

Effects of tropical open-water seaweed farming on seagrass ecosystem structure and function

J. S. Eklöf*, R. Henriksson, N. Kautsky

Department of Systems Ecology, Stockholm University, 106 91 Stockholm, Sweden

ABSTRACT: Seaweed farming is often depicted as a sustainable form of aquaculture, but suspected habitat alterations and spread of algae outside farms have rendered speculations on the actual degree of sustainability. We conducted an experimental field study on Unguja Island (Zanzibar, Tanzania) to investigate the effects of off-bottom seaweed farming on a tropical seagrass ecosystem, using 1.5 × 2.5 m experimental farm plots. After 11 wk, above-ground seagrass biomass was 40% lower than in control plots, owing to a combination of lower shoot density, shoot length and leaf growth rate. Since the biomass was constant between Day 15 and 75 in the farm (F) treatment, but increased by 67 vs. 48% in the 2 controls (control treatment [C] and stick-and-line control treatment [CSL]), the effect exerted by the farm was a lack of potential biomass increase rather than an actual decrease. The effect was transplanted to associated organisms both in terms of lower seagrass epiphyte cover and changes in the abundance of 2 dominating epifauna taxa (>1 cm): sea urchins and sponges. Furthermore, the F treatment caused an accumulation of seagrass leaf litter, but did not affect sediment organic matter (SOM) content. The mechanisms behind these effects were not explicitly tested, but algal shading, emergence stress and mechanical abrasion were identified as likely contributors. Interestingly, the effects were largely restricted to 1 of the 2 seagrass species present, *Enhalus acoroides*, while the other, *Thalassia hemprichii*, remained more or less unaffected. This may be due to reduced interspecific competition or species-specific differences in morphology and stress tolerance, and could in the long-term have implications for (amongst others) associated fish communities. Although seaweed farming at the current level is less detrimental than, for example, intensive shrimp farming, and therefore should be seen as a strong option for future aquaculture developments, intensive farming on seagrasses should be avoided or at least minimized by, for example, implementing other farming methods. The risk of ecosystem-level changes in large-scale and uncontrolled farm enterprises warrants a holistic and integrated coastal management approach which considers all aspects of the tropical seascape including human societies and natural resource use.

KEY WORDS: Environmental effects · Seagrass ecosystems · Seaweed farming · Aquaculture · Algae · *Eucheuma denticulatum*

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Many of the dominating forms of aquaculture (e.g. shrimp and salmon farming) are resource-inefficient and contribute to environmental degradation (e.g. Naylor et al. 2000, Rönnbäck 2001). Therefore, the development of more resource-efficient forms, e.g. the use of integrated systems and farming of species at lower trophic levels (Rönnbäck et al. 2002, Neori et al. 2004) have high priority within coastal management.

Seaweed farming, i.e. mariculture of macroalgae, is often considered as the most environmentally friendly form of aquaculture: it requires little or no input of fertilizers or medicines, does not cause any major physical alterations of the environment (Johnstone & Ólafsson 1995, Bryceson 2002), and can be used to mediate eutrophication and pollution (e.g. Haglund & Lindstrom 1995, Rai et al. 2000). Seaweed farming is therefore heavily promoted as an alternative sustainable aquaculture practice for local coastal communities in

*Email: johane@ecology.su.se

developing countries (Ask 2001, Sievanen et al. 2005), and is currently spreading on a global scale (Ask et al. 2001, Rönnbäck et al. 2002). At the same time, the awareness of environmental side-effects that may compromise the sustainability of large-scale farming operations is growing stronger (Bryceson 2002, Zemke-White & Smith 2006). By altering habitat and involuntary spreading farmed algae to adjacent areas, seaweed farming seems to affect many components of natural communities e.g. bacteria (Johnstone & Ólafsson 1995), meiofauna (Ólafsson et al. 1995), benthic macrofauna (Eklöf et al. 2005), fish (Bergman et al. 2001) and scleractinian corals (Russell 1983). However, as environmental impacts are still disputed (see e.g. Ask et al. 2001), there is a clear need for experimental studies that validate and describe the effects of such farms (Zemke-White & Smith 2006). Experiments can also pin-point the actual causes of effects, and aid in the development of more sustainable farming methods.

In East Africa, seaweed farming was initiated on Unguja Island (Zanzibar, Tanzania) in the late 1980s, with the introduction of Philippine strains of *Eucheuma denticulatum* (Burman) Collins & Harvey and *Kappaphycus alvarezii* Doty. These 2 red seaweeds are farmed in shallow lagoons for their content of the polysaccharide carrageenan, using the 'offbottom' method where algal thalli, tied to strings stretched between wooden sticks driven into the sea bottom, are harvested every 2 to 3 mo. In the mid 1990s, farms covered a total area of approximately 1000 ha (Ólafsson et al. 1995), but due to decreasing seaweed prices and fewer people farming (Bryceson 2002), this figure is probably lower today (J. Eklöf pers. obs.). Seaweed farms are placed in seagrass beds in areas where seagrasses are either the preferred substrate (de la Torre-Castro & Ronnback 2004) or where non-vegetated sites are lacking. Seagrass beds are a common and important feature in inter- and subtidal areas in East Africa, due to their provision of a number of ecological goods and services, e.g. fishing grounds (Gullström et al. 2002, Green & Short 2003, de la Torre-Castro & Ronnback 2004). However, seaweed farmers sometimes manually remove shoots of larger seagrasses (de la Torre-Castro & Ronnback 2004), and there are indications that seagrass beds occupied by seaweed farms have lower seagrass biomass and a different macrofauna community structure compared to those without (Eklöf et al. 2005). Hence, a future expansion of seaweed farming may pose a threat to seagrass ecosystems in the region (Green & Short 2003).

Seagrasses and macroalgae in general often compete for limiting resources e.g. light (Holmquist 1997, Irlandi et al. 2004) and nutrients (Dumay et al. 2002). Reduced growth rates of farmed seaweeds in the pres-

ence of seagrasses could indicate similar competition in seaweed farms (Collén et al. 1995, but see Mtolera 2003). Although the dynamics in seaweed farms probably differ (owing to the fact that they are managed monocultures), similar mechanisms may contribute to and explain decreases of seagrasses in seaweed farms.

The aim of this study was to investigate the short-term effects of off-bottom seaweed farming on seagrass ecosystem structure and function, thereby (1) validating observations from previous studies, (2) elucidating mechanisms behind effects and (3) contributing to a broader understanding of farm sustainability. A number of structural and functional endpoints were investigated in replicated seaweed farms after 1 farming cycle (11 wk), making this the first study to experimentally investigate effects of seaweed farming. In addition to several seagrass variables, the abundance of seagrass epiphytes (algae and sessile invertebrates) and larger epifauna (>1 cm) was assessed. These taxa represent seagrass community components that are likely to be affected by farming, and that are important ecologically as well as socio-economically in the study area (de la Torre-Castro & Ronnback 2004). Further, effect on sediment organic matter (SOM) content was measured and compared with values obtained from areas where farming had been conducted for more than a decade (Eklöf et al. 2005). Finally, the amount of seagrass leaf litter was estimated because it constitutes the main source for regenerated nutrients and may have a significant impact on microbial secondary production (Peduzzi & Herndl 1991).

