



Differences in macrofaunal and seagrass assemblages in seagrass beds with and without seaweed farms

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Abstract

Since it was introduced to Zanzibar (Tanzania), seaweed farming has significantly contributed to local, socio-economic development. However, several investigations have shown impacts on the coastal environment near where the farms are located. As many seaweed farms are located on seagrass beds, there is a risk that seaweed farming could affect seagrass beds, and thereby disturb important ecosystem functions and the flow of ecological goods and services. This study compares characteristics of macrophytes (focusing on seagrasses), benthic macrofauna and sediment in seagrass beds, with and without seaweed farms, and a sand bank without vegetation in Chwaka Bay, Zanzibar. The results showed that seagrass beds underneath seaweed farms generally had less seagrass and macroalgae, finer sediment, lower sediment organic matter content and a reduced abundance and biomass of macrofauna, than seagrass beds without seaweed farms. Further, the macrofaunal community structure in seaweed farms showed more similarities to that on the sand bank than in the unfarmed seagrass beds. Most of the dissimilarity was attributable to *Lucinidae* (suspension-feeding bivalves), which were almost absent in the seaweed farms, resulting in the large difference in biomass between the seaweed farms and the unfarmed seagrass beds. When interpreted together with information from farmers, the observed pattern is believed to be caused by the seaweed farming activities. This indicates that more research is needed to establish the effects of seaweed farming on seagrass beds, and that more attention should be given to the location of farms and the choice of farming methods.

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1. Introduction

Open-water seaweed farming was introduced to Unguja Island (Zanzibar, Tanzania) around 1990 and mainly two species of red algae, *Eucheuma denticulatum* (formerly *E. spinosum*) and *Kappaphycus alvarezii* (formerly *E. cottonii*), are grown and harvested for extraction of hydrocolloid carrageenans (Petterson-

Löfquist, 1995). Unlike other, more destructive and resource-inefficient aquaculture methods (e.g. semi-intensive shrimp and salmon farming), seaweed farming does not require any inputs of fertilisers or pesticides, and is considered not to alter the physical environment in any major way (Johnstone and Ólafsson, 1995; Bryceson, 2002). Further, living standards have increased in many villages following the introduction of seaweed farming (Msuya, 1993; Petterson-Löfquist, 1995; Jiddawi and Ngazy, 2000). This has led to a common perception that seaweed farming is a highly sustainable aquaculture practice (e.g. Saleh, 1998;

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McKnight Foundation, 2002). However, several studies have shown that seaweed farming affects components of ecosystems in which such farms are located, e.g. meiobenthos (Ólafsson et al., 1995), benthic microbial production (Johnstone and Ólafsson, 1995), fish assemblages (Bergman et al., 2001), epifauna and macrophytes (Msuya, unpublished data; Semesi, 2002), and the water column around the algae (Collén et al., 1995). These findings indicate that more research on the subject is needed (e.g. Ólafsson et al., 1995; Bryceson, 2002; Zemke-White, in press).

In Zanzibar, the seaweed farms are located in shallow lagoons, and the dominant farming-method is the “fixed off-bottom” or “tie-tie” method, where fronds of the algae are tied to ropes stretched between wooden sticks fixed to the bottom, and harvested every 2–4 weeks during low water spring tides (Pettersson-Löfquist, 1995). Seaweed farms are often sited on bottoms with seagrass, and farmers often regard the presence of seagrass as being a good indicator of a suitable environment (de la Torre Castro and Rönnbäck, 2004).

Seagrass bed ecosystems have for a long time been more or less neglected in coastal zone management but, due to the growing consensus about their importance (e.g. Duarte, 2000; Gullström et al., 2002), this is currently changing. Seagrass beds are important contributors to primary production in global oceans (Duarte and Chiscano, 1999), their canopy acts as a hydrodynamic barrier in near shore areas (Koch, 1996) and their roots and rhizomes stabilise bottom sediments (Fonseca, 1989).

Perhaps most important, seagrass beds provide habitats for other organisms. A large number of studies have shown that seagrass beds host more diverse and abundant animal communities than unvegetated areas, both in the temperate (e.g. Pihl, 1986; Boström and Bonsdorff, 1997) and tropical zones (e.g. Coles et al., 1993; Arrivillaga and Balz, 1999). The major factors attributed to this pattern are refuge from predation (Hindell et al., 2000; Salita et al., 2003) and the presence of food (Connolly, 1994; Bologna and Heck, 1999). Many of the animals residing in seagrass beds (e.g. fish and macroinvertebrates) are directly utilised by humans, and are thus of economic importance (de Boer and Longamane, 1996; Lynne et al., 2000; Jackson et al., 2001).

Because of their importance to society, seagrass/algal beds have been estimated to generate gross financial benefits amounting to US\$19 000 ha⁻¹ year⁻¹, this being the third highest value of the 16 biomes investigated (Costanza et al., 1997). In addition, there is growing concern about the worldwide decline of seagrass beds (e.g. Fortes, 1988; Short and Wyllie-Echeverria, 1996; Hall et al., 1999; Duarte, 2002). Since seaweed farming has been shown to impact components of the ecosystems in which such farms are placed there is a risk that

seaweed farming could also affect seagrass beds and the associated communities, thereby disturbing important ecosystem functions.

The aim of this study was to investigate seagrass beds with seaweed farms in relation to unfarmed seagrass beds in the seagrass-dominated Chwaka Bay. This was done by comparing seagrass beds with and without seaweed farms and one unvegetated sand bank, using characteristics of three important components of seagrass bed ecosystems – the macrophytes (seagrass and macroalgae), sediment and benthic macrofauna. Because habitat provision is one of the most important functions attributed to seagrass beds, the relationship between macrofauna and environmental variables was also investigated.

The differences between seaweed farms and unfarmed seagrass beds are discussed in terms of the effects of seaweed farming, the implications this might have on ecosystem function, and suggestions regarding future research and management of seaweed farming.

2. Material and methods

2.1. Study area

The study was conducted in Chwaka Bay, an intertidal lagoon located on the east coast of Unguja Island, Zanzibar (6°13–25' S and 39°37–58' E; Fig. 1). Its mean water depth is 3.2 m, and the area of the bay covered with water fluctuates between 50 km² at high-water spring tide and 20 km² at low-water spring tide (Cederlöf et al., 1995). The centre part of the bay is dominated by tidal flats and channels, covered with mixed and monotypic stands of seagrasses and seaweeds. The dominant seagrass species are *Thalassia hemprichii*, *Cymodocea serrulata*, *Cymodocea rotundata*,

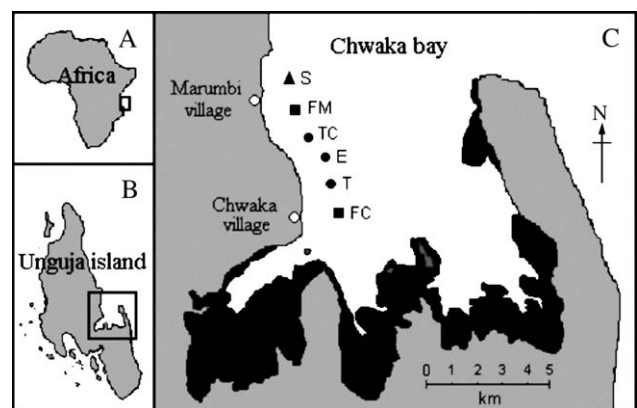


Fig. 1. Map of (A) Africa, (B) Unguja Island (Zanzibar) and (C) Chwaka Bay with the six sampling sites. ■, seaweed farm; ●, seagrass bed; ▲, sand bank. Black areas represent mangroves.

Enhalus acoroides and *Thalassodendron ciliatum* (Mohammed and Jiddawi, 1999).

Seaweed farming was introduced into the bay around 1990 (Mohammed and Jiddawi, 1999), and currently there are five seaweed farming sites, covering a total area of approximately 2.5 km², or approximately 10% to 5% of the total bay area at low and high tides, respectively. All the farms are located on seagrass beds, close to the main villages around the bay.

A total of six sites were included in this study: three seagrass beds, two seaweed farms and one sand bank, designated as follows: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S, sand bank. The sand bank was included as a reference site without vegetation for the macrofaunal and sediment comparisons.

