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Role of the source community for the recovery of seagrass associated meiofauna: a field colonisation experiment with seagrass mimics in Diani Beach, Kenya

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Seagrass communities are subject to frequent disturbances that can affect the associated fauna. Seagrass loss in Kenya has been mainly due to extensive grazing by the sea urchin *Tripneustes gratilla*, leading to habitat fragmentation. The challenge is whether the system can recover fully and function as before. Density, diversity and community structure of meiofauna were studied to evaluate the ability of the ecosystem to recover its associated fauna. Artificial seagrass mimics were planted in natural, replanted and bare seagrass patch types. The associated meiofauna was harvested at different colonisation time intervals (min. 2 days–max. 21 days). Significantly different meiofauna densities between the patch types and the colonisation days were found whereas the harpacticoid copepod densities were only significantly affected by colonisation time. Meiofauna densities on the seagrass mimics recovered quickly in all patch types, i.e. after four days of colonisation their densities were comparable to those on natural seagrasses, but they exhibited an unstable, cyclical pattern. Initial communities consisted mainly of opportunistic non-phytal taxa. Passive and active migrations were deduced for harpacticoid copepods. We recommend the ecosystem approach as seagrass-associated meiofauna (and copepods) responded relatively quickly to new substrates, providing the surrounding (source) communities remains undisturbed.

Keywords: disturbance, ecosystem functioning, harpacticoid copepods, meiofauna, seagrass beds

Introduction

Tropical seagrass beds form a complex and diverse ecosystem that supports a large variety of associated fauna and flora with a diversity of ecological characteristics (Hemminga and Duarte 2000). Notwithstanding this diversity, seagrass communities are subject to frequent anthropogenic and natural disturbances. In severe cases, overgrazing by, for example, sea urchins decimates entire seagrass meadows (Eklöf et al. 2008). These disturbances lead to alterations in vegetation complexity (Fonseca and Bell 1998, Seddon et al. 2000, De Troch et al. 2001), but also affect the associated fauna (Daudi et al. 2012). Such effects are often understudied and more focus has been on the recovery of the plants as this can be easily be observed and evaluated. However, understanding the recovery of associated fauna and flora is essential to evaluate the full recovery of the ecological functions of the seagrass ecosystem after disturbance, and hence the effect of restoration and conservation measures.

Seagrass loss has been reported in several sites along the Kenyan coast due to population explosions of sea urchins (especially *Tripneustes gratilla*) (Alcoverro and Mariani 2002). Overgrazing of seagrasses by sea urchins may be caused by reduced predation by fish such as trigger fish and wrasses (McClanahan and Shafir 1990). In the Diani Chale lagoon, up to half of the seagrass cover disappeared between 2001 and 2006; however, natural recovery has been reported in certain sites but not in all areas (JNU, unpublished data).

Conservation and restoration can be enhanced by transplantation of plants from natural seagrass beds (Paling et al. 2001). The success of seagrass transplantation has been examined to test the feasibility of seagrass rehabilitation for recolonisation and creation of new meadows (Paling et al. 2007). Different methods of transplantation, including seed sowing, single-shoot planting, shoot bundles, peat pot and plugs, and wire frames, have been tested (Fonseca et al. 1994, Orth et al. 1994, Short and Neckles 1999). Several attempts at seagrass transplantation have been successful with survival levels up to 90% (Paling et al. 2003). However, it is not easy to achieve transplantation on a large-scale and long-term basis due to the costly and time-consuming nature of these methods, hence protection and conservation of existing meadows is the most preferred action to take (Fonseca et al. 1994).

More research effort has been spent on seagrass transplantation and on the implementation of marine protected areas than on the restoration and conservation of the functions of seagrass ecosystems (Paling et al. 2001). To guarantee an optimal ecosystem functioning and full restoration, all components, including the seagrass associated flora and fauna, should be fully recovered and be conserved.

Removal of seagrass canopy and alterations to the density and canopy height are common experimental manipulations that have been used to assess effects of seagrass physical structure on faunal distribution and abundance (e.g. Edgar and Robertson 1992, Connolly 1995, Horinouchi and Sano 1999). However, the duration of a manipulative experiment could be limited by the growth rate of the seagrass. Therefore, artificial seagrass units that mimic the physical structure of natural meadows is a good option to take, especially when studying the colonisation of seagrass-associated fauna and epiphytic algae (Virnstein and Curran 1986, Edgar and Robertson 1992, Ceccherelli and Cinelli 1999, Kenyon et al. 1999, De Troch et al. 2005). Seagrass mimics provide flexibility in experimental designs as seagrass presence and other seagrass parameters can be easily manipulated, depending on the experimental requirements, in contrast to working with natural seagrass (Lee et al. 2001).

Knowledge of diversity patterns is important in understanding the organisation and functioning of organisms in an ecosystem and their interaction with the environment (Duarte 2000). Consequently, any loss of biodiversity may result in the loss of ecosystem functions and the several services that they provide to society (Constanza et al. 1997). Testing the link between biodiversity and ecosystem functions and services is therefore essential to understand the vulnerability of an ecosystem in order to choose the correct conservation measures (Tilman 1997).

