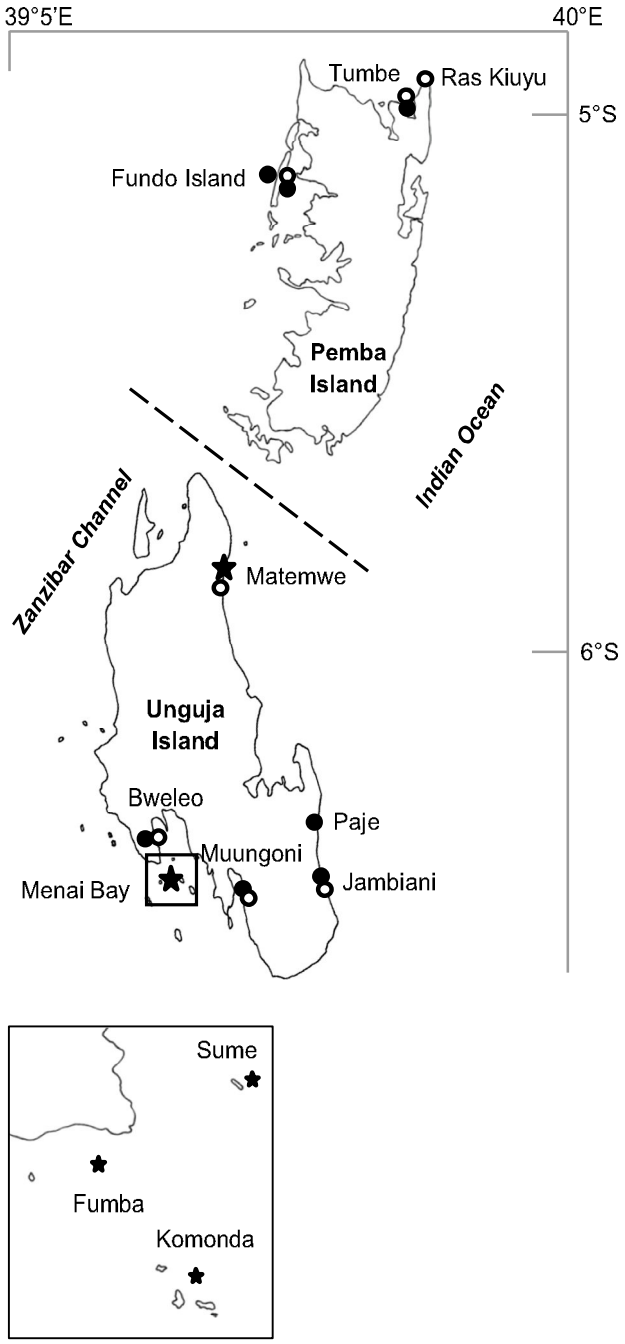


Fig. 1 Map of Unguja and Pemba Islands. *Stars* indicate sites in the study of wild *E. denticulatum*, *hollow dots* indicate farms sampled and *filled dots* indicate sites checked for attached *E. denticulatum* in close vicinity of farms. *Close up* shows sites in the Menai Bay area

collected from seven representative farm settings with active large-scale seaweed farming on Pemba and Unguja Islands for genetic analysis (Fig. 1). The samples were collected from October to November in 2011 with some additional samples collected in October in 2012. Between 5 and 25 samples per site were collected from farms, with the number of samples depending on information from the farmers of the number of varieties farmed, as well as the visible variation of the seaweeds themselves (e.g. colour and shape). Areas surrounding the farms were searched for wild-growing *E. denticulatum*, with the search range commonly being within and around farms by 200 m in all directions possible. All substrates were included, but more focus put on hard substrate areas. For the wild stands surrounding the farms, one sample was taken per patch.

All genetic samples were dried and stored in silica gel until DNA extraction. Total genomic DNA was isolated from the dried samples with a modified CTAB extraction described by Zuccarello and Lokhorst (2005). The *cox*2-3 spacer was generated as described by Zuccarello et al. (1999), and both PCR purification and Sanger sequencing were performed by Macrogen Europe Inc. using an ABI3730XL sequencer. Sequences were quality controlled and aligned using MEGA 5.2 and identified with standard nucleotide BLAST in GenBank® (http://www.ncbi.nlm.nih.gov). The mitochondrial DNA haplotypes were identified by alignment and comparison with sequences from Zuccarello et al. (2006). Furthermore, phylogenetic relationship was calculated using the maximum likelihood (ML) approach, with bootstrapping (1000), and visualised with dendrograms as implemented in MEGA 5.2.