All sampling was conducted during daytime at low-water spring tide (LWST) during November and December 2002. Water salinity was on average 25.5 (ranging from 21 to 28), surface water temperature on average 36.3 °C (ranging from 32 to 39 °C) and water depth on average 0.12 m (ranging from 0 to 0.3 m).

2.2. Field sampling and laboratory analyses

At each of the six sites, 20 seagrass sampling points were randomly chosen within a 150 × 200-m area. This meant that sampling points within farm sites could be located underneath or between farm plots.

In terms of seagrass species composition, the dominant species in decreasing order were noted for each of the five vegetated sites as follows. At each sampling point seagrass shoot density was established by counting and collecting all shoots within two randomly placed 0.0625-m² steel frames. Seagrass canopy height was measured following the method of Short and Coles (2001) at eight places surrounding each of the two steel frames. The percent cover of seagrass, macroalgae and sand was estimated in four randomly placed 0.25-m² steel frames (to the nearest 10%). The cover of the green calcareous algae, *Halimeda* spp., was noted separately due to the dominance of this taxon and its importance in maintaining the sediment structure (Björk et al., 1995; Muzuka et al., 2001).

In the laboratory, all the collected seagrass shoots were cleaned in fresh water and the above-ground biomass (DW) was determined after drying at 80 °C for 72 h. All measured values from each sampling point were averaged to derive single replicate values (which were used in the statistical analyses). The sand bank was not included in the macrophyte statistical analysis, since no seagrass occurred naturally at this site.

Sediment ($n=7$) and macrofaunal samples ($n=7$) were randomly taken within a 30 × 30-m area (located within the 150 × 200-m area). Samples for benthic

macrofauna were sampled using a PVC-tube (inside diameter: 12 cm; depth: 10 cm). In the lab, the samples were roughly cleaned (removing all plant material), rinsed through a 0.5 mm sieve and fixed in 10% borax-buffered formalin. All animals were then coloured using RoseBengal stain and sorted using a stereo microscope (16× magnification). Crustaceans were identified to order/suborder, polychaetes and molluscs to family, and other miscellaneous taxa to phylum. All taxa were classified into one of the following functional groups, based on the literature (Day, 1967; Fauchald and Jumars, 1979; Holdich and Jones, 1983; Richmond, 1997): carnivores (C), herbivores (H), omnivores (O), suspension feeders (S), surface deposit feeders (SD) and burrowing deposit feeders (BD). Biomass (g DW) of each taxonomic group was determined after drying at 60 °C for 96 h. Molluscs were dried and weighed including shells.

The sediment samples for grain size determination were taken adjacent to the macrofauna samples, using a standard core (inside diameter: 6 cm; depth: 10 cm). In the laboratory, the samples were cleaned in fresh water (to remove organic material), dried at 80 °C for 72 h and sieved to obtain the following fractions: >2, >1, >0.5, >0.25, >0.125, >0.063 and <0.063 mm. Each fraction was weighed separately and calculated as percentage of total sample weight (Morgans, 1956). Standard sediment parameters (mean grain size, sorting, skewness and kurtosis) were calculated using the mathematical methods of moments (as described in Boggs, 2001). Mean grain size was expressed in mm, and sorting, skewness and kurtosis by ϕ according to the Udden–Wentworth scale ($\phi = -\log_2 d$, where d = grain diameter in mm). The proportion silt/clay (<0.063 mm), sand (0.063–2 mm) and coarse sand (>2 mm) was also calculated for each site.

Samples for sediment organic matter (SOM) content analysis were collected next to the grain size sampling site using a modified plastic syringe (inside diameter: 3 cm; depth: 5 cm). The samples were stored air-sealed and in the dark at –10 °C. After determining their dry weight, the samples were incinerated (500 °C for 5 h) and weighed again (AFDW). The organic matter content was expressed as proportion (%) of the initial dry weight.

2.3. Statistical analysis

Differences in seagrass, macrofauna and sediment between sites were investigated by one-way analysis of variance (ANOVA). Paired a posteriori comparisons were made using Tukey's HSD test. Prior to the analysis, Cochran's C-test was used to test for the assumption of homogeneity between variances. When assumptions were not met, data were transformed (arcsin and log₁₀) or the non-parametric Kruskal–Wallis

Median test was used. A posteriori comparisons were then made using pair-wise Mann–Whitney *U*-tests (with the significance level adjusted according to the sequential Bonferroni-method, with $\alpha=0.05/10=0.005$; Holm, 1979). Otherwise, the significance level was set at $\alpha=0.05$. All univariate analyses were performed using STATISTICA v. 5.5 '99 ed. (Microsoft).

Differences and similarities in macrofaunal community structure (biomass of taxonomic and functional groups) within and between sites were described using non-metrical multidimensional scaling (MDS) ordination (Clarke, 1993). To examine differences between sites in the similarity matrix, the one-way analysis of similarities (ANOSIM) randomisation test was used (Clarke, 1988). To analyse which taxa or functional groups contributed to the dissimilarity between sites (expressed as δ_i), the similarity percentage (SIMPER) program was used (Warwick and Clarke, 1990). To investigate which variables were important for habitat function in the seagrass beds, the relationship between macrofaunal abundance and ten environmental variables (seagrass shoot density, biomass, cover and canopy height; macroalgal cover and of *Halimeda* spp. alone; total cover of vegetation; cover of sand, mean sediment grain size and SOM) was analysed using the BIO-ENV routine. This program calculates which set of environmental variables best explain variation in the macrofauna data matrix using the Spearman coefficient ρ . Since the seagrass, sediment and macrophyte variables were not sampled at exactly the same points at the sites, the calculated means (per site) were used as input data for these variables. This causes a loss of resolution, but was regarded as adequate for the analysis. All the analyses were run on fourth-root transformed data and the Bray–Curtis coefficient of similarity (Clarke, 1993), using the software package PRIMER (Plymouth Routines In Marine Ecological Research) for Windows v. 5.2.9.

3. Results

3.1. Seagrass and macroalgae

In terms of seagrass species composition, site T was dominated by *Thalassia hemprichii*, with patches of *Cymodocea serrulata* (Table 1). At site TC, the same two species (*T. hemprichii* and *C. serrulata*) were encountered, with roughly equal coverage. At site E, large *Enhalus acoroides* were dominant, but small and concentrated patches of *T. hemprichii* were also encountered. At the seaweed farm FC, the species composition was more mixed, with *T. hemprichii* and *C. serrulata* dominant and small patches of *E. acoroides* (found between farm plots and at farm edges) as well as *Halophila* sp. At the last site, seaweed farm FM,

Table 1

Description of the six sampling sites in Chwaka Bay, Zanzibar

Site name	Site type	Dominating seagrass species
T	Seagrass bed	<i>Thalassia hemprichii</i> , <i>Cymodocea serrulata</i>
TC	Seagrass bed	<i>Thalassia hemprichii</i> , <i>Cymodocea serrulata</i>
E	Seagrass bed	<i>Enhalus acoroides</i> , <i>Thalassia hemprichii</i>
FC	Seaweed farm	<i>Thalassia hemprichii</i> , <i>Cymodocea serrulata</i> , <i>Enhalus acoroides</i> , <i>Halodule uninervis</i>
FM	Seaweed farm	<i>Thalassia hemprichii</i> , <i>Enhalus acoroides</i>
S	Sand bank	-

T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC; seaweed farm Chwaka; FM, seaweed farm Marumbi; S, sand bank.

T. hemprichii was dominant but small patches of *E. acoroides* were encountered between the farm plots.

The mean seagrass shoot density varied greatly between and within the five sites (sand bank excluded), ranging from 123 shoots m^{-2} (site FM) to 1210 shoots m^{-2} (site T; Fig. 2A). There were clear differences between the five sites (Kruskal–Wallis Median test; $P<0.0001$), as the seaweed farms (site FC and FM) had lower shoot densities than the seagrass beds ($P<0.005$ for all comparisons), except for site FC that did not differ from site E ($P=0.055$). When comparing the seagrass beds, shoot density was higher at site T than both other seagrass beds ($P<0.005$ for both comparisons), followed by TC, which was higher than E ($P<0.005$). No difference was found between the two seaweed farms ($P=0.016$).