The present study focuses on meiofauna, especially harpacticoid copepods, because they form an important link between primary producers and higher trophic levels (Klumpp et al. 1992, De Troch et al. 1998). They are found in high abundances in seagrass beds (Bell and Hicks 1991) and can actively migrate from sediments to the water column (Commito and Tita 2002). On account of their small size (passing through a 1 000 µm mesh but retained on a 38 µm sieve), high turnover rate, lack of large-scale larval dispersion, and sensitivity to environmental changes, they are considered a good proxy for monitoring the health of the environment (Kennedy and Jacoby 1999). Changes in meiofauna communities will inextricably be bound up with a modified energy transfer to higher trophic levels, and yet will affect the overall productivity of the seagrass ecosystem.

The main objective of the present study was to determine the recovery of biodiversity of meiofauna, with special emphasis on harpacticoid copepods, in tropical seagrass beds at Diani, Kenya. Sampling of natural seagrass and artificial seagrass mimics was used to evaluate recovery of associated fauna. Colonisation of meiofauna (at higher taxa) and harpacticoid copepods (at family level) on artificial seagrass mimics in natural, replanted and bare sites were investigated. The main hypothesis of our study was that the colonisation of seagrass leaves by meiofauna is strongly governed by the 'source' population and its substrate, i.e. the seagrasses where the meiofauna is associated with and originates from. More specifically, we hypothesised that natural seagrass beds, restored seagrass beds and bare sediment act differently as the source of meiofauna. Finally, we aimed to use the success of this recruitment process as a proxy for the health and the optimal functioning of the source community.

Material and methods

Sampling strategy

Attempts to transplant seagrasses in Kenya were done with varying degrees of success as harsh weather conditions during the inter-monsoon were often detrimental to the trials. The only site along the Kenyan coast where the majority of the transplants remained and transplantation was relatively successful was at Diani Beach. Consequently, the experiments were conducted at this site.

Sampling was conducted between 15 August and 6 September 2008. Diani Beach (4°21' S, 39°33' E) is situated approximately 72 km south of Mombasa on the south coast of Kenya and is separated from the main waterbody of the Indian Ocean by a fringing coral-reef platform. Along the Kenyan coast, this site had been most affected by overgrazing of sea urchins. Sampling was conducted while snorkelling at low tide in mean water depth of 0.7 m. *Thalassodendron ciliatum* is the dominant subtidal species at the site. Average shoot densities of *T. ciliatum* at the site were 280 shoots m^{-2} for the natural seagrass and 50 shoots m^{-2} for the replanted sites. Patch size was not determined for this study.

Meiofauna on T. ciliatum *leaves and in the sediment*

As a control for the colonisation experiment, epiphytic meiofauna on natural seagrass plants (*T. ciliatum*) were sampled in triplicate in natural patches of comparable shoot density. Samples were collected by placing plastic bags over the seagrass plants and cutting them at the base of the stem. An 8% $MgCl_2$ solution was added to the bags for 15 min in order to detach the meiofauna from the leaves prior to rinsing the leaves over 1 mm and 38 µm sieves with filtered seawater. The epiphytic samples were stored in 4% formaldehyde.

Polyvinyl chloride (PVC) cores (3.6 cm inner diameter, 10 cm^2 surface) were used to collect meiofauna from the sediment (benthic meiofauna) around the natural plants and in all areas where the mimics were planted. Sediment cores were sliced into three depth layers (0–1 cm, 1–2 cm and 2–5 cm) and preserved in 4% formaldehyde.

Both epiphytic and benthic control samples were collected at the end of the experiment, at day 21.

Artificial seagrass mimics

Seagrass mimics (plastic seagrasses, http://cgbiomodels.com/) were used to mimic small areas of *T. ciliatum* and to evaluate colonisation of associated fauna from different seagrass patches (see experimental design) towards the mimics. It should be noted that the mimics used here resembled *Thalassia hemprichii*, which has longer and narrower leaves compared to broader-leafed natural *T. ciliatum*. Previous studies have shown that leaf size had no significant effect on meiofauna densities (De Troch et al. 2005, Torres-Pratts and Schizas 2007). Each mimic plant consisted of four green leaves and one brown leaf, resembling natural fresh (green) and dead (brown) leaves respectively. The mimics were 35.7 cm wide (SE 2.3) and 0.8 cm long (SE 0.1). Total leaf length per mimic plant (five leaves) was 178.4 cm (SE 12.9) corresponding to an average plant surface area of 146.8 cm^2 (SE 17.3). Each

mimic sample consisted of four mimic plants (five leaves on each) grouped together as a cluster in order to reduce variability, according to the method of De Troch et al. (2005). The mimics were treated as spatially independent and were planted in the sediment by means of cable ties at three selected sites from the shore in the subtidal areas where *T. ciliatum* is known to be dominant.

Experimental design

Three sets of triplicated mimics were planted (Figure 1). The first set was planted in an area with transplanted seagrass (4°21'10.2'' S, 39°33'57.1'' E) about 200 m away from the beach where there were existing replanted seagrasses 'transplanted'. The replanted seagrasses were at this site for about one year, although most of them were lost during the inter-monsoon season (July 2008). The second set was planted (4°21'10.3'' S, 39°33'57.5'' E) about 12 m from the first set in a 'bare' area and the final set was planted (4°21'10.3'' S, 39°33'58.8'' E) about 36 m from the previous batch in an area with natural *T. ciliatum* (Figure 1).

Colonisation of meiofauna was investigated at six different time intervals (2, 4, 6, 10, 14 and 21 days) according to De Troch et al. (2005) (Figure 1). Seagrass mimics were planted in triplicates at the selected sites and harvested within each of the time intervals (Figure 1). Each replicate (4 × 5 leaves pooled) was spatio-temporally independent.