Study of wild *E. denticulatum*

A detailed study on the cover, density, reproductive structures and genotype composition of wild-growing *E. denticulatum* was carried out at four selected sites around Unguja Island (Fig. 1), chosen due to previous knowledge and reports of presence of wild *E. denticulatum* (Mshigeni 1984). Three of the sites are located in the Menai Bay area at the southwest coast of Unguja: Fumba, where farming has been reported to have occurred at least in 2004 (Halling et al. 2013); Sume, a small uninhabited island separated from the main island by deeper water, where no farming has been reported but local people report regular collection of *E. denticulatum*; Komonda, a set of three small, uninhabited islands, interconnected by a tidal plain and surrounded by deeper water. Trial farming of native *E. denticulatum* has been performed at the site (under the name Pamunda) (Mtolera et al. 1995), but no farming of introduced haplotypes has been reported. The two island sites, Sume and Komonda, are located approximately 3 and 6 kms, respectively, from the closest current farming area at Bweleo, and 4 and 3 kms respectively, from Fumba. The last site, Matemwe, is located at the northeast coast of Unguja, and seaweed farming has been practised more or less regularly since 1994 (Bergman et al. 2001). The study of wild *E. denticulatum* was performed from July to October 2012.

Genetic sampling

Fronds were picked haphazardly without looking from the stands of *E. denticulatum* to avoid active selection. Fronds were collected over the entire area of each site, to obtain samples from all potential microhabitats. The sampling was performed in this fashion to enable a credible assessment of approximate haplotype frequencies at each site, and between one and two samples were taken per patch. Other eucheumoid species were also sampled whenever found. The samples were analysed as described above for the study of farmed *E. denticulatum*.

Estimation of cover and density

At each of the four sites selected for the study of wild *E. denticulatum*, five transects, 25 m long and 2 m wide, were sampled in the beginning of September 2012 and again a month later. The cover of *E. denticulatum* was determined by walking or swimming along a transect line and estimating the cover visually of a 2 m section at the time. For each section, the cover was estimated on a 9-graded scale (0, 1, 5, 10, 15, 25, 50, 75 or 100 % cover). We also estimated the cover of other large macroalgae down to the genus level, the total macroalgal cover and the amount of hard substrate suitable for algal growth using the same 9-graded scale. The cover of *E. denticulatum*, other algae and the total algal cover were then divided by the cover of hard substrate to account for differences in the cover of hard substrate between transects. The analyses are based on mean cover for all sections of the transects.

Additionally, the density of *E. denticulatum* was determined at each site and sampling occasion, by harvesting an area of 20 × 20 cm where the species was present for biomass measurement. Five samples were harvested by hand at each site and sampling occasion, and the collected samples were weighed (wet weight). In cases where *E. denticulatum* was found to occur in small patches of less than 20 × 20 cm^2, smaller samples were taken and for comparability the biomass was calculated per surface area (g WW cm^{-2}).

Reproductive structures

At the four sites where the wild seaweeds were studied, samples of *E. denticulatum* were also collected for investigating reproductive structures. Samples were visually inspected for reproductive structures using a light microscope. Cross and longitudinal sections of thalli were prepared by hand using a scalpel and inspected, as well as longitudinal sections of the spines. Between 20 and 29 fronds per site and sampling occasion were inspected.

Abiotic factors

Temperature and light were measured using HOBO Pendant® Temperature/Light Data Loggers placed at the four sites where the wild seaweeds were studied, at the same water depth as the seaweeds, and set to record every ten minutes from the 2nd to the 30th of September 2012. The measurements of temperature and light incidence were collected to establish if there were any large differences between the sites regarding temperature and light. No large differences were found between the sites. The average water temperature varied between 27.5 and 28.2 °C during the period studied, but minimum and maximum temperatures ranged between 23.2 and 34.5 °C during spring tides. Light varied from 0.3 to 1.6 × 10^5 lux, with the highest light levels occurring during spring low tides when the seaweeds and loggers were emerged.

Statistics

Differences in cover and density of *E. denticulatum* between sites and sampling occasions were analysed with two-way ANOVAs with Tukey's post hoc test in R 2.15 (R Core Team 2014). Visual inspection of the data for normality was made using Q-Q plots and residual models, and transformations were made when necessary. Heterogeneity of the data was also checked by Bartlett's test.