In terms of seagrass biomass, there were also differences between the five sites (Kruskal–Wallis Median test; $P=0.0001$) (Fig. 2B). The biomass was lower in seaweed farm FM than in all three seagrass beds ($P<0.005$, respectively), and lower than in seaweed farm FC ($P<0.005$). However, there were no differences between seaweed farm FC and the seagrass beds ($P=0.59–0.89$), nor between the three seagrass beds ($P=0.21–0.78$).

Cover of seagrass differed between the sites (ANOVA: $P<0.001$; $F=117.14$), and was lower in both seaweed farms than in all three seagrass beds ($P<0.05$ for all comparisons; Fig. 2C). Further, seagrass bed T had higher cover than both TC and E ($P<0.05$, respectively). Again, there was no difference between the two seaweed farms ($P=0.28$).

Also with canopy height there were clear differences between the sites (Kruskal–Wallis Median test; $P<0.0001$), and canopy height was lower in both seaweed farms than in the three seagrass beds ($P<0.005$ for all comparisons; Fig. 2D). Further, the canopy was higher in seagrass bed E, being dominated by the tall *Enhalus acoroides*, than in both other beds

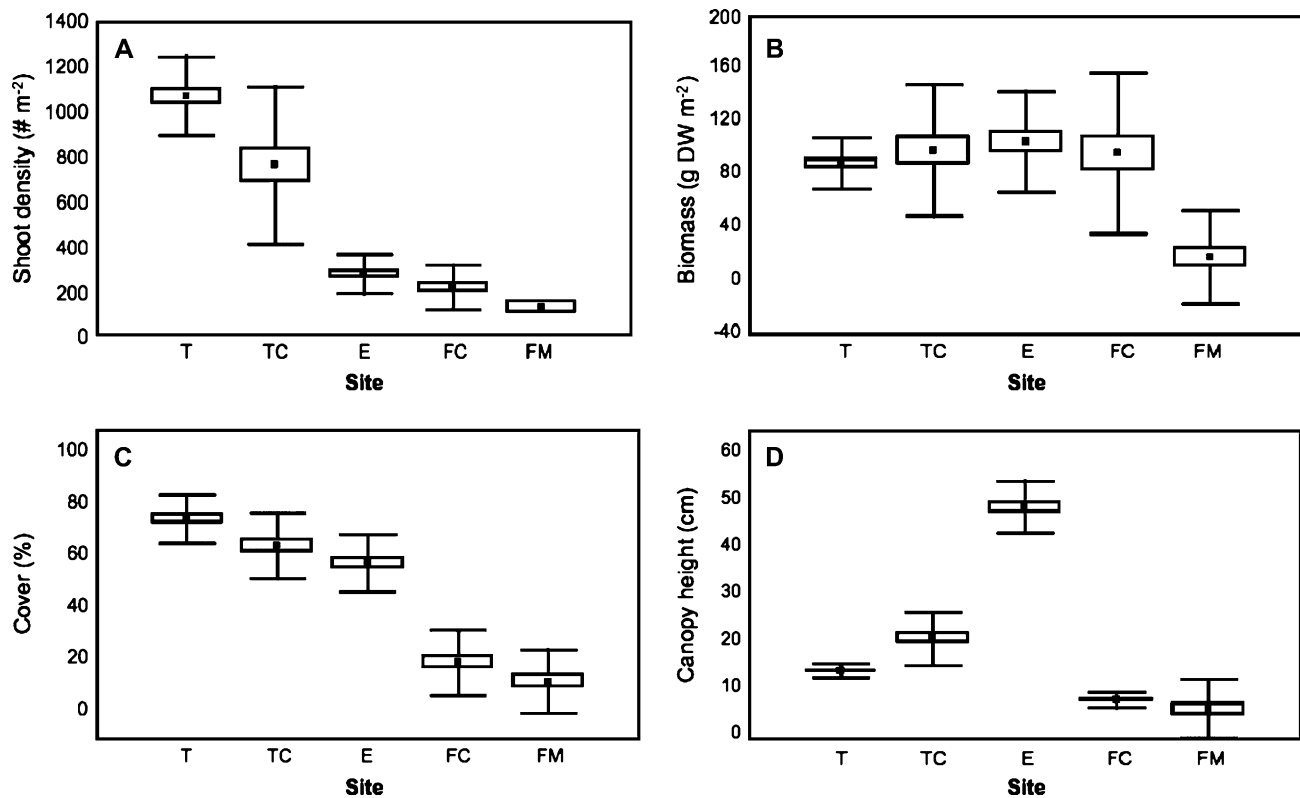


Fig. 2. Seagrass characteristics of the five sites in Chwaka Bay, Zanzibar ($n=20$; central squares, means; boxes, S.E.; whiskers, S.D.) showing seagrass (A) shoot density, (B) biomass, (C) cover and (D) canopy height. The sites were: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi.

(site T and TC; $P<0.005$, respectively), and higher at site TC than site E ($P<0.005$). No difference was found between the two seaweed farms ($P=0.06$).

In terms of other macrophytes, the cover of macroalgae differed between the sites (ANOVA: $P=0.03$; $F=15.98$), with lower cover in the seaweed farms (site FC and FM) than in the three seagrass beds (site T, TC and E; $P<0.05$, respectively; Table 1). No difference was found between the two seaweed farms ($P=0.06$). Among the macroalgae encountered, *Halimeda* spp. (*H. discoidea*, *H. macroloba* and *H. opuntia*) were dominant and were therefore analysed separately (as *Halimeda* spp. in Table 1). The results showed that the cover of *Halimeda* spp. differed between the sites (ANOVA: $P=0.01$; $F=17.04$), and was lower in the seaweed farms (site FC and FM) than in the three seagrass beds (site T, TC and E; $P<0.05$, respectively). No difference was encountered in cover between the two seaweed farms ($P=0.83$).

3.2. Macrofauna

In total, 9510 animals belonging to 53 taxa were collected at the study sites. Their mean contribution to abundance and biomass and assignment to functional groups is given in Table 2. The dominant groups

(in terms of abundance) were crustaceans (13 taxa), polychaetes (21 families) and molluscs (11 families, one class).

Their mean abundance ranged from 1111 m^{-2} (site S) to 41 800 individuals m^{-2} (site T; Fig. 3A), these values being within the range of those found in other studies in tropical soft-sediment bottoms (Ndaro and Ólafsson, 1999; Dittman, 2002).

Macrofaunal abundance differed markedly between the sites (ANOVA; $P<0.001$; $F=25.6$). It was lower in seaweed farm FC than in seagrass bed T ($P<0.05$), but not lower than at site TC ($P=0.12$) or site E ($P=0.89$). The other seaweed farm (site FM), however, had a lower macrofaunal abundance than all three seagrass beds ($P<0.05$ for all comparisons) and site FC ($P<0.05$). There were also differences between the seagrass beds, with a higher abundance at site T than site E ($P<0.05$). Finally, on the sand bank, abundance was lower than at all the other sites ($P<0.05$ for all comparisons), except site FM ($P=0.81$).