Harvesting was done by placing plastic bags over the mimics and cutting the cable ties near the bottom. The mimics were placed in plastic bags containing a small amount of water and sealed with rubber bands and brought to the boat. An 8% $MgCl_2$ solution was added to the bags for 15 min to detach the meiofauna from the leaves prior to rinsing the leaves over 1 mm and 38 µm sieves using filtered seawater. The epiphytic samples were stored in a 4% formaldehyde-freshwater solution.

Sample processing

Benthic samples were decanted 10 times over a 38 µm mesh sieve, centrifuged three times with Ludox (specific density 1.18) and stained with Bengal Rose. The epiphytic meiofauna samples were not centrifuged but directly stained with Bengal Rose. The meiofauna were counted and identified to the highest possible taxon level, based on Higgins and Thiel (1988). The first 100 copepods were collected at random from the samples, mounted *in toto* in glycerine slides and identified to family level (especially for harpacticoid copepods) under a stereomicroscope using identification keys by Boxshall and Halsey (2004) and Lang (1965) as well as original descriptions.

Data analyses

Factorial ANOVA was used to test for significant differences in

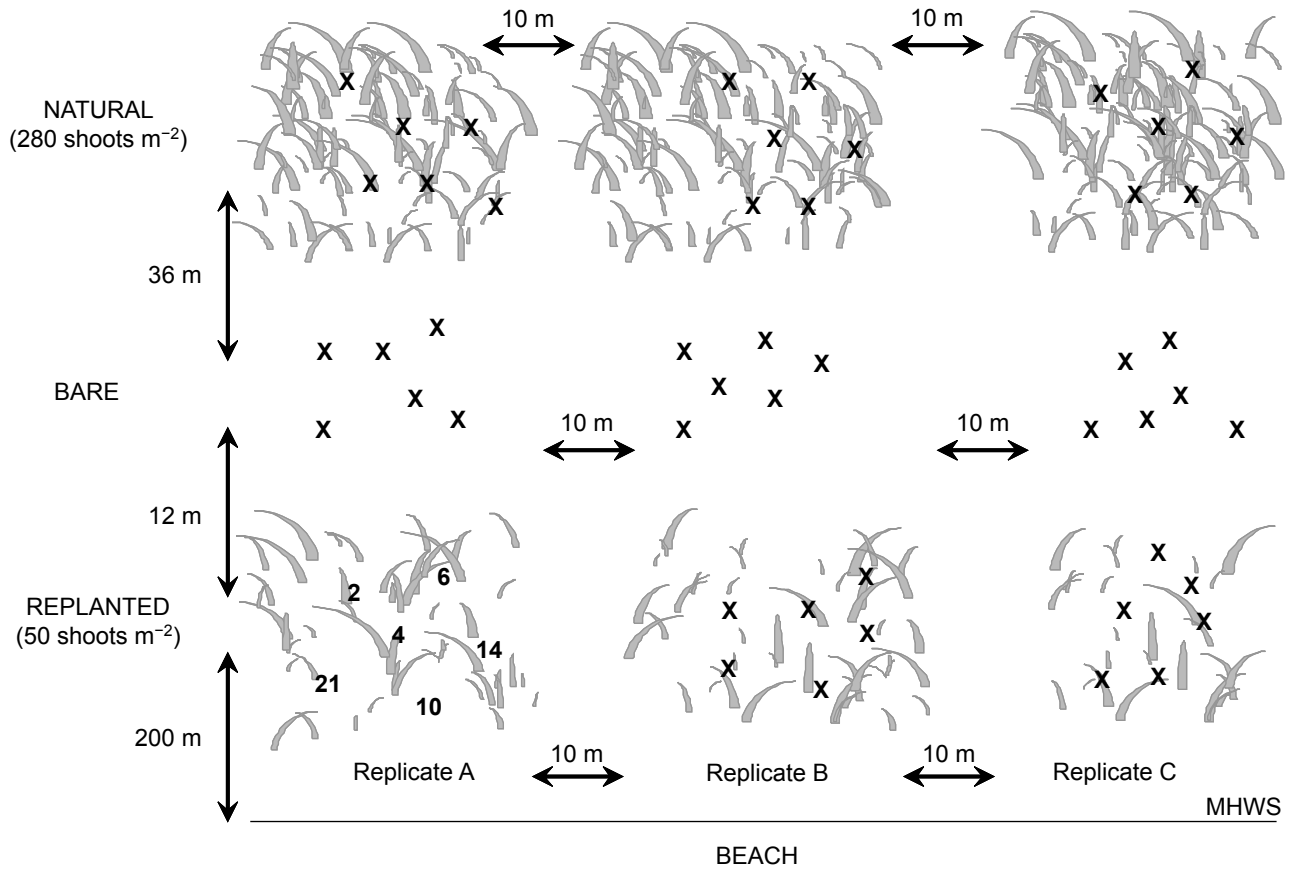

Figure 1: Experimental design. Mean high water at spring tide (MHWS) and numbers of days of collection (i.e. after 2, 4, 6, 10, 14 and 21 days of colonisation) are shown

densities and diversities of the fauna found on the mimics at the different sites (site) and on all harvesting days (time) using STATISTICA 8. Factorial ANOVA *post hoc* analysis was done using the Tukey HSD test. Levene's test was used to test for homogeneity of variances of the data and non-parametric tests were employed to test for differences between the benthic harpacticoid samples. The copepod community structure was analysed by means of multidimensional scaling (MDS) of fourth-root transformed densities in PRIMER 6 software based on Bray-Curtis similarity.