Results

Genetic analyses

All but one of the genetic haplotypes of *E. denticulatum* detected in this study have previously been described, and throughout this study the haplotype numbers designated to them by Zuccarello et al. (2006) and Halling et al. (2013) will be used, and an additional number was designated to the new haplotype. The genetic marker detected five different haplotypes of *E. denticulatum* in the study at large. Two of these, 13 and 32, have been found in farmed and wild samples in Indonesia, the Philippines and Malaysia and have likely been introduced to Zanzibar from South-east Asia (Zuccarello et al. 2006; Halling et al. 2013; Tan et al. 2013). The remaining three haplotypes (60, KOM3 and PAC5) belong to an African group of *E. denticulatum* that is 30 base pairs or more separated from the South-east Asian (SEA) haplotypes (Zuccarello et al. 2006; Halling et al. 2013). The new haplotype detected (KOM3) was only one base pair different from haplotype 60, and also one base pair different from a previously found haplotype (46).

All samples from the study of farmed *E. denticulatum* (i.e. algae collected from the seaweed farms and attached

Table 1 Successfully analysed samples from sites with active seaweed farms sampled for *E. denticulatum* haplotypes and investigated for wild-growing *E. denticulatum* during 2011 and 2012

Farm site	Farmed haplotype	n	Haplotype outside farm	n	Year
Fundo Island	13	2	None[a]	–	2011
Tumbe	13	1	None[a]	–	2011
Ras Kiuyu	13	4	–[b]	–	2011
Jambiani	13	2	13	2	2011
Muungoni	13	21	13	3	2011
Paje	–[c]	–	None[a]	–	2011
Bweleo	13	7	13	7	2011[d] 2012[e]
Matemwe	13	1	See main study	–	2012

[a] No attached plants found

[b] No sampling outside farm

[c] Farm not sampled

[d] Outside farm

[e] Farmed sample

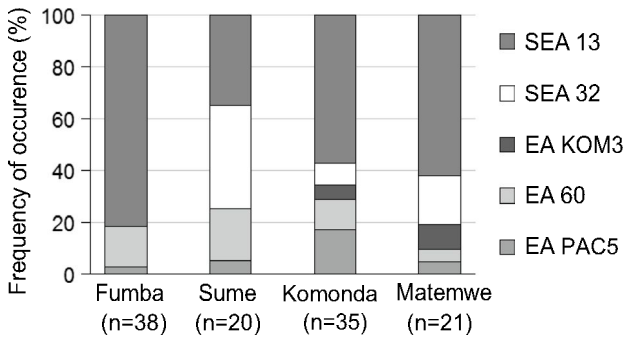


Fig. 2 Frequency of the five different South-east Asian (SEA) and East African (EA) haplotypes of *E. denticulatum* found at the sites over the entire sampling period (July–October, 2012)

specimens in the vicinity of farms) were found to belong to haplotype 13 (Table 1). In total 38 farmed and 12 attached samples, respectively, were successfully analysed.

In the study of wild *E. denticulatum*, the SEA haplotypes of *E. denticulatum* dominated at all of the investigated sites (Fig. 2). At Fumba and Matemwe, the currently farmed haplotype (13) dominated, whereas at Sume the other introduced haplotype (32) was most abundant followed by haplotype 13. Native East African (EA) haplotypes were also present at all sites. Fumba had the lowest frequency of EA haplotypes, with only one specimen being of native origin over all sampling occasions, and Komonda had the highest frequency, with over 50 % native haplotypes during September. Komonda and Matemwe were the only sites where all five haplotypes were present, but the most common haplotype was still 13. In total 114 samples were successfully analysed from the four sites used in the study of wild *E. denticulatum*.

Two other eucheumoid species were found during the study: *K. alvarezii* (haplotype 130) and *E. platycladum* (the new haplotype EP1, which is only one base pair different from the described haplotype 65). Both of these haplotypes are of East African origin (Zuccarello et al. 2006) and were collected at Komonda. All genetic sequences are deposited in GenBank (accession numbers: KT390538–KT390698).

Algal cover and density

The cover of *E. denticulatum* showed a significant interaction between site and sampling occasion (Table 2). The post hoc comparison showed that all sites were significantly different from each other except Komonda and Matemwe, with Sume having the highest *E. denticulatum* cover, with an overall mean and standard deviation of 19.5 ± 6.8 %, followed by Fumba (12.5 ± 14.1 %), and Komonda and Matemwe the lowest (0.9 ± 0.9 and 0.3 ± 0.6 %, respectively) (Fig. 3a). The difference between sampling occasions, although not large, was due to an increase in cover at Fumba between samplings, and the significant interaction between site and sampling occasion can be explained by the fact that Sume and Fumba differed significantly from each other during the September sampling but not during October, due to the increase at Fumba.