MATERIALS AND METHODS

Study site. The study was conducted in Chwaka Bay (Zanzibar, Tanzania; 6° 6' S, 39° 24' E to 6° 13' S, 39° 31' E), a 50 km² semi-enclosed bay with an average vegetation cover of 50% (Gullström et al. 2006), consisting mainly of seagrasses e.g. *Enhalus acoroides* (L.) Royale, *Thalassia hemprichii* (Ehrenberg) Ascherson, *Cymodocea serrulata* (Br) Ascherson & Magnus, and *Thalassodendron ciliatum* (Forskål) den Hartog, as well as benthic macroalgae e.g. *Halimeda* spp., *Caulerpa* spp., and *Dictyosphaeria cavernosa*.

Commercial seaweed farming was initiated in the area in the early 1990s, but wild native strains of *Eucheuma* spp. have been collected since the 1950s (Bryceson 2002). Currently, seaweed farms cover roughly 2.5 km² of the bay surface (de la Torre-Castro & Ronnback 2004).

The study site, located on a subtidal bank close to one of the seaweed farms, was chosen based on (1) a relatively homogenous distribution of seagrasses, (2) site conditions (sediment grain size, relative water

depth and flow velocity) suitable for farming and (3) the lack of signs of previous seaweed farming. The water depth in the area ranged from approximately 2.5 to 0.1 m during high and low water spring tide, respectively.

The seagrass community consisted of *Enhalus acoroides* (51%) and *Thalassia hemprichii* (49%) (mean total shoot density \pm SE = 236 ± 85 shoots m^{-2} ; $n = 57$), with interspersed single individuals or patches of benthic green algae, mainly *Dictyosphaeria cavernosa*, *Halimeda* spp. and *Caulerpa* spp.

Experimental design. The effects of seaweed farming were investigated using a replicated treatment/control design, with experimental plots (2.5×1.5 m) located 1 m apart within a 30×30 m area. The size of and distance between plots were based on logistical constraints (i.e. a site large enough for the plots but with a relatively homogenous vegetation cover). The plots were placed perpendicular to the water current, and randomly assigned 1 of 3 treatments ($n = 19$) to avoid confounding factors. Farm treatment (F) plots consisted of three 2.5 m long, 4 mm thick nylon ropes ('monolines'), fastened 0.15 m above the bottom between a pair of wooden sticks (length 1.0 m, diameter 2 to 3 cm) that were driven 0.4 m into the bottom and placed 0.5 m apart. On each rope, 9 pieces of *Eucheuma denticulatum* (wet wt ~ 100 g per piece) were attached (0.25 m apart) using plastic ribbon (known locally as 'tie-tie'). All materials and methods were carefully chosen to resemble those used in the area. The control treatment (C) consisted of unmarked seagrass plots. Further, to investigate whether farm effects originated from the presence of the algae and/or the sticks and lines, a stick-and-line procedural control treatment (CSL) was included. This consisted of a set-up identical to that of the F treatment, except that no algae were attached to the monolines.

The study ran for ~ 11 wk (75 d) from early November 2004 to January 2005, a time period that corresponded roughly to 1 farm cycle and considered sufficient to distinguish short-term effects from differences observed after more than a decade of farming (Eklöf et al. 2005). Unless stated otherwise, all sampling was conducted at the end of the experiment.

Algal growth. The daily growth rate of farmed algae was estimated by weighing 1 randomly chosen seedling of *Eucheuma denticulatum* per F treatment plot at the start of the experiment (wet wt, to the nearest 1 g; $n = 19$). After 11 wk, the same seedling was reweighed and the daily growth rate (DGR; %) was calculated using the formula:

$$DGR = [(W_t/W_0)^{1/t} - 1] \times 100$$

where W_0 and W_t are initial and final biomass at Day t , respectively (Lignell et al. 1987).

Seagrasses. A non-destructive method was used to estimate above-ground biomass (g dry wt m^{-2}). Initially, 30 shoots of each of the 2 seagrass species growing between the experimental plots were randomly selected. After measuring the length of the longest leaf (to the nearest 1 cm), all shoots were cut off and collected. In the laboratory, all leaves were cleaned of epiphytes and sediment (using 5% HCl and distilled water) and dried at 90°C to constant weight. The biomass was determined as dry wt (to the nearest 0.1 mg), and length-weight regression confirmed that the length of the longest leaf was a reasonable proxy for total shoot biomass for both *Enhalus acoroides* ([shoot biomass mg] = $0.0987e^{0.0406 \times [\text{shoot length in cm}]}$; $R^2 = 0.6779$; $p < 0.001$) and *Thalassia hemprichii* ([shoot biomass mg] = $0.0005[\text{shoot length cm}]^{1.9357}$; $R^2 = 0.6982$; $p < 0.001$). At Days 15 and 75 of the study, the above-ground biomass of 5 randomly chosen shoots per species and experimental plot was estimated (as above). The 5 estimates were averaged to form 1 replicate value. Seagrass shoot density (no. of shoots m^{-2}) was estimated at Days 0, 15, 30, 45, 60 and 75 by counting all shoots (separating the 2 species) within a 0.0625 m^2 frame at 3 random positions in each plot, and averaging the counts to form 1 replicate value. The above-ground biomass (g dry wt m^{-2}) after 15 and 75 d, both per species and in total, was then calculated by multiplying estimated biomass per shoot with estimated shoot density. Statistical comparisons of shoot densities in the plots on Day 0 ensured that there were no initial differences that could confound the treatment effects, either for both species combined (1-way ANOVA; $F = 1.49$; $p = 0.23$), or *E. acoroides* ($F = 0.62$; $p = 0.54$) and *T. hemprichii* ($F = 1.45$; $p = 0.24$) separately.

Seagrass above-ground production (mg growth shoot $^{-1}$ d $^{-1}$) was estimated throughout the whole experiment using the leaf-puncture method (Short & Coles 2001). Due to the heterogeneous distribution of *Thalassia hemprichii* (some plots initially had < 5 shoots m^{-2}), no removal of shoots could be conducted. Therefore, growth measurements were only completed for *Enhalus acoroides*. Within each plot, 3 randomly chosen shoots were marked 3 cm below the leaf sheath using a syringe. Approximately 15 d later, the shoots were collected and 3 new shoots were marked. Over the 11 weeks, this resulted in a continuous measurement of shoot growth via 5 separate estimations. In the laboratory, all leaves were cleaned of sediment and epiphytes (as above) and the growth section was weighed (to the nearest 0.1 mg) after drying at 90°C to constant weight. The total aerial above-ground production for the whole study period (g growth m^{-2}) was calculated by multiplying growth rate with shoot density for each 15 d interval and summing over the 5 periods.

Before data analyses, seagrass shoot density, above-ground biomass and total aerial production were corrected for the removal of shoots for growth measurements.

Seagrass epiphyte cover. Seagrass epiphyte cover was investigated by collecting 1 shoot from each seagrass species in the centre of each plot after 60 d. Epiphyte cover was investigated on both the inside and outside of the upper third of the oldest intact leaf, which hosts the most mature epiphyte community (Short & Coles 2001). Five field views (each comprising 1 cm² for *Enhalus acoroides* and 0.25 cm² for *Thalassia hemprichii*) were investigated using a binocular microscope (20× magnification). Each field view had a gridline that provided 9 intersections, and the % cover of epiphytes was estimated by firstly counting the number of times an intersection overlapped with epiphytes or bare leaf surface and then by summing over the 5 field views, i.e. 45 intersections.