Diversity of epiphytic and benthic meiofauna (highest taxon level) and harpacticoids (family level) was expressed by means of Hill's indices N_0, N_1, N_2 and N_∞ (Hill 1973).

Results

Meiofauna density, composition and diversity

Meiofauna densities ranged between 5 and 97 ind. 100 cm^{-2} during the colonisation experiment (Figure 2). The densities of the epiphytic meiofauna were low at day 2 and increased towards day 4; however, they dropped at day 6 by a factor of three for all sites, and on day 10 increased again by a factor of 10 for those mimics planted within the natural seagrasses and doubled for both those in the replanted and bare sites. The densities stabilised for all sites on day 14 but on day 21 they reduced by a factor of 1.5 for the mimics in the bare and natural sites and by a factor of 6 for the mimics in the replanted sites. The highest densities for mimics in the bare and replanted sites were observed at day 4 whereas those in the natural sites peaked at day 10.

The natural seagrass species *T. ciliatum* was sampled once during the sampling period to compare their associated meiofauna densities with those on mimics and the average epiphytic meiofauna was 83 ind. 100 cm^{-2} (SE 21.1) (Figure 2). In comparison, the highest average meiofauna densities on the mimics at the replanted and bare sites were 76 and 96 ind. 100 cm^{-2} respectively at day 4 whereas the density on the mimics at the natural sites was 62 ind. 100 cm^{-2} at day 10. Meiofauna densities were on average higher on the natural seagrasses than on the seagrass mimics. There were significant differences ($p < 0.05$) in meiofauna densities as regards to colonisation time and site (Table 1).

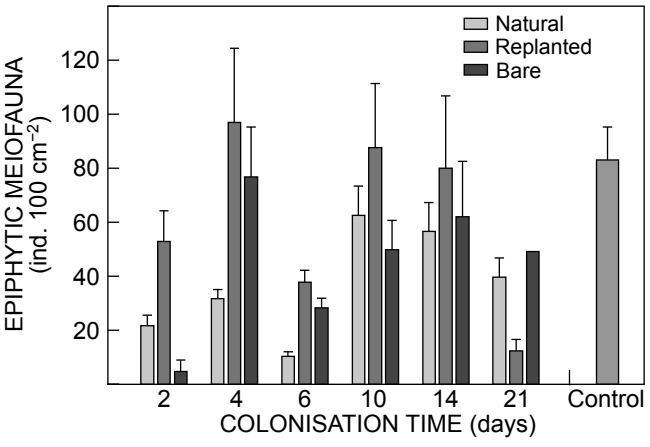

Figure 2: Total meiofauna densities on mimics at different colonisation days and on natural seagrasses. Error bars denote SE

A total of 21 meiofauna taxa was identified in the epiphytic and benthic samples. Initially (until day 4), nauplii dominated the meiofauna community except for the mimics in the bare sites. Later, the dominance shifted towards copepodites and adult copepods. Nematodes were the second most abundant meiofauna. On the mimics at the natural sites, the lowest relative abundance of nauplii was on day 6; relative abundance increased on days 10 and 14 and decreased towards the end of the experiment on day 21. On the mimics at the replanted and bare sites, the highest relative abundance of nauplii was recorded on day 4 (>50%) and this relative abundance reduced further towards day 21. The mimics in the natural seagrasses harboured larger copepod abundances (47%) relative to the other sites.

The diversity of epiphytic meiofauna (expressed as number of major taxa) was generally higher for the natural seagrasses (11) compared to the mimics (10). There were no significant differences in the Hill's diversity indices for the mimics for either site or colonisation time except for N_2 which showed a significant difference for the colonisation time (non-parametric tests, $p < 0.05$).

Benthic meiofauna densities ranged from 200 to 600 ind. 10 cm^{-2} in the top sediment layer (0–1 cm), from 377 to 705 ind. 10 cm^{-2} in the middle layer (1–2 cm) and from to 490 to 685 ind. 10 cm^{-2} in the lowest layer (2–5 cm). Meiofauna densities were high in the top sediment layer in the mimics at the bare site whereas the mimics at the replanted sites had the highest density in the deepest sediment layer (2–5 cm). The mimics at the natural sites had the highest meiofauna density at subsurface (1–2 cm). There were no significant differences in the benthic meiofauna densities ($p > 0.05$). Overall, the benthic samples were dominated by nematodes (65–87%). Hill's diversity indices did not show any statistical significant differences between mimics at different sites and sediment depth for benthic meiofauna.

Harpacticoid copepods

A total of 15 families of the order Harpacticoida was identified in the samples (Table 2). Cyclopoida and Calanoida were also present but were only identified to order level as they are mainly planktonic and are therefore not strongly associated with seagrass. Cyclopoid and calanoid copepods were generally dominant on mimics at all sites during initial colonisation (days 2 and 4). From day 6 onwards, harpacticoid copepods colonised the seagrass mimics and the cyclopoids and calanoids decreased in abundance.