When comparing the biomass between sites, large differences were detected (ANOVA: $P<0.001$, $F=31.3$). The biomass was lower in both seaweed farms than in the seagrass beds ($P<0.05$ for all comparisons; Fig. 3B), but no differences were detected between the two seaweed farms ($P=0.98$). Finally, the biomass on the

Table 2

Mean contribution of 53 major macrofauna taxa to abundance (N/m²) and biomass (g. DW/m²) in six investigated sites in Chwaka Bay, Zanzibar ($n=7$, except for site S where $n=6$)

Taxon	Type	T		TC		E		FC		FM		S	
		N/m ²	g/m ²	N/m ²	g/m ²	N/m ²	g/m ²	N/m ²	g/m ²	N/m ²	g/m ²	N/m ²	g/m ²
Crustacea													
Copepoda	SD/S	4041	<0.1	206	<0.1	245	<0.1	193	<0.1	13	<0.1	—	—
Ostracoda	SD	2445	<0.1	1030	<0.1	1248	0.2	399	<0.1	26	<0.1	—	—
Gammaridea	O	13115	0.9	7104	0.8	5444	0.4	7220	0.5	1236	<0.1	135	<0.1
Caprellidea	C	—	—	13	<0.1	—	—	77	<0.1	—	—	—	—
Tanaidacea	BD	4234	0.18	5032	0.2	4299	0.2	3642	0.5	13	<0.1	—	—
Asellota	H	6332	<0.1	2265	<0.1	1081	<0.1	219	<0.1	914	<0.1	30	<0.1
Flabellifera	C	2008	0.5	412	0.2	425	0.2	64	0.1	3423	0.1	270	<0.1
Anthuridea	C	180	<0.1	129	<0.1	206	0.1	219	<0.1	39	0.2	—	—
Cumacea	S/SD	77	<0.1	1519	0.1	618	<0.1	1776	0.1	77	<0.1	345	<0.1
Mysidacea	O	13	<0.1	26	<0.1	13	—	13	<0.1	26	<0.1	—	—
Brachyura	C	39	2.18	64	4.8	64	3.5	13	0.1	—	—	—	—
Stomatopoda	C	—	—	—	—	—	2.4	—	—	—	—	—	—
Leptostraca	S	—	—	—	—	—	—	283	<0.1	—	—	—	—
Polychaeta													
Aphroditidae	C	—	—	13	<0.1	—	—	—	—	—	—	—	—
Polynoidae	C	—	—	—	0.0	26	<0.1	13	<0.1	—	—	—	—
Amphinomidae	C	450	<0.1	309	<0.1	232	<0.1	51	<0.1	—	—	—	—
Phyllodocidae	C	51	—	219	<0.1	103	<0.1	51	<0.1	—	—	15	<0.1
Hesionidae	C/H	154	<0.1	322	0.1	167	0.2	39	<0.1	51	<0.1	—	—
Syllidae	C	3166	0.26	3591	0.2	2072	0.2	746	0.1	90	<0.1	30	<0.1
Nereididae	C	13	<0.1	64	0.3	51	<0.1	438	<0.1	—	—	—	—
Glyceridae	C	116	0.9	64	0.4	39	0.3	90	0.1	51	<0.1	75	0.2
Eunicidae	C	579	0.1	682	4.3	257	0.8	103	0.1	26	<0.1	—	—
Lumbrineridae	C	13	<0.1	26	<0.1	103	0.4	13	—	26	<0.1	15	<0.1
Oenonidae	C	64	<0.1	13	<0.1	13	<0.1	39	<0.1	—	—	—	—
Spionidae	SD	39	<0.1	309	<0.1	142	<0.1	206	<0.1	26	<0.1	—	—
Cirratulidae	SD	—	—	39	<0.1	64	<0.1	116	<0.1	—	—	—	—
Paraonidae	BD	—	—	528	<0.1	206	0.1	515	<0.1	—	—	—	—
Opheliidae	BD	51	<0.1	51	<0.1	116	<0.1	13	<0.1	—	—	—	—
Capitellidae	BD	438	<0.1	1030	0.1	644	0.1	386	<0.1	90	<0.1	30	<0.1
Maldanidae	BD	528	0.2	438	<0.1	502	0.1	129	0.2	26	0.2	—	—
Oweniidae	S	13	<0.1	51	<0.1	39	1.3	—	—	—	—	—	<0.1
Ampharetidae	SD	—	—	13	0.1	64	<0.1	26	<0.1	13	2.9	—	—
Terebellidae	SD	360	0.1	232	0.5	270	0.1	154	0.1	—	—	—	—
Dorvellidae	C	13	<0.1	142	<0.1	206	0.1	26	—	—	—	—	—
Polych. Unid.	—	—	0.8	—	<0.1	—	0.2	—	0.1	—	<0.1	—	—
Bivalvia													
Lucunidae	S	399	251	1634	998	1158	1055	77	11.2	—	—	—	—
Mytilidae	S	39	1.2	—	—	26	0.1	13	0.2	13	9.7	—	—
Pinnidae	S	—	—	26	29	—	—	—	—	—	—	—	—
Mactridae	S	90	17	77	0.3	116	0.1	77	0.4	64	<0.1	—	—
Cardiidae	S	—	—	51	0.2	—	—	—	—	—	—	—	—
Gastropoda													
Ovulidae	H	26	0.2	13	0.2	13	0.3	—	—	—	—	—	—
Olividae	H	—	—	39	<0.1	77	<0.1	51	0.1	—	—	—	—
Trochidae	H	26	<0.1	26	<0.1	—	—	—	—	—	—	—	—
Terebellidae	H	—	—	13	0.1	26	0.7	—	—	—	—	—	—
Potamididae	H	—	—	—	—	13	0.1	—	—	—	—	—	—
Other taxa													
Polyplacophora	H	—	<0.1	—	—	13	0.1	—	—	—	—	—	—
Ophiuroidea	C	412	<0.1	—	—	283	0.1	39	<0.1	—	—	45	<0.1
Oligochaeta	BD	373	<0.1	644	<0.1	734	<0.1	425	<0.1	51	<0.1	45	<0.1
Chironomidae	SD	219	<0.1	—	—	13	<0.1	13	<0.1	—	—	—	—
Pycnogonida	C	26	<0.1	—	—	—	—	39	—	—	—	—	—
Sipunculida	BD	759	0.4	553	<0.1	386	<0.1	116	<0.1	39	0.2	—	—
Nematoda	BD	978	<0.1	1145	<0.1	1866	<0.1	1081	<0.1	39	<0.1	75	<0.1
Branchiostoma	S	—	—	13	<0.1	—	—	129	<0.1	13	<0.1	—	—
Total		41879	275.9	30167	1041.3	23681	1067.0	19331	14.2	6383	13.6	1111	0.2

Type is functional group, with the following abbreviations: C, carnivores; H, herbivores; O, omnivores; S, suspension feeders; SD, surface deposit feeders; BD, burrowing deposit feeders. Sites are: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S, sand bank.

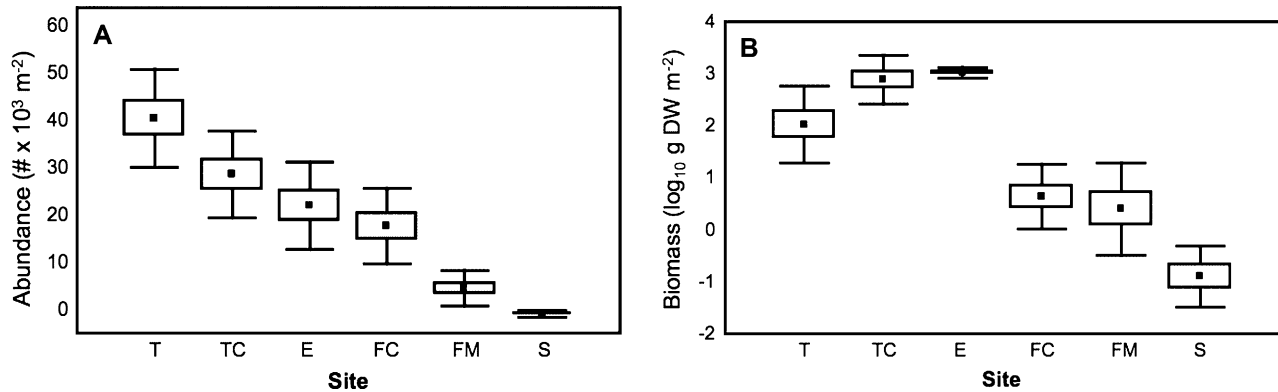


Fig. 3. Macrofaunal (A) abundance and (B) biomass at the six sites in Chwaka Bay, Zanzibar ($n=7$, except site S where $n=6$; central squares, means; boxes, S.E.; whiskers, S.D.). The sites were: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S, sand bank.

sand bank (site S) was lower than at all the other sites ($P < 0.05$ for all comparisons).