Epifauna. All epifauna (defined as all sessile or slow-moving fauna >1 cm encountered on seagrass leaves, farmed alga or the sea bed) were counted and identified to species (n = 17). The community was analyzed in terms of abundance (no. of ind. m⁻²) and diversity (no. of species plot⁻¹, Shannon-Wiener Diversity Index *H'* and Simpson Index of Diversity *D*). As the community was dominated by sea urchins, sponges and sea anemones (constituting 98 to 100% of total abundance in all treatments), their respective abundances were also analyzed separately.

Accumulated seagrass leaf litter. The amount of accumulated seagrass leaf litter (g dry wt m⁻²) was estimated by collecting all dead loose-lying seagrass leaves, roots and rhizomes in the upper 1 cm sediment layer within three 0.0625 m² frames randomly placed within plots (n = 12). The 3 samples were immediately pooled to form 1 replicate sample, and brought to the laboratory. The material was separated by species and weighed (to the nearest 0.1 mg) after drying at 90°C to constant weight.

Sediment organic matter (SOM) content. Sediments were collected using a small corer (Ø = 3 cm, depth = 2 cm) at 3 randomly chosen places within each plot (n = 19). The samples were immediately pooled to form 1 sample per plot, stored in dark airtight plastic bags, and brought to the laboratory for analysis. All non-sediment material (e.g. large stones, shells and plant pieces) was removed, the sediment was dried at 90°C to constant weight (to the nearest 0.1 mg), and was finally burnt (at 500°C for 5 h). After reweighing, the organic content was expressed as % loss-on-ignition.

Algal shading. The shading of the farmed algae was estimated using a QSI 140B Integrating Quantum Solar Irradiance meter (Biospherical Instruments) with a 4π

sensor. Since the required water depth limited the number of estimations that could be performed each day, measurements were conducted over 3 consecutive days at noon ± 2 h during returning spring tide (water depth = 0.85 ± 0.1 m). To minimize effects of time, the measurements were equally divided per treatment and day. Irradiance in the F treatment plots was estimated both directly underneath the algal canopy (Fu: farm under), and at the same height above the bottom but between the algal monelines (Fb: farm between), with all measurements conducted in separate plots. In the control treatments, measurements were conducted at the same height above the bottom in the centre of the plot. The surface irradiance was estimated before and after each bottom measurement period, and was used to calculate the transmittance (% surface irradiance reaching the bottom) for each plot (n = 6).

Data analysis. Treatment effects were tested using 1-way ANOVAs, except for (1) epiphyte cover which was tested using a 2-way ANOVA (with 'treatment' and 'leaf side' as fixed factors) and (2) changes in above-ground seagrass biomass between Days 15 and

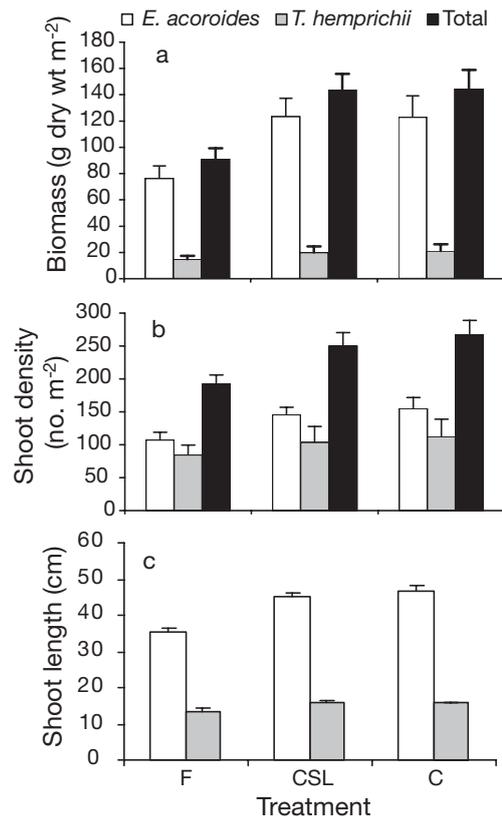


Fig. 1. *Enhalus acoroides*, *Thalassia hemprichii* and both species combined. (a) Above-ground biomass, (b) shoot density and (c) shoot length in experimental plots after 11 wk (n = 19, mean + SE). F: farm; CSL: stick-and-line control; C: control

75, which were separately tested for each of the 3 treatments using paired *t*-tests.

The shading and epiphyte cover data were arcsine-transformed prior to analysis. *A priori* assumptions of homogeneity of variances were tested using Cochran's *C*-test, and when assumptions were not met the data was transformed ($\log x + 1$). Significant main effects were further analyzed using Tukey's Honestly Significant Difference (HSD) post hoc test. If ANOVA assumptions could not be met after transformations, the nonparametric Kruskal Wallis Median Test was used. Post hoc analyses were then performed using the multiple comparisons procedure.

When separately testing effects on abundance of the 3 specific epifauna taxa (sea urchins, sponges and sea anemones) and leaf litter biomass of *Eucheuma acoroides*, *Thalassia hemprichii* and *Thalassodendron ciliatum*, significance levels were adjusted following the sequential Bonferroni method (Holm 1979). Unless stated otherwise, significance levels were set at $\alpha = 0.05$.

RESULTS

Algal growth

The DGR of *Eucheuma denticulatum* was $2.3 \pm 0.12\%$ (mean ± 1 SE). This value is lower than the 7 to 10% reported in the older literature (e.g. Pettersson-Löfquist 1995), but falls within the range of more recent estimations. If, however, it is lower than the normal DGR, this only makes our estimations of farm effects conservative compared to those occurring in actual seaweed farms (see 'Discussion').

Seagrasses

At the end of the experiment, F treatment plots had on average 36 and 37% lower total above-ground biomass of seagrass than controls (Tukey's HSD: $p = 0.01$ and 0.009 for CSL and C, respectively) (Table 1, Fig. 1a). This pattern was similar for *Enhalus acoroides*, where the biomass was 38% lower than in both controls (Tukey's HSD: $p = 0.044$ and 0.047 for CSL and C, respectively; Table 1); in contrast, *Thalassia hemprichii* biomass was unaffected (Table 1). Between Days 15 and 75, the above-ground biomass in the F treatment was constant ($t = 1.04$; $p = 0.31$), whereas it increased by 67% in CSL ($t = 5.71$; $p < 0.001$) and 48% in C ($t = 3.89$; $p = 0.001$) (Fig. 2). The increase probably reflects normal seasonal fluctuations of *E. acoroides* (e.g. Erfteimeijer & Herman 1994).

Total shoot density (Fig. 1b) in F treatment plots was 37% lower than in controls (Table 1) (Tukey's HSD: $p =$

Table 1. Results of 1-way ANOVAs for effects of seaweed farming on seagrass biomass, shoot density and shoot length (for total seagrass, *Enhalus acoroides* and *Thalassia hemprichii*), and total aerial above-ground production of *E. acoroides* over 11 wk ($n = 19$); *p*-values in **bold** indicate significant differences ($p < 0.05$)

Source	df	MS	F	p
Biomass				
Total	2	17523.9	6.31	0.003
<i>E. acoroides</i>	2	13883.9	4.01	0.023
<i>T. hemprichii</i>	2	23.08	0.22	0.53
Shoot density				
Total	2	11216.85	8.66	<0.001
<i>E. acoroides</i>	2	12068.02	3.73	0.030
<i>T. hemprichii</i>	2	3845.90	0.41	0.666
Shoot length				
<i>E. acoroides</i>	2	722.07	22.14	<0.001
<i>T. hemprichii</i>	2	33.79	5.55	0.007
Production				
<i>E. acoroides</i>	2	16721	5.40	0.007

0.001 and 0.003 for CSL and C, respectively). For *Enhalus acoroides* there were 30% less shoots than in C treatment plots (Tukey's HSD: $p = 0.034$) but no less than in CSL treatments (Tukey's HSD: $p = 0.103$). For *Thalassia hemprichii*, no effect was detected (Table 1).

