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Experimental harvest in a tropical seagrass meadow leads to shift in associated benthic communities

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Abstract: Seagrass meadows represent key ecosystems in coastal areas worldwide, hosting a great biodiversity of associated communities and thereby providing a large range of ecosystem services. In this study we present an experimental approach to investigate the effects of seagrass losses on related macrofauna assemblages. Over a three year period, seagrass canopies were removed in experimental plots and changes in epifauna, infauna and respective functional groups were recorded. The experimental removal of seagrass leaves resulted in a decline of 74% of overall macrofaunal abundance and the loss of several taxa. The immediate response of associated communities was followed by the establishment of an alternative assemblage, characterized by an increased number of bioturbators and deposit feeders. The colonization of disturbed seagrass plots by burrowing shrimps (Callianassidae) might have hindered the reestablishment of seagrass after the removal. Our findings highlight the important role of seagrasses as habitat forming species that provide relevant functioning and services in coastal ecosystems.

Nomenclature for plants: Green and Short (2003) and Richmond (2011).

Introduction

Seagrass beds are among the most productive ecosystems in coastal areas. Altogether they form one of the largest shallow marine ecosystems in the world (approximately 177,000 km^2, Green and Short 2003). They occur at the coast of all continents except Antarctica, typically showing higher species richness in tropical compared to temperate regions (Laffoley and Grimsditch 2009). Together with mangroves and coral reefs, seagrasses are among the most important foundation species in coastal tropical areas, with key roles in community structure and ecosystem functioning (Duarte et al. 2008, Unsworth et al. 2015). Seagrasses form natural barriers against land erosion (Ondiviela et al. 2014), promote carbon capture and storage (Warwick 1984, Nagelkerken et al. 2004, Dorenbosch et al. 2005, Duarte et al. 2013), provide nursery grounds for economically important fish species (Unsworth et al. 2014) and supply habitat, shelter and food for a diversity of organisms, varying from invertebrates to marine mammals (Verweij et al. 2006, Valentine and Duffy 2006). Especially in tropical regions, local communities strongly rely on seagrass meadows as fishing grounds. This dependence might strengthen in the future, as the health of coral reefs is predicted to decline (Unsworth et al. 2014, Nordlund et al. 2017). The ecosystem services provided by seagrass meadows are crucial for the well-being of coastal communities, therefore being viewed as coupled socio-ecological systems (Unsworth et al. 2014).

Seagrass meadows are among the most threatened ecosystems on earth, with global losses estimated up to 7% of areal distribution per year (Waycott et al. 2009). On a global scale, threats are represented by land erosion, eutrophication and mechanical damage due to dredging and anchoring (Orth et al. 2006). Within the Indo-Pacific region, physical disturbance of seagrass, eutrophication, pollution, disease and the impacts of river runoff have been identified as the most common threats (Coles et al. 2011). Perturbation of seagrass habitats can lead to considerable changes in the structure of associated communities (Herkül and Kotta 2009, Gartner et al. 2010, Do et al. 2013). However, responses can vary based on local ecosystem conditions and the type, severity and duration of perturbations (Coles et al. 2011). These perturbations might be reinforced by faunal species benefitting from seagrass declines, especially if these species are also able to act as ecosystem engineers. The resulting regime shift in seagrass meadows and related communities, can finally lead to profound changes in primary production, carbon sequestration and habitat formation (Kneer et al. 2013, Maxwell et al. 2017).

In this article we present the effects of long-term removal of seagrass canopy on the associated macrofaunal communities in Gazi Bay, Kenya. This study was done in parallel to the work described in Githaiga et al. (2019). The intertidal seagrass meadows in Gazi Bay are intensively used for artisanal fishing activities (Harcourt et al. 2018) and the Bay is home to one of the major fish landing sites in South East

Kenya (FAO 2015). These activities resulted in visible scars within the seagrass meadows and are thought to have contributed to the decline of ~2% yr^{-1} in seagrass coverage between 2000 and 2016 (Harcourt et al. 2018). The overall aim of this study was to identify impact pathways of seagrass perturbation by investigating changes in infauna and epifauna abundance as well as overall fauna community structure, resulting from seagrass removal.