The only other eucheumoid species found in the transects was *K. alvarezii* at Komonda, having an average cover and standard deviation of 0.02 % (±0.04). The most common macroalgal genera at the sites were *Turbinaria* sp., *Sargassum* sp. and *Ulva* sp., with *E. denticulatum* being the dominating species only at Sume. The overall algal cover at the Fumba and Komonda was comparatively high (63.1 ± 15.5 and 65.6 ± 11.2 %, respectively), with Sume having intermediate cover (35.1 ± 6.8 %) and Matemwe

Table 2 ANOVA of cover (log-transformed) and density of *E. denticulatum*

	Cover				Density			
	Df	Mean sq	*F* value	Pr (>*F*)	*Df*	Mean sq	*F* value	Pr (>*F*)
Site	3	18.023	60.814	**1**.56e–13	2	0.9170	27.512	6.16e–07
Sampling	**1**	1.533	5.172	0.0296	1	0.0113	0.339	0.5661
Site/sampling	3	0.997	3.354	0.0302	2	0.1575	4.725	0.0186
Residuals	33	0.296	–	–	24	0.0333	–	–

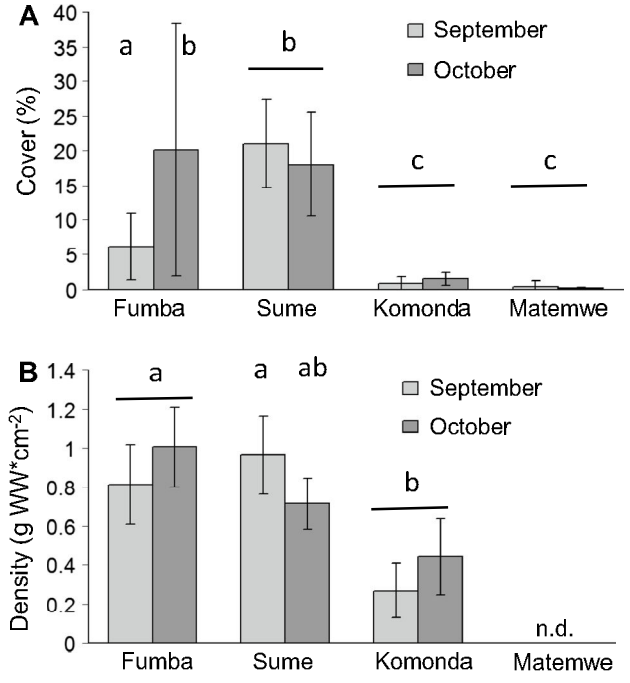


Fig. 3 Overall mean cover per hard substrate surface area (**A**) and density in wet weight (**B**) of *E. denticulatum* in September and October 2012. *Error bars* are standard deviation. *Different letters* indicate statistical significance ($p < 0.01$)

distinguishing itself from the other sites by having extremely low algal cover (1.3 ± 1.6 %).

There was a significant interaction between site and sampling occasion for the density of *E. denticulatum* per surface area where the species occurs (Fig. 3b, Table 2). The post hoc analysis showed a significantly lower density at Komonda than the other two sites during September and lower than Fumba during October. Due to low quantity of *E. denticulatum*, Matemwe was excluded from the biomass sampling, and as the algae were positioned between tightly growing coral branches, any attempts to sample algal biomass would have been overly destructive.

Reproduction

Out of the 189 fronds investigated for reproductive structures, such were only found in two specimens. Both specimens containing tetraspores were collected at Komonda during September 2012, and were of East African origin (haplotype PAC5 and 60, respectively). No sampling of reproductive structures was made at Matemwe in October due to an unforeseen weather event.

Discussion

Free-living introduced South-east Asian haplotypes of *E. denticulatum* have now been located at numerous sites around Zanzibar—in this study alone, seven sites around Unguja Island have been found to harbour attached non-native haplotypes of *E. denticulatum*, and two others are shown by Halling et al. (2013). At two of the sites in the current study, Komonda and Sume, cultivation of foreign haplotypes has never occurred, but even so more than 50 % of sampled *E. denticulatum* in these locations consist of non-indigenous haplotypes. Both of the sites are located off-shore and separated from the mainland of Unguja Island by deeper channels, which shows that introduced haplotypes are capable of spreading over deeper waters and establishing outside farming areas where they may compete with native haplotypes. Moreover, the results show that South-east Asian (SEA) haplotypes are the dominating forms of wild-growing *E. denticulatum* at all of the investigated sites, and further that at both sites with more than 5 % cover of *E. denticulatum*, as much as 75 to 97 % consists of introduced haplotypes.