The shoot length was also lower in farm plots (Table 1, Fig. 1c): shoots of *Enhalus acoroides* were 25% shorter (Tukey's HSD: $p < 0.001$, both controls) and *Thalassia hemprichii* 15% shorter compared to those in control plots (Tukey's HSD: $p = 0.010$ and 0.026 for CSL and C, respectively).

Finally, above-ground production of *Enhalus acoroides* over the 11 weeks was 30% lower in farm plots than in either control treatment (Tukey's HSD: $p = 0.04$ and 0.008 for CSL and C, respectively) (Table 1).

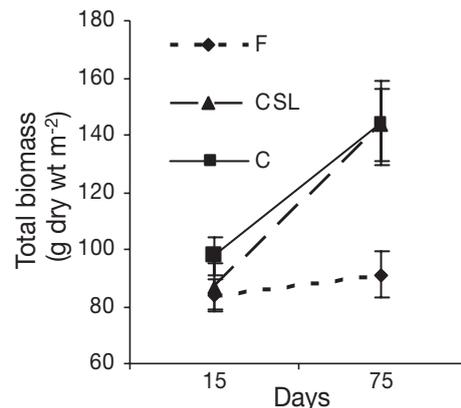


Fig. 2. *Enhalus acoroides* and *Thalassia hemprichii*. Total above-ground seagrass biomass in experimental plots after 15 and 75 d ($n = 19$, mean ± 1 SE). F: Farm; CSL: stick-and-line control; C: control

Table 2. Results of 2-way ANOVAs for effects of seaweed farming (Treatment) and Leaf side on percent epiphyte cover of *Enhalus acoroides* and *Thalassia hemprichii* (n = 19); p-values in **bold** indicate significant differences (p < 0.05)

Source	df	MS	F	p
<i>E. acoroides</i>				
Treatment (T)	2	956	3.14	0.046
Leaf side (L)	1	6340	20.87	<0.001
T × L	2	381.2	1.25	0.289
<i>T. hemprichii</i>				
Treatment (T)	2	2575	5.89	0.003
Leaf side (L)	1	4.55	0.01	0.918
T × L	2	156	0.35	0.35

Epiphyte cover

Epiphyte communities on both *Enhalus acoroides* and *Thalassia hemprichii* leaves were dominated by encrusting coralline and filamentous algae. After 60 d, there was an F treatment effect on leaves of *E. acoroides* (p = 0.047) (Table 2, Fig. 3a), which, although non-significant in the post hoc analyses (p = 0.07 and 0.09 for CSL and C, respectively), showed that the F treatment reduced epiphyte cover by 25% (pooling both leaf sides) compared to control treatments CSL and C. Further, epiphyte cover on the inside of *E. acoroides* leaves was 40% lower (pooling all 3 treatments) than on the outside (Tukey's HSD: p = 0.0001) (Table 2), a pattern that sometimes occurs because the outside can be more exposed to settlement of epiphyte spores (Short & Coles 2001 and references therein).

On leaves of *Thalassia hemprichii* (Fig. 3b) there was a 40% reduction in epiphyte cover (Tukey's HSD: p = 0.0077 and 0.033 for CSL and C, respectively) (Table 2), but no difference between leaf sides.

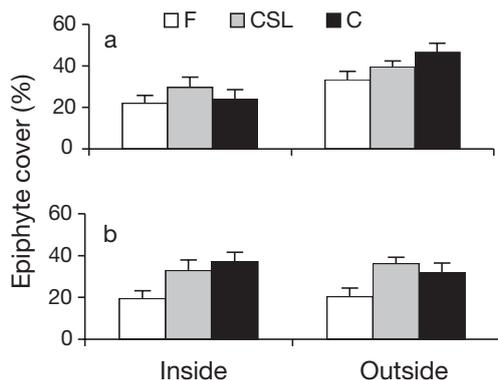


Fig. 3. Epiphyte cover on inside and outside of leaves of (a) *Enhalus acoroides* and (b) *Thalassia hemprichii* in experimental plots after 60 d (n = 19, mean + SE). F: farm; CSL: stick-and-line control; C: control

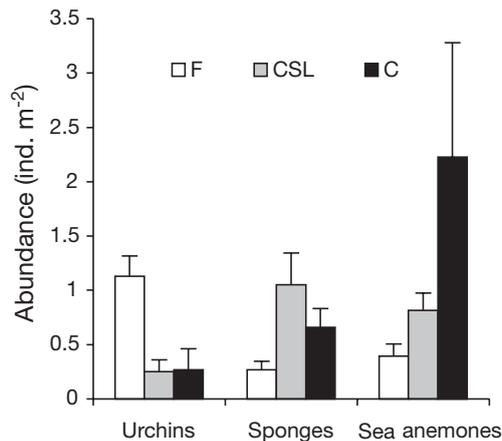


Fig. 4. Abundance of sea urchins, sponges and sea anemones in experimental plots after 11 wk (n = 17, mean + SE). F: farm; CSL: stick-and-line control; C: control

Epifauna abundance and diversity

A total of 16 epifauna species was observed in the plots, of which *Heteroxenia fuscescens* (Actinaria), *Spongia ceyloensis* (Porifera) and *Echinometra mathei* (Echinoidea) dominated (constituting 41, 23 and 20% of total abundance, respectively). In terms of major taxonomic groups, sea urchins (2 species), sponges (7 species) and sea anemones (2 species) contributed 98 to 100% of total abundance in each of the 3 treatments (Fig. 4). There were no effects on either total epifauna abundance or diversity (based on number of species, Shannon-Wiener H' and Simpson's Index D ; Table 3). When comparing abundances of the 3 dominating taxa separately, sea urchins were 4 times more common (Tukey's HSD: p < 0.001, CSL and C) (Table 3) and sponges 4 times less abundant in F treatment plots compared to CSL (Tukey's HSD: p = 0.01); however, there was no difference when compared to treatment C (Tukey's HSD: p = 0.17). For sea anemones, only a decreasing trend was noted (Kruskal Wallis' Median Test: p = 0.07).