Material and methods

Study site

Seagrass meadows located in the intertidal zone of Gazi Bay (S04°25’33”; E39°31’7”), Kwale County, Kenya were selected for this study (Fig. 1). The surface area of Gazi Bay is approximately 13.5 km^2 of which 70% is covered by seagrass (Coppejans et al. 1992). The bay is sheltered by a fringing coral reef in the South East and by an extensive mangrove forest in the North East. The tidal range within the bay can be as much as 3.2 m (Kitheka 1997) and the bay receives freshwater input from the seasonal rivers Kidogoweni and Mkurumuji (Bouillon et al. 2004). Twelve seagrass species are found in Gazi Bay, of which the following four species are most dominant: *Enhalus acoroides*, *Syringodium isoetifolium*, *Thalassia hemprichii* and *Thalassodendron ciliatum* (Githaiga et al. 2019). Regular mounts (10-20 cm in height) produced by burrowing shrimps further characterize the intertidal and shallow subtidal seagrass meadows within the bay.

This study focused on monospecific meadows of *T. hemprichii* and *E. acoroides*. These seagrass species are both classified as persistent: relatively slow growing, exhibiting a long life-span and resistance to disturbance, thereby fulfilling the role of a stable and long-lasting foundation species (Kilminster et al. 2015).

Study design and sampling

In February 2015, eight experimental plots of 3 m × 2 m were randomly selected in the intertidal seagrass meadows of Gazi Bay. In half of the selected plots, aboveground biomass of seagrass was removed on a monthly basis for the entire duration of the experiment (harvested plots). The remaining half was left undisturbed and considered as a control. Sampling