The analysis of macrofaunal community structure based on taxonomic groups (53 taxa) showed clear differences between the sites (ANOSIM, $r=0.538$, $P=0.001$). The resulting MDS-plot (stress=0.16) is presented in Fig. 4A. Both seaweed farms (FC and FM) were separated from the three seagrass beds (site T, TC and E; $r=0.549-0.877$, $P=0.001-0.002$). Further, the seaweed farms were themselves separated ($r=0.582$, $P=0.001$). The sand bank (site S) was separated from all three seagrass beds ($r=0.861-0.877$, $P=0.001-0.002$) and from seaweed farm FC ($r=0.847$, $P=0.004$), but not from seaweed farm FM ($r=0.443$, $P=0.003$). The SIMPER analysis showed that the differences between the seagrass beds (T, TC and E) and the seaweed farms and the sand bank (FC, FM and S) were mostly attributable to a higher biomass of *Lucinidae* (Bivalvia) ($\delta_i=16-32\%$) in the seagrass beds. The difference between the seaweed farms was caused by a higher biomass of *Tanaiidacea* (Crustacea) at site FC ($\delta_i=6,4\%$),

which also separated this site from the sand bank ($\delta_i=7,3\%$).

The analysis using functional groups (six trophic groups) interestingly revealed a similar pattern (ANOSIM, $r=0.533$, $P=0.001$). The resulting MDS plot (stress=0.07) is presented in Fig. 4B. Both seaweed farms (FC and FM) were largely separated from all three seagrass beds (site T, TC and E; $r=0.586-0.966$, $P=0.001-0.004$), the exception being site T which did not separate from FC ($r=0.485$, $P=0.004$). In terms of functional groups, the seaweed farms were similar ($r=0.219$, $P=0.012$), contrary to the analysis on the taxonomical groups. The sand bank (site S) was separated from all three seagrass beds ($r=0.906-0.991$, $P=0.001$) and from seaweed farm FC ($r=0.646$, $P=0.002$), but not from seaweed farm FM ($r=0.443$, $P=0.003$). The SIMPER analysis showed that the differences between the seagrass beds (T, TC and E) and the seaweed farms and the sand bank (FC, FM and S) were mostly attributable to suspension feeders ($\delta_i=48-71\%$) with a higher biomass than the seagrass beds. The same

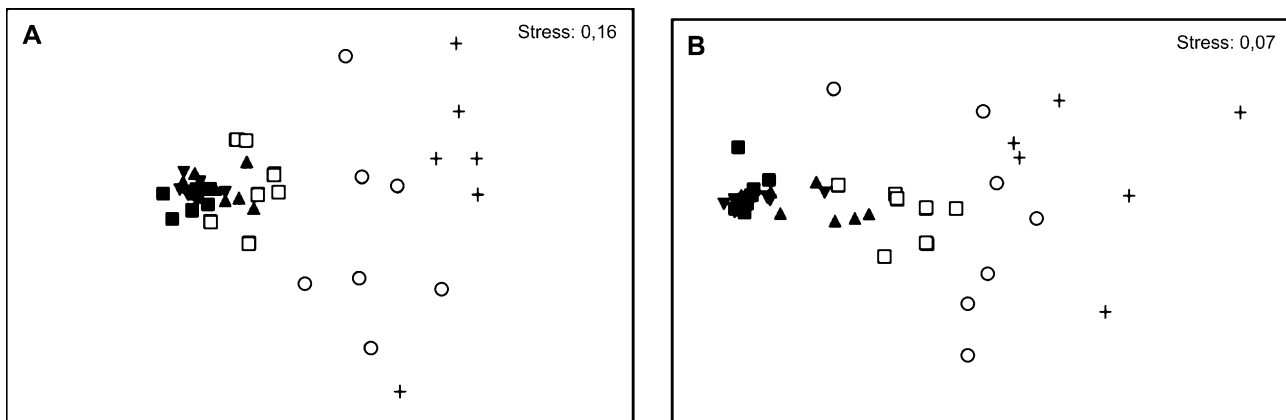


Fig. 4. MDS plots of macrofaunal community structure based on biomass of (A) taxonomic groups and (B) functional groups at six sites in Chwaka bay, Zanzibar ($n=7$, except for site S where $n=6$). Site markers are: ▲, T (*Thalassia hemprichii*-bed); ▼, TC (*Thalassia hemprichii*/*Cymodocea serrulata*-bed); ■, E (*Enhalus acoroides*-bed); □, FC (seaweed farm Chwaka); ○, FM (seaweed farm Marumbi); +, S (sand bank).

Table 3

Sediment variables from the six investigated sites in Chwaka Bay, Zanzibar ($n=7$; mean \pm S.D.)

Site	T	TC	E	FC	FM	S
Coarse sand (%)	23.74 \pm 4.56	13.41 \pm 6.34	20.10 \pm 5.50	6.19 \pm 2.05	2.91 \pm 4.70	0.36 \pm 0.19
Sand (%)	72.07 \pm 1.28	82.23 \pm 7.60	75.50 \pm 4.52	89.76 \pm 2.71	96.77 \pm 4.58	99.50 \pm 0.53
Silt/clay (%)	4.19 \pm 1.28	4.35 \pm 2.08	4.39 \pm 1.93	4.05 \pm 1.23	0.31 \pm 4.58	0.14 \pm 0.36
Mean grain size (μm)	0.73 \pm 0.12	0.42 \pm 0.08	0.56 \pm 0.11	0.35 \pm 0.03	0.29 \pm 0.10	0.26 \pm 0.01
Sorting (ϕ)	1.70 \pm 0.08	1.62 \pm 0.14	1.77 \pm 0.08	1.43 \pm 0.10	0.91 \pm 0.19	0.75 \pm 0.05
Skewness (ϕ)	0.65 \pm 0.19	-0.16 \pm 0.22	0.24 \pm 0.14	-0.20 \pm 0.16	-0.86 \pm 0.28	-1.08 \pm 0.16
Kurtosis (ϕ)	2.53 \pm 0.35	2.27 \pm 0.18	1.99 \pm 0.10	2.72 \pm 0.18	5.05 \pm 1.40	4.65 \pm 0.53
Organic matter (%)	5.12 \pm 0.58	4.06 \pm 0.35	4.42 \pm 0.39	3.42 \pm 0.44	3.10 \pm 0.14	2.95 \pm 0.05

Sites: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S, Sand bank.

functional group contributed to most of the dissimilarity between seaweed farm FC and the sand bank ($\delta_i=26\%$).

3.3. Sediment

All sites were dominated by sand (0.063–2 mm), with varying proportions of coarse sand and silt/clay (Table 3). The mean grain size differed between the sites (ANOVA: $P<0.001$; $F=31.6$). The mean grain size was larger at site T than all the other sites ($P<0.05$ for all comparisons; Fig. 5A). The grain size at site E was also larger than in both seaweed farms ($P<0.05$ for both FC and FM), but not larger than in the third seagrass bed (site TC; $P=0.06$). Further, there was no difference between seagrass bed TC and the seaweed farms ($P=0.063$ for FC, $P=0.054$ for FM), or between the seaweed farms ($P>0.72$). Finally, the mean grain size on the sand bank (site S) was smaller than in the seagrass beds ($P<0.05$ for all comparisons), but was no different to the seaweed farms ($P=0.36$ for FC, $P=0.99$ for FM).

Analysis for skewness in the grain size distribution at the six sites showed that the sediment sizes in both seaweed farms and on the sand bank are strongly negatively skewed (Table 3). This indicates that the

sediments lack the normal proportion of smaller grain size fractions in proportion to the grain size distribution.

SOM differed between the sites (ANOVA: $P<0.001$, $F=5.73\times 10^{-5}$), with a lower content in the seaweed farms and on the sand bank than in the seagrass beds ($P<0.05$ for all comparisons; Fig. 5B). Further, there were differences between the seagrass beds, with site T having a higher content than both sites TC and E ($P<0.05$). No differences were encountered between the two seaweed farms ($P=0.59$), nor between the seaweed farms and the sand bank ($P=0.19$ for FC, $P=0.97$ for FM).