In Zanzibar, *E. denticulatum* is farmed by tying seaweed fronds to ropes, which are then anchored to the sediment in shallow areas with high tidal influence. Parts of plants easily rip off, especially during strong winds and water movements, and occasionally large amounts of seaweeds are found drifting at sites around Unguja Island (Halling et al. 2013; pers. obs.). Such fragments have the potential to re-attach to suitable substrate as *E. denticulatum* readily attaches by spine and branch tips (Doty 1988, 1987). This might be a potential source for establishment also in areas remote from seaweed farms.

E. denticulatum 13 was the only haplotype found in farms during the current study, as well as in the study by Halling et al. (2013), suggesting that this is the major type of *E. denticulatum* being farmed since at least 2004. Also *E. denticulatum* haplotype 32 is likely to have been introduced to Zanzibar by seaweed farming (Halling et al. 2013) since it has been found in samples collected in the wild in Indonesia and Hawaii (to where it has been introduced), and in farms in the Philippines (Zuccarello et al. 2006), and is genetically well separated from the EA haplotypes. Since haplotype 32 has not been found in any samples from seaweed farms since 2004, its occurrence in the wild implies that it has established stable populations that are not sustained by a continuous inflow of seaweeds from surrounding farms. Similarly this particular haplotype of *E. denticulatum* has become established on patch reefs in Kaneohe Bay, Hawaii (Zuccarello et al. 2006; Conklin et al. 2009). Even though the seaweed overgrowing the reefs in Hawaii

was previously thought to be *Kappaphycus* sp., it appears to be identical to *E. denticulatum* haplotype 32 (Zemke-White and Smith 2006; Conklin et al. 2009).

There is no truly comparable data for *E. denticulatum* cover in the area prior to the introduction of SEA haplotypes, but some eucheumoid studies exist from Tanzania from the 1970s. Mshigeni (1984) performed field observations of eucheumoids during spring low tide and estimated the species abundance using a grid point method in areas where eucheumoids were found. The season of the study is not specified, but the water temperatures reported by Mshigeni (1984) suggest that the survey took place during the cold season, with water temperatures much resembling those found in the current study. As eucheumoids in Tanzania are suggested to be perennial (Mshigeni 1979), with higher abundances during the South East Monsoon (pers. obs.), it appears likely that the studies took place during roughly the same time of the year. According to Mshigeni (1984) the mean cover of *E. denticulatum* in Tanzania during the 1970s was approximately 22 %, and as the seaweed beds in Fumba Bay were described as rich (Mshigeni 1984), a reasonable assumption is that the cover was at least 22 % on suitable substrates. As this was prior to the introduction of foreign haplotypes, the populations were solely native *E. denticulatum*. When comparing this to the current state of *E. denticulatum* in the Fumba area, the cover is within the same size range, but it is comprised of 97 % of introduced haplotypes. This clearly points to a shift from native to introduced *E. denticulatum* in the wild population and constitutes a cryptic invasion by introduced haplotypes.

Apart from *E. denticulatum*, three other eucheumoid species were reported to occur at Fumba during the 1970s (Mshigeni 1979): *E. platycladum*, *Kappaphycus striatum* and *K. cottonii* (the latter two reported as *E. striatum* and *E. okamurai*). However, the identification of these four eucheumoids was carried out based solely on morphology. The eucheumoids are characterised by a large morphological plasticity, and application of molecular methods has to a large extent changed the understanding of the taxonomy of this group (Zuccarello et al. 2006; Conklin et al. 2009). Three eucheumoid species have so far been identified in Tanzania using molecular methods (*E. denticulatum*, *E. platycladum* and *K. alvarezii*) (Zuccarello et al. 2006; Halling et al. 2013). *Kappaphycus striatum* and *K. cottonii* have so far only been reported from South-east Asia (Zuccarello et al. 2006; Lim et al. 2013). Using the descriptions and pictures by Mshigeni (1979; 1984), it appears that the species classified as *E. striatum* is actually *K. alvarezii*, and that *E. okamurai* is a morphologically differing version of one of the other eucheumoid species. However, despite nomenclature difficulties, at least three species of eucheumoids occurred at Fumba during the 1970s (Mshigeni 1979), whereas now the only species found at Fumba is *E. denticulatum*, which also was the case in 2004 (Halling et al. 2013). During the current study, two other eucheumoid species were found, however, only at one site (Komonda) and in very low abundances—*K. alvarezii* had a cover of 0.02 %, while *E. platycladum* was not found in any of the transects, but was sampled during site surveys. Mshigeni (1984) reported a mean cover of 19.2 % of *E. striatum* (possibly *K. alvarezii*) and 8.2 % of *E. platycladum* in Tanzania during the 1970s, which indicates that also other eucheumoids may have decreased dramatically or even disappeared since.