Table 1: ANOVA results for meiofauna densities collected on seagrass mimics. Significant *p*-levels (<0.05) are indicated in bold

Factors	df	SS	MS	*F*	*p*
Intercept	1	4 003 893	4 003 893	154.1246	0.0000
Day	5	648 427	129 685	4.9921	**0.0016**
Site	2	187 271	93 636	3.6044	**0.0384**
Day × Site	10	294 661	29 466	1.1343	0.3677
Error	33	857 283	25 978		
Total	50	1 970 629			

There was a significant difference in copepod densities at the different sampling events (colonisation time) and the interaction between day number and site (two-way ANOVA, $p < 0.05$, Table 3). Densities of copepods increased from day 2 to day 4 for all mimics but declined at day 6 by a factor of 1.5. From day 10 onwards, densities increased again, by a factor of 1.5, and remained stable until day 21. However, copepod densities for the mimics at the replanted sites declined towards day 21 by a factor 2.5 (Figure 3).

Table 2: Presence (*) of epiphytic harpacticoid families found on mimics at the different sites

Family	Natural	Replanted	Bare
Thalestridae	*	*	*
Tisbidae	*	*	*
Ectinosomatidae	*	*	*
Ameiridae	*	*	*
Laophontidae	*	*	*
Longipediidae	*	*	*
Miraciidae	*	*	*
Porcellidiidae	*	*	*
Unidentified	*	*	*
Harpacticidae	*	*	*
Tegastidae	*	*	*
Cletodidae			*
Canuellidae	*	*	
Rhizotrichidae	*		
Canthocamptidae	*		

Table 3: ANOVA results for copepod densities on seagrass mimics. Significant *p*-levels (<0.05) are indicated in bold

Factors	df	SS	MS	*F*	*p*
Intercept	1	183 056.8	183 056.8	992.4337	0.0000
Day	5	9 303.1	1 860.6	10.0873	**0.0000**
Site	2	1 115.3	557.7	3.0234	0.0647
Day × Site	10	5 763.2	576.3	3.1245	**0.0084**
Error	28	5 164.7	184.5		
Total	45	22 215.8			

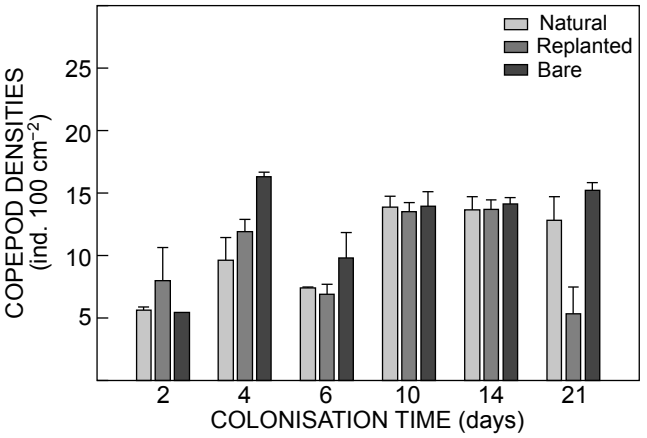

Figure 3: Average epiphytic copepod densities on mimics for different colonisation days. Error bars denote SE

Based on the MDS (Figure 4), the initial copepod community (days 2–4) differed from the later colonisation days in the bare and replanted site. In the natural site, this initial community grouped days 2, 4 and 6. For all sites, the copepod community on day 21 differed from the previous days.

Taxa richness for harpacticoid copepods (Hill's diversity indices) differed significantly between colonisation time ($p < 0.05$) but not between sites. In all, eight harpacticoid copepod families were identified in the sediments in all sites. Other orders such as Cyclopoida and Siphonomastoida were also present. The composition of the benthic harpacticoid copepods in the natural sites was dominated by