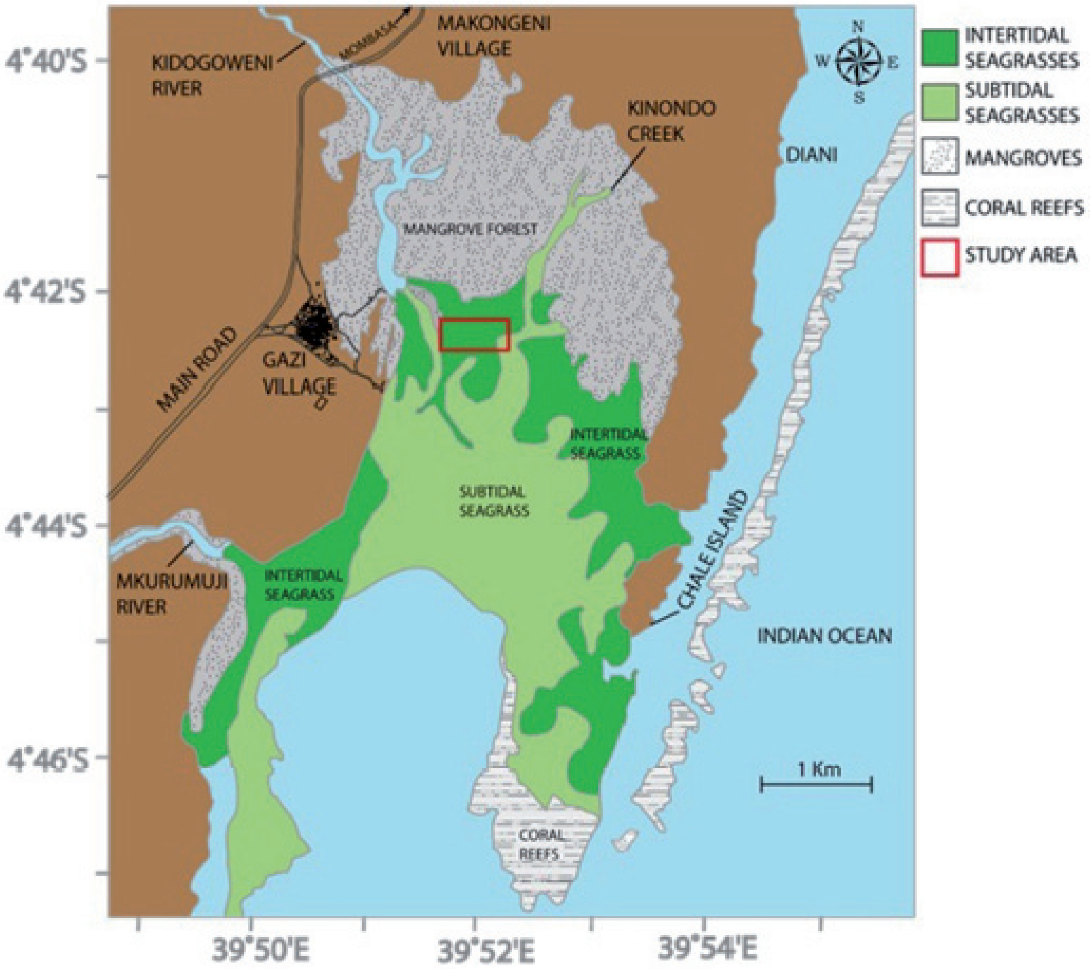

Figure 1. Map of the sampling area, sampling sites are located in the intertidal seagrass meadows between Kinondo creek and Kidogoweni River (map from Githaiga et al. 2019).

Table 1. Variability in sampling effort for epifauna and infauna over the duration of the study.

Sample type	Fauna sampled	# samples 2015	# samples 2016	# samples 2017
core	infauna	2 plot^{-1}	3 plot^{-1}	3 plot^{-1}
dropsample	epifauna	-	2 plot^{-1}	1 plot^{-1}

started one month after the first removal of seagrass canopy and took place annually in 2015, 2016 and 2017. In order to avoid a seasonal bias in macrofaunal composition, sampling was always performed between February and April.

Infauna samples were taken using cores, while epifauna was collected employing drop samples, randomly placed within the surveyed plots. Cores were taken in accordance with established sampling strategies (e.g., Bowden et al. 2001), extending the core with a diameter of 10.5 cm to a depth of 15 cm. Core samples were placed in freezer bags, transported to the lab and sieved through 500 µm mesh sieves. Seagrass biomass was removed, separated in aboveground and belowground biomass, dried at 60°C for 48 h and weighed. All fauna was manually removed from the remaining sample. For drop samples a metal frame (50 cm × 50 cm) with a height of 40 cm was placed on the sediment at low tide (< 30 cm) and pushed down to seal the sample. Fauna was carefully removed from the water retained in the frame using a 500 µm sieve, keeping sediment resuspension at a minimum in order to avoid sampling of infauna. This process was repeated until two consecutive sieves did not contain any fauna and the frame could be considered empty. Fauna was stored in a 120 ml sampling jar with seawater and transported to the lab. The sampling followed a nested design with subsamples (cores and drop samples) being nested within plots. The sampling effort varied with time, as drop samples were introduced in the second year of the study to improve the sampling of epifauna. In addition, differences in resource availability for field work resulted in changes in the number of obtained replicates (Table 1).

All samples were stored in a solution of 10% formalin for a minimum of 48 h, washed and preserved in a solution of 70% ethanol (Eleftheriou and McIntyre 2005). Fauna was identified to the lowest taxonomic level possible (family level) using taxonomic literature specific for the Western Indian Ocean (Day 1967, Smith and Heemstra 1999, Richmond 2011, Wambiji et al. 2015) and descriptions of marine fauna from other regions when necessary (Hayward and Ryland 2000, Alonso 2003, Ngoc-Ho 2003, Haye et al. 2004, Pagliosa 2005, Campbell 2007, Poore and Bruce 2012, Conway 2015, Jumars et al. 2015).

Data analysis

To identify the impact of seagrass canopy removal on fauna, results from cores and drop samples were averaged per plot. Due to the variability in sampling effort (Table 1), a separate one-way ANOVA was performed in R (R Core Team 2012) for each of the three sampling events, testing for differences in faunal abundance and seagrass belowground

Table 2. Biological characteristics used to categorize taxa into functional groups. Functional groups were constructed by a four letter combination of traits presented.