We cannot conclude whether the introduced haplotypes of *E. denticulatum* have displaced the native populations or whether the present dominance of SEA haplotypes is rather a consequence of a decline in native populations driven by other factors. Introduced species may not necessarily be the driver causing declines in native species abundance, but may simply be passengers utilising space freed up by other factors such as environmental change (e.g. Didham et al. 2005; MacDougall and Turkington 2005). It is known that the extensive algal collection (including a variety of all native eucheumoids) during the 1970s reduced the abundance of the native populations of *E. denticulatum* (Pettersson-Löfquist 1995) and may have opened up space for the establishment of introduced haplotypes. Disturbance of native seaweed communities has been documented to increase the risk for establishment of non-native seaweeds (e.g. Levin et al. 2002, Valentine and Johnson 2003, Britton-Simmons 2006), but is less likely to explain the current dominance by the SEA haplotypes. A growth trial in Uroa, Zanzibar, showed that the growth rate of SEA *E. denticulatum* was more than twice that of native specimens (Mtolera et al. 1995). Additionally, Lirasan and Twide (1993) found that EA seedlings had lower growth rates than the SEA ones, and that they showed relatively good growth only during the colder period of the year. This could mean that the introduced haplotypes have a competitive advantage over the native, but controlled experiments of the competitive interaction between native and introduced haplotypes would be needed to establish whether the decline in the native eucheumoid populations can be explained by competition from SEA haplotypes, changing environmental conditions (e.g. increasing sea surface temperature) or a combination of the two.

The finding that wild *Eucheuma* populations now to a large extent are composed of non-native haplotypes calls for further studies of the potential effects, both on the native haplotypes of *E. denticulatum* and other components of the ecosystem. To date we lack information about population dynamics and genetic diversity of East African *Eucheuma* populations and how these are affected by the spread of SEA haplotypes. The fact that introduced haplotypes occur

abundantly alongside the native ones could result in hybridisation between native and introduced haplotypes. We found very few reproductive structures and only on native haplotypes, indicating that the risk of hybridisation is small at least during the period of the study, but this should be evaluated by further genetic analyses of populations containing both native and introduced haplotypes. However, the decrease seen in the population of native *E. denticulatum*, coupled with what appears to be a very low rate of sexual reproduction, indicates that the effective population size of EA *E. denticulatum* may be very low. The potentially reduced fitness of a small effective population, arising from such factors as inbreeding, could lead to limitations in the populations ability to adapt to changing environmental conditions (Willi et al. 2006), which may also negatively affect the possibility of using wild populations as future seed stock.

There is little known on the ecological function of *E. denticulatum*, or the potential differences between native and introduced haplotypes, which means that we cannot predict the ecological effects of the spread of non-native haplotypes. In the case of the common reed (*Phragmites australis*) in North America, an introduced haplotype has not only replaced the native strains in many locations (Saltonstall 2003), but has also invaded other habitats where it is outcompeting other species and causing changes to community structure (Able and Hagan 2000; Benoit and Askins 1999). Introduced eucheumoids have been shown to become invasive and overgrow and smother corals in other areas (Chandrasekaran et al. 2008; Conklin and Smith 2005; Kamalakannan et al. 2010), and further studies of the ecology of introduced genotypes could show if there is a risk for a similar development in East Africa.

Conclusions

The results from this study show that the populations of East African *E. denticulatum* around Unguja Island have declined over the last decades and that at many sites the introduced South-east Asian haplotypes are now dominating. This cryptic invasion by their foreign congeners and the low occurrence of sexual reproduction, may threaten the genetic diversity and adaptive potential of East African *E. denticulatum*. This calls for more research on potential effects on native populations and ecosystems by the spread of the introduced haplotypes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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