3.4. Relationship between macrofaunal abundance and environmental variables

Three of the variables investigated, viz. sediment grain size, cover of *Halimeda* spp., seagrass cover, were correlated with other variables and were thus removed from the dataset prior to analysis. The BIO-ENV procedure revealed that, of the remaining six variables, the combination of % vegetation cover (seagrass and macroalgae) and SOM had the highest correlation to macrofaunal abundance ($\rho=0.996$). Separate correlations between macrofaunal abundance and these two

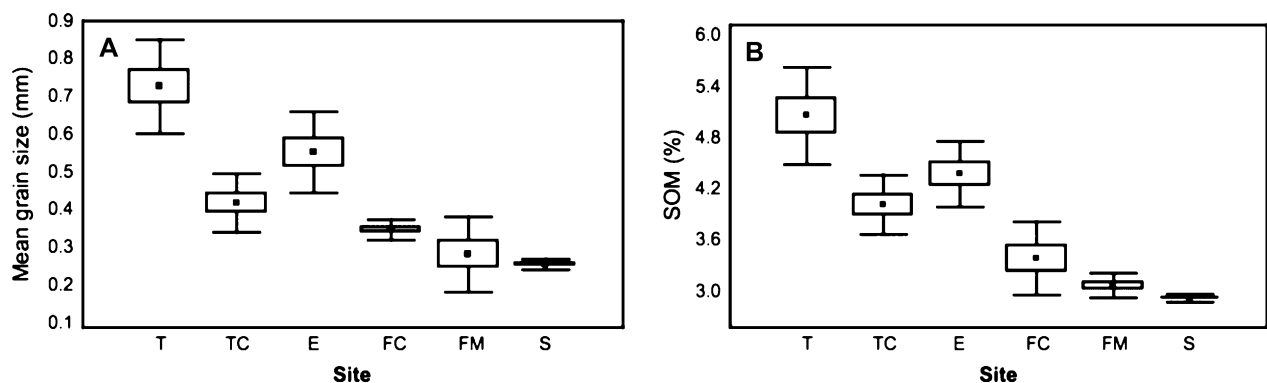


Fig. 5. Sediment (A) mean grain size and (B) organic matter content at the six sites in Chwaka Bay, Zanzibar ($n=7$; central squares, means; boxes, S.E.; whiskers, S.D.). The sites were: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S, sand bank.

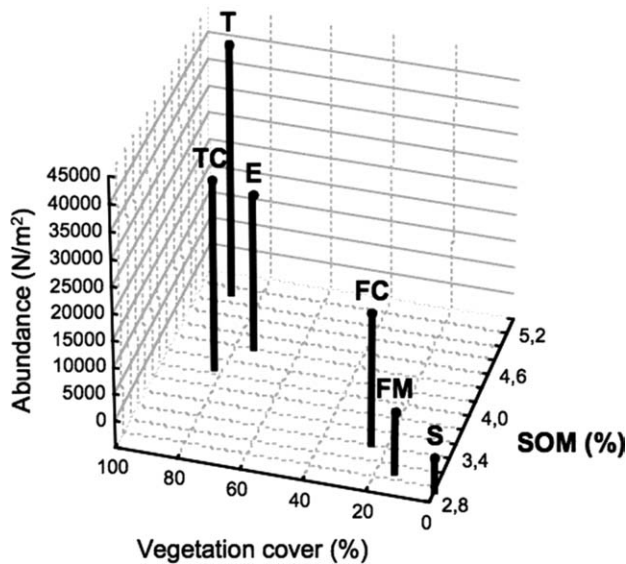


Fig. 6. Relationship between macrofaunal abundance, vegetation cover (%) and SOM (%) at six sites in Chwaka Bay, Zanzibar. Values presented are means per site. The sites were: T, *Thalassia hemprichii*-bed; TC, *Thalassia hemprichii*/*Cymodocea serrulata*-bed; E, *Enhalus acoroides*-bed; FC, seaweed farm Chwaka; FM, seaweed farm Marumbi; S: sand bank.

variables yielded similar results (SOM: $r=0.938$, $P=0.006$, $n=6$; vegetation cover: $r=0.933$, $P=0.007$, $n=6$). The relationship between the three variables is presented in Fig. 6.

4. Discussion

4.1. Seagrass and macroalgae

Seagrass shoot density, biomass, cover and canopy height were, in most cases, lower in the two seaweed farms than in the three seagrass beds. The cover of macroalgae was also lower in the seaweed farms than in the seagrass beds. Exceptions were high seagrass biomass in farm FC (Fig. 2B), caused by the presence of the conspicuous *Enhalus acoroides* in four of the samples (reflected by the large S.D.). These were sampled between farm plots in the outer parts of the seaweed farming area. The low shoot density at site E was also possibly explained by the presence of *E. acoroides* which has quite large individual plants. The variability found between the three seagrass beds (three different seagrass assemblages were deliberately chosen) reflects the spatial heterogeneity in the bay.

As the four investigated seagrass variables are more or less dependent on each other (reflecting the underlying characteristics of the seagrass), the results together form the picture that seaweed farming might affect underlying seagrasses, causing a thinning of the

meadows. This corresponds well with information obtained from interviews in another study, where seaweed farmers explain that, when a seaweed plot is set up, the seagrass underneath the algae starts to decrease in cover, and sometimes even disappears after a few months (de la Torre Castro and Rönnbäck, 2004). The lower content of SOM also support this, as its major part originates from decaying fragments of seagrass and macroalgae (e.g. Hemminga and Duarte, 2000).

The actual reasons why seaweed farming should have a negative effect on seagrass and macroalgae has not been investigated, but possible factors can be suggested: shading and competition for nutrients in the water (Collén et al., 1995) might reduce seagrass primary production and growth rates; mechanical abrasion by the algae fronds, trampling and deliberate removal of shoots by farmers (de la Torre Castro and Rönnbäck, 2004) might reduce shoot density; and excretion of hydrogen peroxide and halogenated toxic substances by the algae (Mtolera et al., 1995, 1996) could stress seagrass. None of the suggested factors are mutually exclusive; instead, the observed patterns could be caused by their synergistic action.

4.2. Macrofauna

In terms of macrofauna, the lower abundance and biomass in the farmed seagrass beds compared to unfarmed beds is most likely to be caused by the differences in seagrass and algae at these sites, as macrofaunal abundance was closely correlated to SOM (which originates mostly from decaying macrophytes, i.e. seagrass and algae) and vegetation cover (% seagrass and algae). This is supported by results from other studies identifying macrophytes (e.g. seagrass) and SOM as being important for macrofaunal abundance (e.g. Paula et al., 2001). The extreme differences in macrofaunal biomass (more than two orders of magnitude) were caused by the almost complete absence of bivalves at the farm sites, these being encountered in numbers ranging from 600 to 1800 individuals m^{-2} in the seagrass beds, constituting 91–99% to the total biomass. The family *Lucinidae*, which contributed most of the biomass, are filter-feeding bivalves normally found buried in sand/gravel sediments (Richmond, 1997). Thus, the results suggest that seaweed farming over seagrass indirectly affects the habitat function of the seagrass beds (e.g. by reducing shelter function and/or food availability), lowering the abundance and biomass of macrofauna as observed in this study.

The multivariate analyses of macrofaunal community structure also separated the seagrass beds with and without seaweed farms, and showed that the seaweed farm community at site FM was more similar to that on the sand bank. This is interesting, since this seaweed

farm is located on a seagrass bed where there still is seagrass, and it therefore would be expected to differ from the vegetation-free sand bank. Again the taxon and functional group responsible for most of the dissimilarity in the analyses was the *Lucinidae* (functional group: suspension feeders). Bivalves in general are known to benefit from seagrass for shelter (Blundon and Kennedy, 1982; Peterson, 1982; Coen and Heck, 1991), and a low seagrass cover in farms probably results in low availability of shelter, high predation rates and finally the lower macrofaunal abundance and biomass observed. In addition, seaweed farmers might remove bivalves manually.