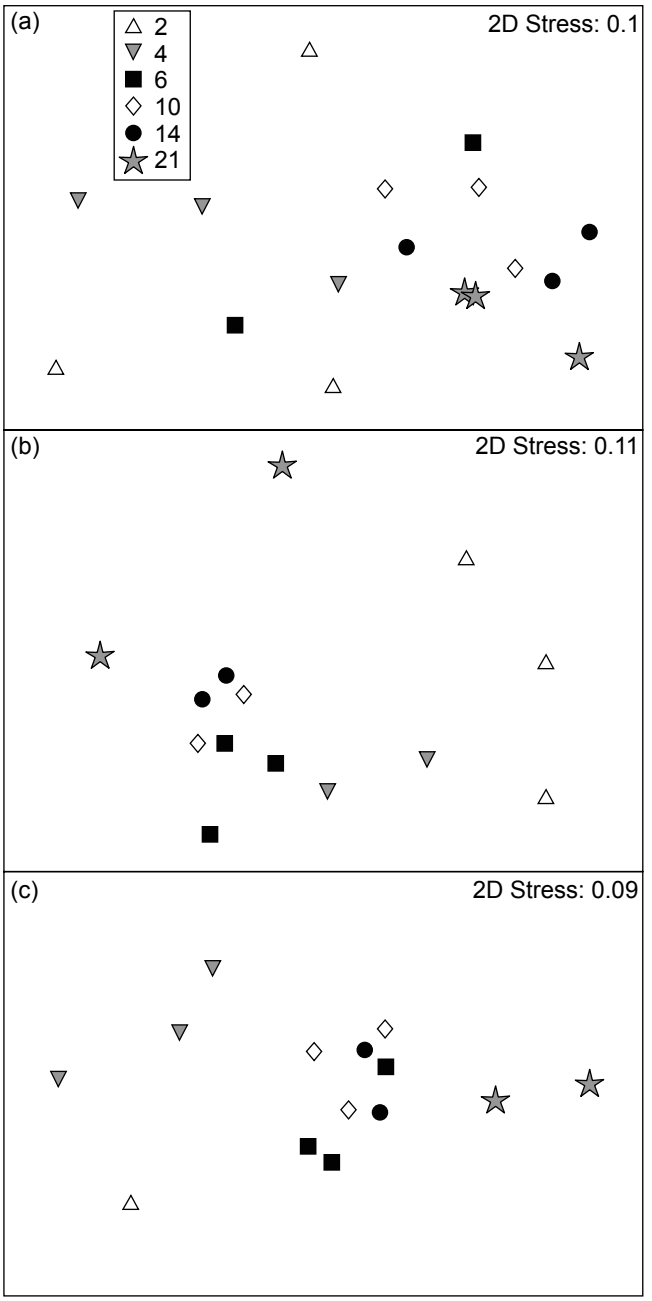

Figure 4: Copepod community structure on mimics: (a) bare, (b) replanted and (c) natural (numbers represent the day of collection)

Ectinosomatidae in the top sediment layer and Cletodidae and Ameiridae were abundant in the deeper sediment layers. In the bare sites, Ameiridae were abundant in the top and lower layers and Miraciidae in the middle layer. In the replanted sites, Ectinosomatidae dominated in the top sediment layer and Ameiridae in the deeper sediment layers.

Close to the natural and replanted sites, high copepod densities were recorded in the deepest sediment layer whereas the highest densities in the bare sites were found in the top layer (Figure 4). There were no significant differences in copepod densities between sites or sediment layers.

In general, there was higher taxon richness for benthic harpacticoid copepods in the bare sites (five taxa) than in the natural sites (three taxa). There was a high dominance of species in the bare and the replanted sites in the lowest sediment layer relative to the other layers. In contrast, the highest dominance of species at the natural sites was in the top layer. The most abundant epiphytic harpacticoids on natural seagrasses were Thalestridae and Ectinosomatidae.

Discussion

Meiofauna densities recorded in the present study were much lower compared to those found in other studies in tropical seagrass beds (Mirto and Danovaro 2004, De Troch et al. 2005) but were comparable to the densities reported from other artificial hard substrata (da Fonsêca-Genevois et al. 2006). Meiofauna recovered relatively quickly after four days of colonisation, and the densities on seagrass mimics were comparable to those in undisturbed natural seagrass beds. However, there was higher variation in meiofauna densities on the mimics than on natural seagrasses. Moreover, there was a cyclical trend in the meiofauna abundance, with an increase towards day 4 followed by a decrease on day 6 and so on. This might suggest more unstable conditions of the new environment (the mimics). This could be attributed to the short experimental time, which did not allow the establishment of a stable epiphytic biofilm consisting of bacteria and diatoms, the main food sources for meiofauna. The short experimental period was chosen to allow comparison with other similar studies using mimics or artificial substrates (De Troch et al. 2005, da Fonsêca-Genevois et al. 2006), in addition to the challenges involved in maintaining mimics in the field for a long period. Our study focused on the ability of meiofauna to colonise new substrates and the role of nearby seagrass sources in that recruitment process. This allowed us to evaluate the health of differential patch types (natural, replanted and bare sand) in terms of associated meiofauna and the way they serve as sources to colonise new substrates. The data showed the importance of the status of the source community for the colonisation of new substrate by meiofauna. The data on meiofauna colonisation proved our hypothesis that natural seagrass beds, restored seagrass beds and bare sediment act differently as a source of meiofauna. This different success of recruitment can be used as a proxy for the health and the optimal functioning of the source community.

Distinct differences in faunal communities in vegetated and unvegetated habitats over small spatial scales have been reported by Boström and Bonsdorff (1997) and Connolly (1997). The preference of harpacticoid copepods to inhabit the edges rather than the interior of seagrass patches (Warry et al. 2009) could explain the low copepod densities found on mimics planted within natural seagrasses, which were characterised by a fragmented distribution rather than a continuous meadow. The first colonisation phase in all patches was typified by planktonic copepods (mainly cyclopoids and calanoids) whereas densities of (benthic) harpacticoids increased as colonisation progressed. Thus, colonisation by copepods seemed to be initially fuelled from the water column and later from the sediment and other seagrass patches nearby. This sequence is in contrast to that reported by De Troch et al. (2008) from field experiments in which initial high meiofauna densities mainly consisted of opportunistic nematodes that originated from the sediment. Other studies have also found harpacticoid copepods to be the fastest meiofaunal colonisers (da Fonsêca-Genevois et al. 2006).

Finding copepods on mimics from day 6 in the replanted and bare sites and on day 10 in the natural site suggests that recolonisation by harpacticoid copepods in the study site is faster in areas with the lowest seagrass cover. The fact that harpacticoid copepods tend to colonise faster in bare areas or areas with very sparse vegetation cover than areas with dense seagrass cover indicates their ability to close new areas quickly. However, in contrast to the meiofauna data, the colonisation success of copepods was not significantly influenced by the source community. Thus, our hypothesis that natural seagrass beds, restored seagrass beds and bare sediment act differently as the source of meiofauna does not hold for harpacticoid copepods.