Biological traits	Type modalities	Legend
Body type	Soft	S
	Rigid (exoskeleton)	R
	Vertebrate	V
	Calcified (molluscs)	C
Adult body size	< 1 mm	S
	1-5 mm	M
	> 5 mm	L
Feeding behaviour	Predator	P
	Deposit feeders/grazers	D
	Suspension feeding	S
	Omnivorous	M
Sediment interaction	Mobile or burrowing	B
	Tube building	T
	Pelagic	P
	Sessile	A
	Commensal	C
	Other (interface between sediment and water)	S

Table 3. List of functional groups used in the analysis of community composition. Summarized functional attributes refer to functional groupings from Table 2.

Functional group number	Summarized functional attributes
1	Large burrowing crustaceans and at sediment surface, mixed feeding and predators
2	Large burrowing and tube-building worms, omnivorous and predators
3	Deposit feeders and grazers
4	Suspension feeders
5	Large predatory, pelagic fish
6	Predators and omnivores, commensal or water column
7	Small predators and omnivores, sessile or tube-building, commensal or burrowing organisms

biomass between disturbed and control plots. Normality of the data was tested using a Shapiro-Wilk test and the data were transformed when assumptions were not met. The relationship between seagrass belowground biomass and infauna abundance was investigated using linear model (LM) and a linear regression (LR) using Pearson and Spearman correlations.

To identify the changes in abundance of specific fauna taxa, an analysis of functional groups was performed. This analysis is similar to Biological Trait Analysis (BTA), using a series of morphological and behavioural characteristics of species to indicate aspects of their ecological functioning (Tilman et al. 1997, Paganelli et al. 2012, Peng et al. 2013, Greenfield et al. 2016). Diet, interaction with sediment, body type and body size were defined for each taxon, based on prior studies of functional groups in macrofauna (Borja et al. 2009, Lavesque et al. 2009, Valença et al. 2012, Gamito et al. 2012, Peng et al. 2013, Rodil et al. 2013, Barnes and Hendy 2015) (Table 2). Macrofauna taxa were summarized in functional groups (Table 3), according to similarities in the aforementioned categories (e.g., grazers were included within the deposit feeders as these two feeding behaviours are often combined in small invertebrates). The groups that showed low abundances in the samples were deliberately included in the analysis, due to their disproportionate importance and expected impact on the system, e.g., large predatory fish.

Community analysis was performed using PRIMER 7 for both taxonomic and functional data (Clarke and Warwick 2001). To reduce the influence of the most dominant taxa, fourth root transformation was applied to abundance data and square root transformation to functional group data (Clarke and Warwick 2001). In order to assess the impact of treatment and time on the community, Bray-Curtis similarities were calculated and used for cluster analysis. The results were plotted using non-metric multidimensional scaling (nMDS). Permutational analysis of variance (PERMANOVA, Anderson et al. 2008) was applied for both taxonomic and functional data, to test for differences in community composition between treatments and years. To distinguish taxa responsible for community differences between treatments, the SIMPER routine was performed on combined abundance data for epifauna and infauna for the years 2016 and 2017, using Bray-Curtis similarities with treatment and year as factors.

Results

Community structure

Within the fauna samples a total of 71 taxa were identified, with 52 taxa occurring in both epifauna and infauna samples. 33 taxa were found exclusively within control plots, while only 5 taxa (Poecilochaetidae, Trichobranchidae, Sphaerodoridae, Dendrobranchiata and Stomatopoda) were exclusively found in harvested plots. Thirteen taxa were exclusively found in infauna samples, of which the majority consisted of polychaete families. Six taxa were exclusively found in epifauna samples, e.g., Chaetognaths and Thaliacea.

Experimental treatment

Average faunal abundance was significantly higher in control plots (14395 ± 4999) compared to harvested plots (3929 ± 1173) for each sampling event and no effect of time was detected (Fig. 2). The removal of seagrass leaves resulted in an average loss of 72% of infauna and 89% of epifauna abundance. In total, the abundance declined by 74% over the study period. Noticeably, within one month after removal of the seagrass canopy, the abundance of infauna had already declined by 76%, but without significant difference between treatments ($p = 0.0697$); fauna abundance was significantly higher in control plots in 2016 and 2017, compared with harvested plots ($p < 0.01$) (Table 4.a). On average, 11 (10) taxa were lost in 2016 (2017), respectively, as a result of seagrass removal. There is no significant difference in seagrass belowground biomass between treatments in 2015 ($p = 0.602$) and