4.3. Sediment

It has been suggested that sediments within farms lose finer particles because of the mechanical abrasion from the frondose algae (Ólafsson et al., 1995) and the same effect has been observed in seagrass beds when sediment-binding seagrasses are mechanically removed (e.g. Daby, 2003). The results of the present study revealed the opposite pattern, i.e. finer sediment was found in seaweed farms, which could suggest that (1) the differences may not be caused by the impacts of farming, but instead reflect spatial differences in bay hydrodynamics, or (2) the differences are due to an effect of seaweed farming, causing a reduction of coarser grain fractions in the seaweed farms. Most probably, the coarser grain size in the two seagrass beds (sites T and E) is caused by the higher cover of *Halimeda* algae in these sites (14.4–15.5% cover in the seagrass beds, and 1.6–2.6% in the seaweed farms). *Halimeda* spp. are calcareous, encrusting, sand-producing algae common in the western part of Chwaka Bay, and have been shown to contribute a high proportion of sand grains in the coarser sediment fractions (Björk et al., 1995; Muzuka et al., 2001). Although the differences in mean grain size did not correlate with any effects of seaweed farming (in terms of loss of finer sediments), other sediment parameters may be more useful for the detection of small changes. The sediment analyses at the six sites revealed that, in both seaweed farms and on the sand bank, the grain size distribution was strongly negatively skewed (Table 2). This means that, in relation to the calculated mean grain size and the shape of the distribution curve, the sediments lack a high proportion of finer particles at these sites. This could be caused by the lower seagrass cover, and/or mechanical abrasion by frondose algae in the farms, but remains to be experimentally tested.

4.4. Implications for ecosystem function

Seagrass forms both the energetic and structural base of seagrass beds, suggesting that an effect of seaweed

farming on seagrass is likely to affect ecosystem structure and function. If macrophyte (seagrass and algae) biomass and primary production are decreased by farming, and a major component (the farmed algae) is removed by harvesting, less energy could be channelled through the food web. The effects would be transferred to higher trophic levels, here perhaps illustrated by the lower abundance and biomass of macrofauna in the seaweed farms.

The lower abundance of macrofauna could itself have substantial effects at the system level, as benthic macrofauna perform a number of important functions in seagrass beds, e.g. detritivory and filtration (Snelgrove, 1998; Levin et al., 2001). An example is suspension-feeding bivalves (nearly absent in the seaweed farms), which have been shown to benefit from seagrass for shelter, while simultaneously increasing sediment nutrient levels and benefiting seagrasses in a mutualistic relationship (e.g. Peterson and Heck, 2001). This implies that the lower abundance of bivalves encountered could have a negative feed-back effect on the seagrass, further decreasing the primary production and causing even more thinning of the seagrass beds.

Further, many meio- and macrofaunal taxa constitute important food for benthic fish in seagrass beds (e.g. Ndaro and Ólafsson, 1995), implying that a reduced abundance and biomass of macrofauna (in combination with the changed habitat provided by the algae) could result in an altered fish community residing in the seagrass beds under seaweed farms. This is supported by results from Bergman et al. (2001), who found lower abundances of benthic fish in seaweed farms compared to control areas with only seagrass.

The results of this study suggest that seaweed farming affects key functional groups in seagrass beds (e.g. primary producers and filter feeders), which could result in changes in ecosystem function. This could cause a loss of ecological resilience, or the ability to withstand disturbance without going through a phase shift (sensu Holling, 1973) in seagrass beds under farms. However, considering the current farm sizes in the bay, it is uncertain whether these adverse effects could result in any dramatic ecosystem change (e.g. a complete seagrass die-off) as seagrasses are still present in farms more than a decade after the introduction of seaweed farming. Nevertheless, as the global demand for carrageenan products is estimated to increase by 3–5% year⁻¹ over the next decade (Taylor, 2000), the demand for cultured seaweeds will probably increase and result in more and intensified farming. Together with the expected overall increase in other anthropogenic (e.g. over-harvesting of organisms, agricultural runoff and mechanical damage) and natural disturbances (e.g. storms and disease; Short and Wyllie-Echeverria, 1996; Green and Short, 2003) to seagrass beds, unregulated seaweed farming may contribute to a further decline in seagrasses.

4.5. Conclusion

The results of this study suggest that seaweed farming in Chwaka Bay affects the underlying seagrass beds by decreasing the cover of seagrass and macroalgae, SOM and macrofaunal biomass and abundance, and altering the macrofaunal community structure. This indicates that seaweed farming may not, contrary to what has been suggested, be a fully environmentally sustainable activity. Therefore, researchers and coastal zone managers need to address the environmental aspects of seaweed farming, e.g. by further investigating the actual causes of adverse effects; the possibilities of trade-offs between seaweed farming and the flow of other ecological goods and services from seagrass beds; the underlying driving forces causing seaweed farming expansion; and the management and institutional arrangements of other activities in the coastal zone. The results should be used to assess the carrying capacities of seaweed farms, and evaluate and perhaps modify current farming methods and/or locations to increase the overall sustainability of the activity.

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References

- Arrivillaga, A., Balz, D.M., 1999. Comparison of fishes and macro-invertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science* 65 (2), 301–319.
- Bergman, K.C., Svensson, S., Öhman, M.C., 2001. Influence of algal farming on fish assemblages. *Marine Pollution Bulletin* 42 (12), 1379–1389.
- Björk, M., Mohammed, S.M., Björklund, M., Semesi, A., 1995. Coralline algae, important reef builders threatened by pollution. *Ambio* 24 (7–8), 502–505.
- Blundon, J.A., Kennedy, V.S., 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidum* (Rathbun), predation in Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 65, 67–81.
- Boggs, J.R.S., 2001. *Principles of Sedimentology and Stratigraphy*, third ed. Prentice Hall, New Jersey, USA, 726 pp.
- Bologna, P.A.X., Heck, K.L., 1999. Macrofaunal associations with seagrass epiphytes — relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology* 242 (1), 21–39.
- Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research* 37, 153–166.
- Bryceson, I., 2002. Coastal Aquaculture Developments in Tanzania: Sustainable and Non-sustainable Experiences. *Western Indian Ocean Journal of Marine Science* 1 (1), 1–10.
- Cederlöf, U., Rydberg, L., Mgendi, M., Mwaipopo, O., 1995. Tidal exchange in a Warm Tropical Lagoon: Chwaka Bay, Zanzibar. *Ambio* 24 (7–8), 458–464.
- Clarke, K.R., 1988. Detecting change in benthic community structure. In: *Proceedings, XIVth International Biometric Conference, Namur: Invited Papers*, pp. 131–142.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Coen, L.D., Heck Jr., K.L., 1991. The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria mercenaria* (L.)) growth in a subtropical seagrass (*Halodule wrightii* Aschers.) meadow. *Journal of Experimental Marine Biology and Ecology* 145 (1), 1–13.
- Coles, R.G., Lee Long, W.J., Watson, R.A., 1993. Distribution of seagrasses, and their fish and Penaeid prawns communities, in Cairns Harbour, a tropical estuary, Northern Queensland, Australia. *Australian Journal of Marine and Freshwater Research* 44, 193–210.
- Collén, J., Mtolera, M., Abrahamsson, K., Semesi, A., Pedersén, M., 1995. Farming and physiology of the red algae *Eucheuma*: growing commercial importance in East Africa. *Ambio* 24 (7–8), 497–501.
- Connolly, R.M., 1994. The role of seagrass as preferred habitats for juvenile *Sillagonides punctata* (cuv and val) (*Sillaganidae*, Pisces) — habitat selection or feeding. *Journal of Experimental Marine Biology and Ecology* 180 (1), 39–47.
- Costanza, R., d'Arge, R., Groot, R.D., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van der Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Daby, D., 2003. Effects of seagrass bed removal for tourism purposes in a Mauritian bay. *Environmental Pollution* 125 (3), 313–324.
- Day, J.H., 1967. *A Monograph on the Polychaeta of Southern Africa*, vol. 1–2. British Museum (Natural History), London, 458 pp.
- de Boer, W.F., Longamane, F.A., 1996. The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. *Biological Conservation* 78 (3), 295–303.
- de la Torre Castro, M., Rönnbäck, P., 2004. Links between humans and seagrasses — An example from tropical East Africa. *Ocean and Coastal Management* 47, 361–387.
- Dittman, S., 2002. Benthic fauna in tropical tidal flats — a comparative perspective. *Wetlands Ecology and Management* 10 (3), 189–195.
- Duarte, C.M., 2000. Marine biodiversity and ecosystem services: an elusive link. *Journal of Experimental Marine Biology and Ecology* 250 (1–2), 117–131.
- Duarte, C.M., 2002. The future of seagrass meadows. *Environmental Conservation* 29 (2), 192–206.
- Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: a reassessment. *Aquatic Botany* 65, 159–174.
- Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17, 193–284.
- Fonseca, M.S., 1989. Sediment stabilisation by *Halophila decipiens* in comparison to other seagrasses. *Estuarine, Coastal and Shelf Science* 29, 501–507.
- Fortes, M.D., 1988. Mangrove and seagrass beds of East-Asia — habitats under stress. *Ambio* 17 (3), 207–213.
- Green, E.P., Short, F.T., 2003. *World Atlas of Seagrasses*. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, CA, 298 pp.