Table 3. Results of 1-way tests (ANOVA and Kruskal Wallis' Median Test [K-W]) for effects of seaweed farming on epifauna community variables (n = 17); p-values in **bold** indicate significant differences (p < 0.05 or the adjusted counterpart)

Source	Test	df	MS	F	p
Abundance (no. ind.)	K-W	2	–	–	0.483
Diversity (no. species)	ANOVA	2	1.78	1.76	0.183
Shannon-Wiener (H')	ANOVA	2	0.57	3.04	0.057
Simpson's Index (D)	ANOVA	2	0.23	1.95	0.153
Sea urchins (no. ind.)	ANOVA	2	0.97	45.79	<0.001
Sponges (no. ind.)	ANOVA	2	20.58	5.13	0.010
Sea anemones (no. ind.)	K-W	2	–	–	0.07

Table 4. Results of 1-way ANOVA for effects of seaweed farming on accumulation of seagrass leaf litter (from *Enhalus acoroides*, *Thalassia hemprichii* and *Thalassodendron ciliatum*, and total), sediment organic matter (SOM) content and algal shading; p-values in **bold** indicate significant differences ($p < 0.05$, or the adjusted counterpart)

Source	Test	n	df	MS	F	p
Seagrass leaf litter						
Total	ANOVA	12	2	3.80	20.65	<0.001
<i>E. acoroides</i>	ANOVA	12	2	1.95	11.4	<0.001
<i>T. hemprichii</i>	ANOVA	12	2	7.35	7.13	0.003
<i>T. ciliatum</i>	ANOVA	12	2	4.29	18.97	<0.001
SOM content	ANOVA	19	2	2	0.13	0.872
Algal shading	ANOVA	6	3	3	24.8	<0.001

Accumulated seagrass leaf litter and SOM content

Around 3 times more leaf litter was accumulated in F treatment plots, and the pattern was similar when analyzing the biomass of the 3 seagrass species separately (*Enhalus acoroides*, *Thalassia hemprichii* and *Thalassodendron ciliatum*) (Tukey's HSD: $p < 0.001$ for all comparisons) (Table 4, Fig. 5). Interestingly, dead leaves of *Thalassodendron ciliatum*, which did not grow in the study site, constituted 50, 41 and 34 % of total leaf litter biomass in treatments F, CSL and C, respectively.

No effect on SOM content could be detected: this was approximately 3.5 % in all treatments (Table 4) and was within the range of values reported by Eklöf et al. (2005).

Algal shading

At the end of the study, the farmed algae strongly shaded seagrasses directly underneath the monolines (Tukey's HSD: $p < 0.001$ for all comparisons) (Table 4), with only 3.6 % of surface light penetrating to the bottom (Fig. 6). However, the algal canopy was not dense or wide enough to shade the seagrasses between the monolines (Tukey's HSD: $p = 0.13$ for both comparisons).

DISCUSSION

Effects of farming

The results of this study clearly demonstrate that off-bottom seaweed farming affects seagrass above-ground biomass and production negatively, and thereby validates previously observed patterns (Eklöf

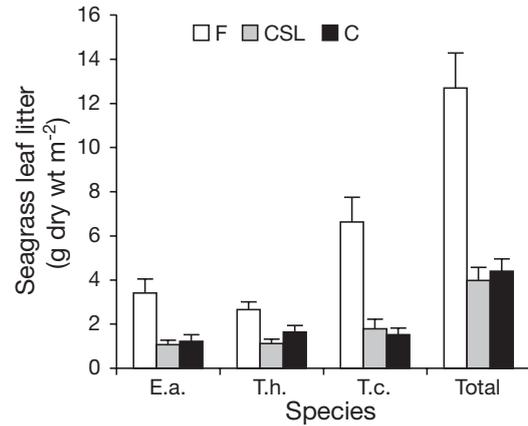


Fig. 5. Accumulated seagrass leaf litter in experimental plots after 11 wk, per species and in total ($n = 12$, mean + SE). E.a.: *Enhalus acoroides*; T.h.: *Thalassia hemprichii*; T.c.: *Thalassodendron ciliatum*; Total: all species combined; F: farm; CSL: stick-and-line control; C: control

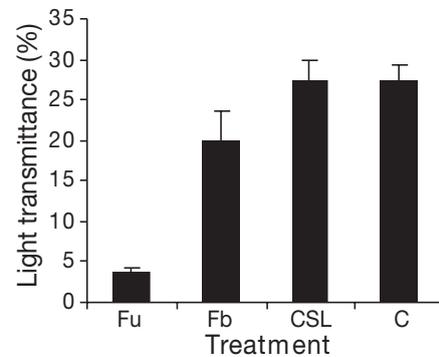


Fig. 6. Algal shading (% surface light reaching leaf canopy) in experimental plots after 11 wk ($n = 6$, mean + SE). Fu: farm treatment under algae; Fb: farm treatment between algae; CSL: stick-and-line control; C: control

et al. 2005). Given the constant biomass in farm plots over time compared to the 40 % increase in control plots, the farming effect was actually represented by a lack of potential biomass increase, rather than by an actual decrease. In a longer time perspective, which includes natural fluctuations in seagrass biomass, this will ultimately result in a decrease in total biomass (Eklöf et al. 2005). Since no manual removal of shoots was conducted, farming-related disturbances were minimized, and there were no differences between the 2 control treatments (CSL and C); we conclude that indirect or direct effects of the farmed algae caused the observed pattern.

First, the algal DGR should roughly indicate whether the increase in algal biomass in the experimental plots over time, and thereby the farming effects, are of the same magnitude as those in the actual seaweed farms. The experimental algal bio-

mass increased by 2.3% d⁻¹, which is lower than the 7 to 10% previously reported for *Eucheuma denticulatum* (Pettersson-Löfquist 1995). However, these figures were recorded more than a decade ago in other areas, and since then the growth rate of both *E. denticulatum* and *Kappaphycus alvarezii* has declined, possibly due to epiphytism (Shunula 1996); a study conducted in 1998 reported rates of 5 and 3.3% growth d⁻¹ for *E. denticulatum* and *K. alvarezii*, respectively (Mtolera 2003). In addition, the tsunami that followed the earthquake north of Indonesia on 26 December 2004 caused substantial loss of seaweed biomass in both experimental farm plots and seaweed farms located in the bay (J. Eklöf pers. obs.), and since the DGR was based on initial and final biomass, any losses occurring during the study period will result in a lower average DGR. In conclusion, it is possible that the growth rate in the experimental plots may have been somewhat lower than that normally achieved. However, this only means that the effects in real farms, where the DGR could be higher, may be more substantial.

The cause(s) of negative effects on seagrasses due to the presence of farmed algae were not explicitly tested, but based on the results and additional observations we identify 3 probable mechanisms. First, the farmed algae shaded the seagrasses, with only 3.6% of surface light reaching underneath the algal canopy. Seagrass growth rates, shoot density and biomass are negatively affected by shading (e.g. Grice et al. 1996), e.g. due to macroalgal mats (e.g. Hauxwell et al. 2001). Thus, shading is probably a strong contributor to the observed effects. The degree of shading probably increases gradually with the build-up of algal biomass, suggesting that effects should be strongest at the end of a farming cycle. Second, *Enhalus acoroides* leaves were frequently found entangled in the farmed algae, and thereby became fully exposed during low water spring tides. This seemed to cause a brownish discoloration of the upper third of many leaves, after which they became fragile. As daylight tidal exposure is known to cause such 'leaf burning' with a subsequent loss of biomass (Erftemeijer & Herman 1994), we conclude that emergence stress probably contributed to the observed effects. Third, discovery of broken-off leaves entangled in the farmed algae, attached leaves completely buried in the sediment and visual observations of algae moving in a 'circular' motion with the waves (J. Eklöf pers. obs.) suggest that mechanical abrasion by the algae (noted by e.g. Ólafsson et al. 1995, Eklöf et al. 2005), is a third likely contributor. In addition, a fourth factor previously suggested is allelopathy: the farmed algae produce potentially toxic hydrogen peroxide when stressed by the presence of seagrasses (Collén et al. 1995, Mtolera

et al. 1995). However, the exudates from the farmed algae did not affect meiofauna in laboratory mesocosms (Ólafsson et al. 1995), and the continuous exchange of water in real seaweed farms probably diminishes the possibility of effects even further. Hence, we regard allelopathy as a possible but not major contributor.