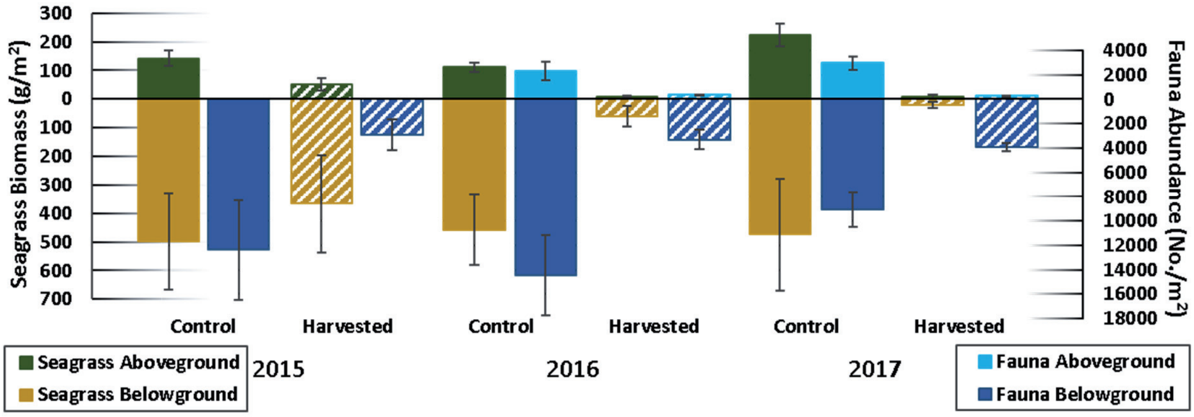

Figure 2. Temporal changes in fauna abundance and seagrass biomass sampled above and belowground for control and harvested plots. Abundance of epifauna sampled by drop sampling (light above baseline) and infauna sampled by cores (dark below baseline) as well as biomass of seagrass leaves (dark above baseline) and seagrass roots and rhizomes (light below baseline) are depicted. Error bars indicate standard error for control (solid) and harvested (striped) treatments. Note that no data on epifauna abundance are available for 2015.

Table 4. a: ANOVA table for the effect of treatments (Control and Harvested) on infauna abundance in 2015 and on macrofauna abundance in 2016 and 2017. **b:** ANOVA table for the effect of treatments (Control and Harvested) on seagrass belowground biomass in 2015, 2016 and 2017.

a

	df	2015			2016			2017		
		SS	F	P	SS	F	P	SS	F	P
Treatment	1	178268443	4.859	0.0697	344939491	21.69	**0.00348**	121156543	16.86	**0.00632**
Residuals	6	95427647			95427647			43119459		

b

	df	2015			2016			2017		
		SS	F	P	SS	F	P	SS	F	P
Treatment	1	34765	0.302	0.602	314434	9.348	**0.0223**	412368	5.357	0.0599
Residuals	6	689986			201813			461857		