- Gullström, M., de la Torre Castro, M., Bandeira, S.O., Björk, M., Dahlberg, M., Kautsky, N., Rönnebeck, P., Öhman, M.C., 2002. Seagrass ecosystems in the Western Indian Ocean. *Ambio* 31 (7–8), 588–596.
- Hall, M.O., Durako, M.J., Fourqurean, J.W., Zieman, J.C., 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22 (2B), 445–459.
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, UK, 310 pp.
- Hindell, J.S., Jenkins, G.P., Keough, M.J., 2000. Evaluating the impact of predation by fish on the assemblage structure of fishes associated to seagrass (*Heterozostera tasmanica*) (Martens ex Acherson) den Hartog, and unvegetated sand habitats. *Estuarine, Coastal and Shelf Science* 255 (2), 153–174.
- Holdich, D.M., Jones, J.A., 1983. *Tanaids* Keys and notes for the identification of species. In: Kermack, D.M., Barnes, R.S.K. (Eds.), *Synopsis of the British Fauna*, vol. 27. Cambridge University Press, Cambridge, 98 pp.
- Holling, C.S., 1973. Resilience and the stability of ecological systems. *Annual Review of Ecology and Systematics* 4, 1–23.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6, 65–70.
- Jackson, J.L., Rowden, A.A., Attrill, M.J., Bossey, S.J., Jones, M.B., 2001. The importance of seagrass beds as habitats for fishery species. *Oceanography and Marine Biology* 39, 269–303.
- Jiddawi, N.S., Ngazy, Z., 2000. A gift from the ocean: The importance of *Eucheuma* farming to the livelihood security of the people of Zanzibar. In: Mshigeni, E., Asman, J., Bisanda, E. (Eds.), *Opportunities from Africa's Bioresources*. Proceedings of the Second International Training workshop on the Zero Emissions Research Initiatives, UNDP. University of Namibia, pp. 132–146.
- Johnstone, R., Ólafsson, E., 1995. Some environmental aspects of open water algal cultivation: Zanzibar, Tanzania. *Ambio* 24 (7–8), 465–469.
- Koch, E.W., 1996. Hydrodynamics of a shallow *Thalassia testudinum* bed in Florida, USA. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), *Seagrass Biology International Workshop*, Rottne Island, Western Australia, pp. 105–110.
- Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4 (5), 430–451.
- Lynne, C.S., Boland, J.W., Edyvane, K.S., Jones, G.K., 2000. Development of a seagrass-fish habitat model — 1: A seagrass residency index for economically important species. *Environmetrics* 11 (5), 541–552, doi: 10.1002/1099-095X(200009/10)11:5<541::AID-ENV416>3.0.CO;2-A.
- McKnight Foundation, 2002. CARE Living With, and Not Off, the Land, vol. 2003: The McKnight Foundation. URL: http://www.mcknight.org/international/profile_care.asp. Accessed 2003/06/11.
- Mohammed, S.M., Jiddawi, S.M., 1999. The ecology and socio-economy of Chwaka Bay, Zanzibar. Zanzibar Town: Report prepared for Jozani-Chwaka Bay Conservation Project, CARE, Tanzania, 47 pp.
- Morgans, J.F.C., 1956. Notes on the analysis of shallow-water soft substrata. *Journal of Animal Ecology* 26, 367–387.
- Muya, F., 1993. Seaweed farming in Zanzibar: An amazing story. *ALCOM News* 11, 11–15.
- Mtolera, M.S.P., Collén, J., Pedersén, M., Semesi, A.K., 1995. Destructive hydrogen peroxide production in *Eucheuma denticulatum* (Rhodophyta) during stress caused by elevated pH, high light intensities and competition with other species. *European Journal of Phycology* 30, 289–297.
- Mtolera, M.S.P., Collén, J., Pedersén, M., Ekdahl, M., Abrahamsson, K., Semesi, A.K., 1996. Stress-induced production of volatile halogenated organic compounds in *Eucheuma denticulatum* (Rhodophyta) caused by elevated pH and high light intensities. *European Journal of Phycology* 31, 89–95.
- Muzuka, A.N.N., Kangwe, J.W., Nyandwi, N., Wannäs, K.O., Mtolera, M.S.P., Björk, M., 2001. Preliminary results on the sediment sources, grain size distribution and percentage cover of sand-producing *Halimeda* species and associated flora in Chwaka Bay. In: Richmond, M.D., Francis, J. (Eds.), *Marine Science Development in Tanzania and Eastern Africa*. Proceedings of the 20th Anniversary Conference on Advances in Marine Science in Tanzania. IMS/WIOMSA, Zanzibar, Tanzania, pp. 51–60.
- Ndaro, S., Ólafsson, E., 1995. A note on the selection of meiobenthic prey *Gerres oyena* in a tropical lagoon in eastern Africa. *Ambio* 24 (7–8), 517–519.
- Ndaro, S., Ólafsson, E., 1999. Soft-bottom fauna with emphasis on nematode assemblage structure in a tropical intertidal lagoon in Zanzibar, eastern Africa: I, spatial variability. *Hydrobiologia* 405, 133–148.
- Ólafsson, E., Johnstone, R.W., Ndaro, S.G.M., 1995. Effects of intensive seaweed farming on the meiobenthos in a tropical lagoon. *Journal of Experimental Marine Biology and Ecology* 191 (1), 101–117.
- Paula, J., Costa, P.F.E., Martins, A., Gove, D., 2001. Patterns of abundance of seagrasses and associated anfaunal communities at Inhaca Island, Mozambique. *Estuarine, Coastal and Shelf Science* 53, 307–318.
- Peterson, C.H., 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Marine Biology* 66, 159–170.
- Peterson, B.J., Heck Jr., K.L., 2001. Positive interactions between suspension-feeding bivalves and seagrass — a facultative mutualism. *Marine Ecology Progress Series* 213, 143–155.
- Petterson-Löfquist, P., 1995. The development of open-water algae farming in Zanzibar: reflections on the socioeconomic impact. *Ambio* 24 (7–8), 487–491.
- Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research* 20, 75–83.
- Richmond, M., 1997. A Guide to the Seashores of East Africa and the Western Indian Ocean. SIDA, SAREC, 448 pp.
- Saleh, 1998. Inside Africa — seaweed farming, vol. 2003: Sunday Times. URL: <http://www.suntimes.co.za/1998/10/04/insight/in09.htm>. Accessed 2003/06/11.
- Salita, J.T., Ekau, W., Saint-Paul, U., 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. *Marine Ecology Progress Series* 247, 183–195.
- Semesi, S., 2002. Ecological and socio-economic impacts from *Eucheuma* seaweeds in Zanzibar, Tanzania. Masters thesis, Noragric, Agricultural University of Norway, 77 pp.
- Short, F.T., Coles, R.G. (Eds.), 2001. *Global Seagrass Research Methods*. Elsevier Science B.V., Amsterdam, 473 pp.
- Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbances of seagrasses. *Environmental Conservation* 23 (1), 17–27.
- Snelgrove, P.V.R., 1998. The biodiversity of macrofaunal organisms in marine sediments. *Biodiversity and Conservation* 7, 1123–1132.
- Taylor, D., 2000. Mindanao seaweed growers, Traders organize to prop up industry, vol. 2003. URL: <http://www.mindanao.org/news/0009/18.htm>. Accessed 2003/06/11.
- Warwick, R.M., Clarke, K.R., Suharsono, 1990. A statistical analysis of coral community responses to the 1982–1983 El Niño in the Thousand Islands. *Coral Reefs* 8 (4), 171–179.
- Zemke-White, W.L. Assessment of the current knowledge on the environmental impacts of seaweed farming in the tropics. Proceedings of the Asia-Pacific Marine Science and Technology Conference, Kuala Lumpur, 2002, in press.