The relative absence of effects on *Thalassia hemprichii* (besides the 15% decrease in shoot length) was not further investigated, but can probably be accounted for by the following mechanisms. First, the negative effects on *Eucheuma acoroides* shoot length and density could actually have benefited the more shade-sensitive *T. hemprichii* (Bach et al. 1998) by reducing interspecific competition for sunlight. Together with the shading imposed by the farmed algae, each individual shoot may have received the same net amount of light and thereby maintained a physiological status quo. Second, *T. hemprichii* is highly resilient to emergence stress (Stapel et al. 1997). Third, the shoots are on average 3 times shorter than those of *E. acoroides* (Fig. 1c), and are thus less likely to be exposed to air and suffer from 'leaf burning'.

Besides the effects on seagrasses, seagrass epiphytes and larger epifauna were also negatively affected by the F treatment. The lower cover of epiphytes can be accounted for in 3 ways. First, the observed decrease in seagrass shoot length of both species was probably due to breakage of fragile leaf tips, i.e. the section of a leaf where most epiphytes are attached, thus resulting in lower epiphyte cover. Second, the suggested mechanical abrasion by the farmed algae could have scraped off encrusting coralline algae. A similar mechanism has been described for *Thalassia testudinum* in Florida (Irlandi et al. 2004), where algal mats scrape off epiphytes. Third, the observed shading by the farmed algae is likely to affect the growth and abundance of all autotrophs in the farmed plots, including epiphytic algae that constituted a substantial proportion of the epiphytes on the leaves.

We also demonstrated farm effects on the large epifauna (>1 cm). The lack of effects on total abundance and diversity, which contrasts previous findings (e.g. Russell 1983, Bergman et al. 2001), is probably accounted for by the relative short term of this study (11 wk), where the decrease of one structurally important habitat component (seagrass shoots) compared to controls was compensated for by the addition of another (farmed algae). However, the abundance of sea urchins was 4 times higher in farm plots compared to controls. Around 95% of the urchins encountered were *Echinometra mathei*, a potential grazer of *Eucheuma denticulatum* (e.g. Bryceson 2002). This suggests that the urchins were attracted to the farm plots by a potential food source, and it cannot be ruled

out that the 3-dimensional structural complexity of the algae also provided shelter.

The abundance of sponges was 4 times lower in F treatment plots compared to CSL plots, but was not lower than in C plots ($p = 0.17$), and there was a similar non-significant trend for sea anemones. Hence, these results are inconclusive and require further investigation. Should the trends actually represent negative effects on the abundance of these 2 taxa, this could be due to direct physical disturbance by the algae or to habitat alterations, e.g. decreased food supply by altered micro-currents. It should be noted that the deliberate exclusion of highly mobile and small (<1 cm) organisms limits the extrapolation of our results to the whole epifaunal community. In fact, algal mats in seagrass beds can increase abundance of many mobile organisms e.g. crustaceans (Holmquist 1997) and fish (Adams et al. 2004). However, the aim of this study was to specifically investigate effects on larger and slow-moving epifauna species, due to their local importance for invertebrate collection (de la Torre-Castro & Ronnback 2004).

The substantial increase in accumulated seagrass leaf litter underneath the farmed algae was probably due to an accumulation of broken-off leaf tips, and to a minor extent to the entrapment of leaves that originated from outside the farmed plots. Whether this increase in itself has any effect requires further investigation, but a greater amount of leaf litter is likely to increase microbial activity (Peduzzi & Herndl 1991) and thereby stimulate seagrass growth. However, it could simultaneously decrease oxygen levels within sediments and contribute to decreased light influx, and thus negatively affect the production of new seagrass shoots.

There was no effect on SOM content, which contrasts with previous findings where seagrass beds with seaweed farms had approximately 30% lower values than those without (Eklöf et al. 2005). Since sediment deposition rates and SOM content is high both within seagrass (Gacia et al. 1999) and macroalgal canopies (Romano et al. 2003), we suggest that the loss of one sediment-trapping structure (seagrass canopy) was compensated for by the addition of another (farmed algae), resulting in a net zero loss of sediment trapping. Over a longer time period, the accumulated leaf litter (not included here in the SOM samples) could increase SOM content when the tissue is decomposed. Again, this effect could be compensated for by an increased thinning of the seagrass canopy. There is probably a 'threshold' limit of seagrass canopy loss, beyond which the farmed algae cannot compensate and SOM content is decreased. Given the temporal scale of this study, we can only conclude that this limit lies beyond the effects on seagrasses observed here.

Implications for ecosystem structure and function

Since seagrasses in real seaweed farming areas are also subjected to other farming-associated disturbances (e.g. manual removal of shoots, trampling, boat moorings), and since there is a great difference in scale—experimental plots covered 3.75 m² for 11 wk, whereas farms cover several km² for decades—the magnitude of effects is probably much greater than shown in this study. After more than a decade of farming, seaweed farms in Chwaka had on average a 15 to 20% cover of seagrasses (Eklöf et al. 2005). Since this figure also includes remnant patches between plots, the actual cover underneath farmed plots was much lower. This undoubtedly affects the habitat structural complexity, and although the farmed algae seem to counter-balance part of this change (Bergman et al. 2001, Eklöf et al. 2006), it will certainly affect the structure of associated communities (Bergman et al. 2001, Eklöf et al. 2005, this study). For some taxa, e.g. fish, it is possible that these effects are further accentuated if farming activities are stopped and the algae are removed (Eklöf et al. 2006). Some of the organisms that are negatively affected by farming contribute to important ecological functions within and outside farms. For instance, the abundance of lucinid bivalves, which indirectly benefit seagrasses due to their ability to reduce levels of toxic hydrogen sulfide in sediments (Barnes & Hickman 1990), was several orders of magnitude lower in seagrass beds with seaweed farms than in those without (Eklöf et al. 2005). Furthermore, the presence of *Kappaphycus alvarezii* on Hawaiian coral reefs decreased fish herbivore control of the invasive macroalgae *Dictyosphaeria cavernosa* because the former was a preferred food source (Stimson et al. 2001). These 2 examples illustrate the possibility of indirect implications for ecosystem functioning, not only within but also outside farms.

Another equally important function of seagrass beds that is likely to be affected by farming is primary production. Our results show a 30% decrease in production of *Enhalus acoroides*, while total production within farms (in terms of both g C and biomass production per time) will probably increase due to the rapid growth of farmed algae (Zemke-White & Smith 2006). However, their contribution to the food web is restricted to minor grazing by herbivores (e.g. rabbit fish and urchins), and continuous harvest of algal biomass in combination with effects on both seagrasses and other primary producers (Eklöf et al. 2005, this study) instead suggest a net loss of nutrients. This could cascade up the seagrass food web: for instance, the epiphytized leaf tips (seemingly broken off by the farmed algae) constitute a primary food source for grazing fish (e.g. Zieman et al. 1984). Additionally, sec-

ondary production in adjacent unvegetated habitats, which normally receive substantial input of detritus and DOM (e.g. Hyndes & Lavery 2005), could be negatively affected.