The colonisation by copepods was successful as all true phytal-dwelling harpacticoid families (Hicks and Coull 1983), with the exception of Peltidiidae, were found on all mimics. The relative abundance of these families increased after six days of colonisation. The fact that more non-phytal harpacticoid families were recorded on the mimics in the replanted and bare sites than in natural sites suggests the potential of the sediments to act as source for copepods in these canopy-deficient areas. Harpacticoid copepods are known for their high propensity to emerge from sediments and colonise a variety of artificial substrata (Bell and Sherman 1980, Palmer 1988, Teasdale et al. 2004).

Ectinosomatidae and Thalestridae were the most abundant harpacticoid families throughout our experiment. The former is mainly an itinerant form, found both on leaf surfaces and in sediment (Hicks and Coull 1983). Ameiridae, a sediment-dwelling harpacticoid, was also found in high abundances in the mimics planted in natural patches, and high densities were also recorded in the sediments around the replanted and bare sites, but not on the mimics planted at these sites. This suggests that Ameiridae prefer the natural seagrasses as they form a canopy structure that enables them to actively emerge from the sediments in spite of their sediment-dwelling behaviour.

The initial colonisation by planktonic copepods was followed by benthic harpacticoids. Given that harpacticoid copepods are not good swimmers, their movement towards the mimics will be driven by passive migration from natural seagrass blades by currents or active emergence from the sediment.

Previous experiments in tropical seagrass beds showed a fast recovery in terms of copepod densities (De Troch et al. 2005). The diversity of copepods in our study was high on the mimics and typical epiphytic families. Thus, full recovery is possible in terms of both density and diversity of copepods.

Generally, biodiversity and community composition can be positively or negatively affected by changes in size, shape and location of the remaining habitat patches (Fahrig 1997). In addition, the recovery of harpacticoid copepods may also depend on the time necessary for the recovery of the epiphytic biofilm, their main food source. The primary factor is the recovery time of seagrass plants themselves, which may take approximately four years (Alcoverro and Mariani 2002).

The present study focused on the area of Diani Beach, the only site along the Kenyan coastline where seagrass replantation has been applied as a conservation strategy, as well as being the area that had been mostly affected by overgrazing of sea urchins. As such, the experimental design was restricted to deploying the treatments within the same area, albeit at 10 m intervals. However, a larger spatial scale could potentially hamper the interpretation of ecological studies on seagrass ecosystems as other environmental factors may act at different sites. Natural recovery of seagrasses has been observed in several areas along the Kenyan coast, which have shown a potential recovery when additional anthropogenic stressors are eliminated (Uku et al. 2009). In terms of conservation measures, and on the basis of the results presented here, we recommend an ecosystem approach, including attention to the organisms at the basis of the marine food web (primary producer–consumer interface), which consequently influence the overall ecosystem functioning. The status of the source population has been shown to be important for the final colonisation of new plants by meiofauna. Seagrass-associated meiofauna responded relatively quickly to new substrates as long as the surrounding (source) communities remained undisturbed.

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References

Alcoverro T, Mariani S. 2002. Effects of sea urchin grazing over a Kenyan mixed seagrass bed. *Biologia Marina Mediterranea* 7: 195–198.

Bell SS, Hicks GRF. 1991. Marine landscapes and faunal recruitment: a field test with seagrasses and copepods. *Marine Ecology Progress Series* 73: 61–68.

Bell SS, Sherman KM. 1980. A field investigation of meiofauna dispersal: tidal resuspension and implications. *Marine Ecology Progress Series* 3: 245–249.

Boström C, Bonsdorff E. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) in beds in the northern Baltic Sea. *Journal of Sea Research* 37: 153–166.

Boxshall GA, Halsey SH. 2004. *An introduction to copepod diversity*. London: The Ray Society.

Ceccherelli G, Cinelli F. 1999. A pilot study of nutrient enriched sediments in a *Cymodocea nodosa* bed invaded by the introduced alga *Caulerpa taxifolia*. *Botanica Marina* 42: 409–417.

Commito JA, Tita G. 2002. Differential dispersal rates in an intertidal meiofauna assemblage. *Journal of Experimental Marine Biology and Ecology* 268: 237– 256.

Connolly RM. 1995. Effects of removal of seagrass canopy on assemblages of small, motile invertebrates. *Marine Ecology Progress Series* 118: 129–137.

Connolly RM. 1997. Differences in composition of small, motile inverterbrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia* 346: 137–148.

Constanza R, d'Arge R, Groot RD, Farber S, Grasso MT. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.

da Fonsêca-Genevois V, Somerfield PJ, Neves MHB, Coutinho R, Moens T. 2006. Colonization and early succession on artificial hard substrata by meiofauna. *Marine Biology* 148: 1039–1050.

Daudi LN, Lugomela C, Uku JN, De Troch M. 2012. Effect of nutrient enrichment on seagrass associated meiofauna in Tanzania. *Marine Environmental Research* 82: 49–58.

De Troch M, Fiers F, Vincx M. 2001. Alpha and beta diversity of harpacticoid copepods in a tropical seagrass bed: the relation between diversity and species' range size distribution. *Marine Ecology Progress Series* 215: 225–236.

De Troch M, Mees S, Wakwabi EO. 1998. Diets of abundant fishes from beach seine catches in seagrass beds of a tropical bay (Gazi Bay, Kenya). *Belgian Journal of Zoology* 128: 135–154.