A number of anthropogenic disturbances such as eutrophication (Duarte 1995), loss of epiphyte grazing (Hauxwell et al. 1998) or introduction of exotic species (Dumay et al. 2002) can indirectly cause seagrass communities to shift from seagrass to algal dominance, which alters not only associated community structure (e.g. Deegan et al. 2002) but sometimes even the production of associated ecological goods such as fish. In areas with intensive and large-scale seaweed farming on seagrass beds, the loss of seagrass biomass in combination with the presence of large biomasses of farmed algae could in a way be considered an analogous community shift, with possible implications for the ecological goods and services produced. However, the lack of reliable information on pre-farming conditions (i.e. the extent of seagrasses prior to the establishment of seaweed farms on Zanzibar), and difficulty in separating direct and indirect effects of seaweed farming from those of other activities (e.g. destructive fishing), currently makes it difficult to extrapolate the findings of this and other studies to assess the net effects of seaweed farming on seagrass ecosystems and their production of ecological goods and services in Zanzibar. However, another study that used local 'madema' fish traps in the same area showed that fish catches in seaweed farms differed from catches in a seagrass bed without seaweed farming and an adjacent sand bank (Eklöf et al. 2006). This could be important because fisheries constitutes the primary livelihood option in many coastal areas e.g. Chwaka Bay (de la Torre-Castro & Ronnback 2004). Interestingly, the farmed algae themselves attracted certain species, which seemed to counter-balance effects of seagrass loss. Undoubtedly, this is a complex and important issue that requires more investigation.

When discussing ecological effects of seaweed farming, a relevant aspect yet to be addressed is how long any negative effects will remain if farms are removed. A crucial factor is probably the scale of the disturbance, i.e. the intensity and duration of farming. According to local seaweed farmers in Chwaka Bay, seagrasses can partially recover in certain areas during periods when farming is not conducted (de la Torre-Castro & Jiddawi 2005). Patches of seagrasses remaining in and between farm plots observed in 2 seaweed farms in the area (Eklöf et al. 2005) would probably contribute to a more rapid seagrass recovery if farming ceases. However, the different responses of the 2 species in this study suggest that farming in multispecific beds could affect competitive interactions between different seagrass species, perhaps facilitating the domi-

nance of those species less sensitive to farming, here *Thalassia hemprichii*. Despite the fact that seagrasses per se still remain, implications could still persist; for instance, seagrass beds dominated by *T. hemprichii* have a lower fish abundance than those dominated by *Enhalus acoroides* (Nakamura & Sano 2004). If farming is so intense that all seagrasses eventually disappear, finer sediment fractions will most likely erode, which increases turbidity and could further hamper possible recovery. In such cases of total seagrass loss, recovery may be very slow to virtually non-existent (Holmquist 1997, Hauxwell et al. 2001).

Management suggestions

Although the present short-term study and a previous study that assessed differences after more than a decade of farming (Eklöf et al. 2005) both showed negative effects on seagrasses of seaweed farming, seagrass still remained within the farming area, probably because seaweed farming on Zanzibar is currently conducted at a rather limited scale. Hence, it should still be seen as a strong option compared to other more destructive forms of aquaculture, e.g. intensive shrimp farming. However, farming on seagrass beds or other important coastal habitats should be avoided or restricted, e.g. by limiting the scale of farming. Smaller farms with less algal biomass per area, perhaps rotated between different areas over time, are probably preferable from a seagrass point-of-view, and could also decrease the risk of algal disease outbreaks such as the bacterial, stress-induced infection known as the 'ice-ice' syndrome (Collén et al. 1995). Leaving strips of seagrasses between farms plots could reduce the risk of total seagrass loss and speed up recovery once a farm is abandoned. Also, seagrasses within or near farms could in fact stimulate algal production by making sediment micronutrients available (Mtolera 2003). This would provide a direct economical incentive for active seagrass conservation, but remains to be thoroughly investigated before taken as a fact. Another more costly option is the implementation of alternative farming methods where algae are suspended higher above the substratum e.g. by floating long-lines (Hurtado & Agbayani 2002) or rafts. The impact of shading and direct physical interactions with seagrasses are probably less likely using such methods, but should be experimentally investigated before large-scale implementation.

Today, seaweed farming is mainly conducted by low-paid farmers with little or no capital available, and declining seaweed prices as well as a low demand for *Eucheuma denticulatum* has caused many farmers on Zanzibar to abandon the activity. Hence, a change in

production methods will ultimately require economical support from the international seaweed companies, NGOs or local governments promoting the activity, which is now generally lacking. Metaphorically speaking, tropical open-water seaweed farming seems to be at a crossroads. At present, low seaweed prices indirectly diminish possible environmental side-effects but mean low socio-economical sustainability. If, however, prices or production rates increase, there is a potential for large-scale expansion of seaweed farming in many tropical coastal areas like Zanzibar, similar to that seen in South-East Asia during the past 30 years. If left uncontrolled, such a development could in the worst case contribute to large-scale ecosystem changes (i.e. extensive seagrass loss, or spread of farmed algae to adjacent coral reefs) with implications for the production of several ecological goods and services. Irrespective of which direction seaweed farming takes, there is a clear need for holistic and adaptive seaweed farming management. This includes the following: choosing species and methods based on the prerequisites of each site; maintaining farming intensity within the carrying capacity of the local environment; acknowledging seaweed farming as an integrated component of the tropical seascape while continuously assessing potential environmental effects across scales; and striving for increased socio-economic sustainability. In this way, seaweed farming will come closer to becoming a truly sustainable form of aquaculture.

Acknowledgements. We thank M. A. Manzi, R. Mcha, A. Mcha, U. A. Makame, M. M. Mwadini, C. A. Mahawi and K. U. Said for field and laboratory assistance; M. Kyewalyanga (Institute of Marine Science, University of Dar es Salaam) for logistic support; P. O. Moksnes for statistical advice; A. Blomberg for lodging; and S. Sjöling, S. Wikström, A. Norström, I. Bryceson, R. Elmgren, S. Seppälä, E. Bonsdorff and 3 anonymous referees for valuable comments on earlier versions of this article. Financial support was provided by the Knut and Alice Wallenberg foundation to J.S.E., the Anna Whitlock foundation to R.H. and Sida/SAREC to N.K.

LITERATURE CITED

- Adams AJ, Locascio JV, Robbins BD (2004) Microhabitat use by a post-settlement stage estuarine fish: evidence from relative abundance and predation among habitats. *J Exp Mar Biol Ecol* 299:17–33
- Ask EI (2001) Creating a sustainable commercial *Eucheuma* cultivation industry: the importance and necessity of the human factor. In: Chapman ARO, Anderson RJ, Vreeland VJ, Davison IR (eds) 17th Int Seaweed Symposium. Oxford University Press, Oxford, p 13–18
- Ask EI, Batibasaga A, Zertuche-Gonzalés JA, de San M (2001) Three decades of *Kappaphycus alvarezii* (Rhodophyta) introduction to non-endemic locations. In: Chapman ARO, Anderson RJ, Vreeland VJ, Davison IR (eds) 17th Int Seaweed Symposium. Oxford University Press, Oxford, p 49–57
- Bach SS, Borum J, Fortes MD, Duarte CM (1998) Species composition and plant performance of mixed seagrass beds along a siltation gradient at Cape Bolinao, the Philippines. *Mar Ecol Prog Ser* 174:247–256
- Barnes PAG, Hickman CS (1990) Lucinid bivalves and marine angiosperms: a search for causal relationships. In: Walker DI, Wells FE (eds) The seagrass flora and fauna of Rottnest Island. Western Australia Museum, Perth, p 215–238
- Bergman KC, Svensson S, Ohman MC (2001) Influence of algal farming on fish assemblages. *Mar Pollut Bull* 42: 1379–1389
- Bryceson I (2002) Coastal aquaculture developments in Tanzania: sustainable and non-sustainable experiences. *Western Indian Ocean J Mar Sci* 1:1–10
- Collén J, Mtolera M, Abrahamsson K, Semesi A, Pedersen M (1995) Farming and physiology of the red algae *Eucheuma*: growing commercial importance in East Africa. *Ambio* 24:497–501
- Deegan LA, Wright A, Ayvazian SG, Finn JT, Golden H, Mereson RR, Harrison J (2002) Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquat Conserv Mar Freshw Res* 12:193–212
- de la Torre-Castro M, Jiddawi N (2005) Seagrass-related research and community participation: 'Fishermen, fisheries and seagrasses'. Participatory workshop, 6–11 Sep 2004, Chwaka Bay, Zanzibar. WIOMSA book series no. 3. Western Indian Ocean Marine Science Association, Zanzibar
- de la Torre-Castro M, Ronnback P (2004) Links between humans and seagrasses—an example from tropical East Africa. *Ocean Coast Manag* 47:361–387
- Duarte CM (1995) Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41:87–112
- Dumay O, Fernandez C, Pergent G (2002) Primary production and vegetative cycle in *Posidonia oceanica* when in competition with the green algae *Caulerpa taxifolia* and *Caulerpa racemosa*. *J Mar Biol Assoc UK* 82:379–387
- Eklöf JS, de la Torre-Castro M, Adelsköld L, Jiddawi NS, Kautsky N (2005) Differences in macrofaunal and seagrass assemblages in seagrass beds with and without seaweed farms. *Estuar Coast Shelf Sci* 63:385–396
- Eklöf JS, de la Torre-Castro M, Rönnbäck P, Nilsson C (2006) How do seaweed farms influence fishery catches in a seagrass-dominated setting in Chwaka Bay, Zanzibar? *Aquat Living Resour* 19:137–147
- Ertfemeijer PLA, Herman PMJ (1994) Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. *Oecologia* 99:45–59
- Gacia E, Granata TC, Duarte CM (1999) An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. *Aquat Bot* 65: 255–268
- Green EP, Short FT (2003) World atlas of seagrasses, Vol 1. University of California Press, Berkeley, CA
- Grice AM, Loneragan NR, Dennison WC (1996) Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. *J Exp Mar Biol Ecol* 195:91–110
- Gullström M, de la Torre-Castro M, Bandeira SO, Björk M, Dahlberg M, Kautsky N, Rönnbäck P, Öhman MC (2002) Seagrass ecosystems in the Western Indian Ocean. *Ambio* 31:588–596
- Gullström M, Lundén B, Bodin M, Kangwe J, Öhman MC, Mtolera M, Björk M (2006) Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. *Estuar Coast Shelf Sci* 67:399–408

- Haglund K, Lindstrom J (1995) The potential use of macroalgae for removal of nutrients from sewage water in East Africa. *Ambio* 24:510–512
- Hauxwell J, McClelland J, Behr PJ, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 21:347–360
- Hauxwell J, Cebrian J, Furlong C, Valiela I (2001) Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82:1007–1022
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Holmquist JG (1997) Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. *Mar Ecol Prog Ser* 158:121–130
- Hurtado AQ, Agbayani RF (2002) Deep-sea farming of *Kappaphycus* using the multiple raft, long-line method. *Bot Mar* 45:438–444
- Hyndes GA, Lavery PS (2005) Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? *Estuar Coast Shelf Sci* 63:633–643
- Irlandi EA, Orlando BA, Biber PD (2004) Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Mar Ecol Prog Ser* 279:81–91
- Johnstone R, Ólafsson E (1995) Some environmental aspects of open water algal cultivation: Zanzibar, Tanzania. *Ambio* 24:465–469
- Lignell A, Ekman P, Pedersén M (1987) Cultivation technique for marine seaweeds allowing controlled and optimized conditions in the laboratory and on a pilot scale. *Bot Mar* 30:417–424
- Mtolera MSP (2003) Effects of seagrass cover and mineral content on *Kappaphycus* and *Euचेuma* productivity in Zanzibar. *Western Indian Ocean J Mar Sci* 2:163–170
- Mtolera MSP, Collén J, Pedersen M, Semesi AK (1995) Destructive hydrogen peroxide production in *Euचेuma denticulatum* (Rhodophyta) during stress caused by elevated pH, high light intensities and competition with other species. *Eur J Phycol* 30:289–297
- Nakamura Y, Sano M (2004) Comparison between community structures of fishes in *Enhalus acoroides*- and *Thalassia hemprichii*-dominated seagrass beds on fringing coral reefs in the Ryukyu Islands, Japan. *Ichthyol Res* 51:38–45
- Naylor RL, Goldburg RJ, Primavera JH, Kautsky N, and 6 others (2000) Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024
- Neori A, Chopin T, Troell M, Buschmann AH, Kraemer GP, Halling C, Shpigel M, Yarish C (2004) Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture* 231:361–391
- Ólafsson E, Johnstone RW, Ndaró SGM (1995) Effects of intensive seaweed farming on the meiobenthos in a tropical lagoon. *J Exp Mar Biol Ecol* 191:101–117
- Peduzzi P, Herndl GJ (1991) Decomposition and significance of seagrass leaf litter (*Cymodocea nodosa*) for the microbial food web in coastal waters (Gulf of Trieste, northern Adriatic Sea). *Mar Ecol Prog Ser* 71:163–174
- Pettersson-Löfquist P (1995) The development of open-water algae farming in Zanzibar: reflections on the socioeconomic impact. *Ambio* 24:487–491
- Rai LC, Kumar HD, Mohn FH, Soeder CJ (2000) Services of algae to the environment. *J Microbiol Biotechnol* 10:119–136
- Romano C, Widdows J, Brinsley MD, Staff FJ (2003) Impact of *Enteromorpha intestinalis* mats on near-bed currents and sediment dynamics: flume studies. *Mar Ecol Prog Ser* 256:63–74
- Rönnbäck P (2001) Mangroves and seafood production. The ecological economics of sustainability. PhD thesis, Stockholm University
- Rönnbäck P, Bryceson I, Kautsky N (2002) Coastal aquaculture development in eastern Africa and the Western Indian Ocean: prospects and problems for food security and local economies. *Ambio* 31:537–542
- Russell DJ (1983) Ecology of the imported red seaweed *Euचेuma striatum* Schmitz on Coconut Island, Oahu, Hawaii. *Pacific Sci* 37:87–107
- Short FT, Coles RG (eds) (2001) Global seagrass research methods, Vol 1. Elsevier Science, New York
- Shunula JP (1996) Epiphytes on farmed seaweeds in Zanzibar: is it a problem? *Window* 7:6
- Sievanen L, Crawford B, Pollnac R, Lowe C (2005) Weeding through assumptions of livelihood approaches in ICM: seaweed farming in the Philippines and Indonesia. *Ocean Coast Manag* 48:297–313
- Stapel J, Manuntun R, Hemminga MA (1997) Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. *Mar Ecol Prog Ser* 148:251–262
- Stimson J, Larned ST, Conklin E (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. *Coral Reefs* 19:343–357
- Zemke-White, WL, Smith JE (2006) Environmental impacts of seaweed farming in the tropics. In: Critchley AT, Ohno M, Largo DB (eds) World seaweed resources — an authoritative reference system. ETI BioInformatics, Wokingham, DVD-Rom
- Zieman JC, Iverson RL, Ogden JC (1984) Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Mar Ecol Prog Ser* 15:151–158

Editorial responsibility: Erik Bonsdorff (Contributing Editor),
Turku/Åbo, Finland

Submitted: November 10, 2005; Accepted: April 21, 2006
Proofs received from author(s): October 10, 2006