De Troch M, Raes M, Muthumbi A, Gheerardyn H, Vanreusel A. 2008. Spatial diversity of nematode and copepod genera of the coral degradation zone along the Kenyan coast, including a test for the use of higher-taxon surrogacy. *African Journal of Marine Science* 30: 25–33.

De Troch M, Vandepitte L, Raes M, Suarez-Morales E, Vincx M. 2005. A field colonization experiment with meiofauna and seagrass mimics: effect of time, distance and leaf surface area. *Marine Biology* 148: 73–86.

Duarte CM. 2000. Marine biodiversity and ecosystem services: an elusive link. *Journal of Experimental Marine Biology and Ecology* 250: 117–131.

Edgar GJ, Robertson AI. 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed. *Journal of Experimental Marine Biology and Ecology* 160: 13–31.

Eklöf JS, Torre-Castro MDL, Gullström M, Uku J, Muthiga N, Bandeira S, Lyimo T. 2008. Sea urchin overgrazing of seagrasses: a review of current knowledge on causes, consequences and management. *Estuarine, Coastal and Shelf Science* 79: 569–580.

Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603–610.

Fonseca MS, Bell SS. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series* 171: 109–121.

Fonseca MS, Kenworthy WJ, Courtney FX, Hall MO. 1994. Seagrass planting in the south-eastern United States: methods for accelerating habitat development. *Restoration Ecology* 2: 198–212.

Hemminga MA, Duarte CM. 2000. *Seagrass ecology*. Cambridge: Cambridge University Press.

Hicks GRF, Coull BC. 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology: an Annual Review* 21: 67–175.

Higgins RP, Thiel H. 1988. *Introduction to the study of meiofauna*. London: Smithsonian Institution Press.

Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 555–557.

Horinouchi M, Sano M. 1999. Effects of changes in seagrass shoot density and leaf height on abundances and distribution of juveniles of three gobioid fishes in a *Zostera marina* bed. *Marine Ecology Progress Series* 183: 87–94.

Kennedy AD, Jacoby CA. 1999. Biological indicators of marine environmental health: meiofauna — a neglected benthic component? *Environmental Monitoring and Assessment* 54: 47–68.

Kenyon RA, Haywood MDE, Heales DS, Loneragan NR, Pendrey RC, Vance DJ. 1999. Abundance of fish and crustacean postlarvae on portable artificial seagrass units: daily sampling provides quantitative estimates of the settlement of new recruits. *Journal of Experimental Marine Biology and Ecology* 232: 197–216.

Klumpp DW, Salita-Espinosa JS, Fortes MD. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. *Aquatic Botany* 43: 327–349.

Lang K. 1965. *Copepoda: Harpacticoidea from the Californian Pacific Coast*. *Kungliga Svenska Vetenskapakademiens* 10: 1–560 (published in German).

Lee SY, Fong CW, Wu RSS. 2001. The effects of seagrass *Zostera japonica* canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. *Journal of Experimental Marine Biology and Ecology* 259: 23–50.

McClanahan TR, Shafir SH. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral-reef lagoons. *Oecologia* 83: 362–370.

Mirto S, Danovaro R. 2004. Meiofaunal colonization on artificial substrates: a tool for biomonitoring the environmental quality on coastal marine systems. *Marine Pollution Bulletin* 48: 919–926.

Orth RJ, Luckenbach MW, Moore KA. 1994. Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology* 75: 1927–1939.

Paling EI, Van Keulen M, Wheeler KD, Phillips J, Dyhrberg R. 2003. Influence of spacing on mechanically transplanted seagrass survival in a high wave energy regime. *Restoration Ecology* 11: 56–61.

Paling EI, Van Keulen M, Wheeler K, Phillips J, Dyhrberg R. 2001. Mechanical transplantation in Western Australia. *Ecological Engineering* 16: 331–339.

Paling EI, Van Keulen M, Tunbridge DJ. 2007. Seagrass transplanting in Cockburn Sound, Western Australia: a comparison of manual transplantation methodology using *Posidonia sinuosa* Cambridge et Kuo. *Restoration Ecology* 15: 240–249.

Palmer MA. 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine Ecology Progress Series* 48: 81–91.

Seddon S, Connolly RM, Edyvane KS. 2000. Large-scale seagrass dieback in northern Spencer Gulf, South Australia. *Aquatic Botany* 66: 297–310.

Short FT, Neckles H. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63: 169–196.

Teasdale M, Vopel K, Thistle D. 2004. The timing of benthic copepod emergence. *Limnology and Oceanography* 49: 884–889.

Tilman D. 1997. *Biodiversity and ecosystem functioning*. Washington, DC: Island Press.

Torres-Pratts H, Schizas NV. 2007. Meiofaunal colonization of decaying leaves of the red mangrove rhizophora mangle, in south-western Puerto Rico. *Caribbean Journal of Science* 43: 127–137.

Uku J, Ndirangu S, Muthama C, Kimathi A, Kilonzi J. 2009. An evaluation of the effect of sea urchin herbivory in the Diani-Chale lagoon: recovery potential of the seagrass habitat. Final Technical Report. A KMFRI/CORDIO collaborative project report, Kenya.

Virnstein RW, Curran MC. 1986. Colonization of artificial seagrass versus time and distance from source. *Marine Ecology Progress Series* 29: 279–288.

Warry F, Hindell J, Macreadie P, Jenkins G, Connolly R. 2009. Integrating edge effects into studies of habitat fragmentation: a test using meiofauna in seagrass. *Oecologia* 159: 883–892.

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