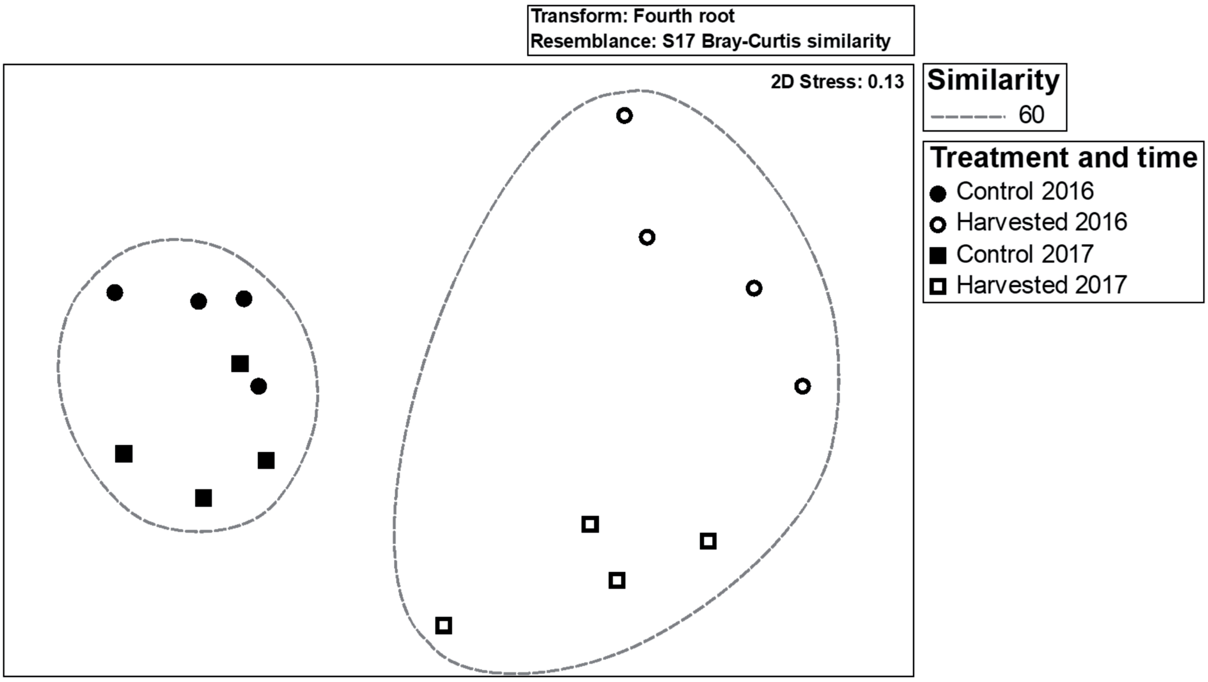

Figure 3. nMDS plots of total fauna abundance (treatment and time as fixed factors) for the different experimental plots. Outcomes of the cluster analysis are superimposed at 60% similarity.

2017 ($p = 0.0599$), however a significant decline was detected ($p = 0.0223$) in 2016 (Table 4.b). The LM showed a significant relationship between loss of seagrass belowground biomass and infauna abundance in harvested plots ($p < 0.01$). The LR showed no significant relationship between infauna abundance and seagrass belowground biomass in harvested plots ($p = 0.15$). The macrofauna community analysis resulted in a clear separation of control and harvested treatments, showing a similarity of 60% within the separate clusters, highlighted in the nMDS plot (Fig. 3). Within the group of harvested plots, a temporal separation for sampling events in 2016 and 2017 is visible. The control plots show an overall higher similarity than harvested plots. The PERMANOVA confirmed a significant ($p < 0.01$) effect of treatment on the community structure, but no effect of time ($p = 0.643$) (Table 5). The SIMPER analysis revealed that within harvested plots, the taxa Amphipoda, Orbiniidae/Paraonidae, Nematoda/Nemertea/Plathelminthes, Capitellidae and Syllidae are the main contributors to within group similarity (Table 6). Comparing treatments, the taxa Ostracoda, Amphipoda and Asellota as main contributors to community dissimilarity (Table 7).

Table 5. PERMANOVA results for effects of the factors treatment and time (both fixed factors) on macrofauna abundance and functional group structure. P-values in bold indicate statistical significance at α = 0.05.

Macrofauna abundance				
Source of variation	df	SS	Pseudo-F	P (perm)
Time	1	1141.6	0.47506	0.643
Treatment	2	4806.3	6.5633	0.001
Residuals	12	4393.8		
Functional group abundance				
Source of variation	df	SS	Pseudo-F	P (perm)
Time	1	149.54	0.063456	1
Treatment	2	4713.3	23.142	0.001
Residuals	12	1222		

Table 6. Mean abundance and Bray-Curtis similarity (SIMPER analysis) of macrofaunal species, averaged for harvested plots. Species are ranked in order of their overall contribution to similarity (%). A cut-off at 50% of overall contribution was applied to the list of taxa.

Taxa	Av. Abundance	Average Similarity	Contribution %
Amphipoda	5.85	7.51	11.09
Orbiniidae/Paraonidae	5.46	7.11	10.50
Nematoda, Nemertea, Platyhelminthes	3.64	4.91	7.24
Capitellidae	3.54	4.70	6.95
Syllidae	3.36	4.34	6.41
Terebellidae	2.99	3.92	5.79

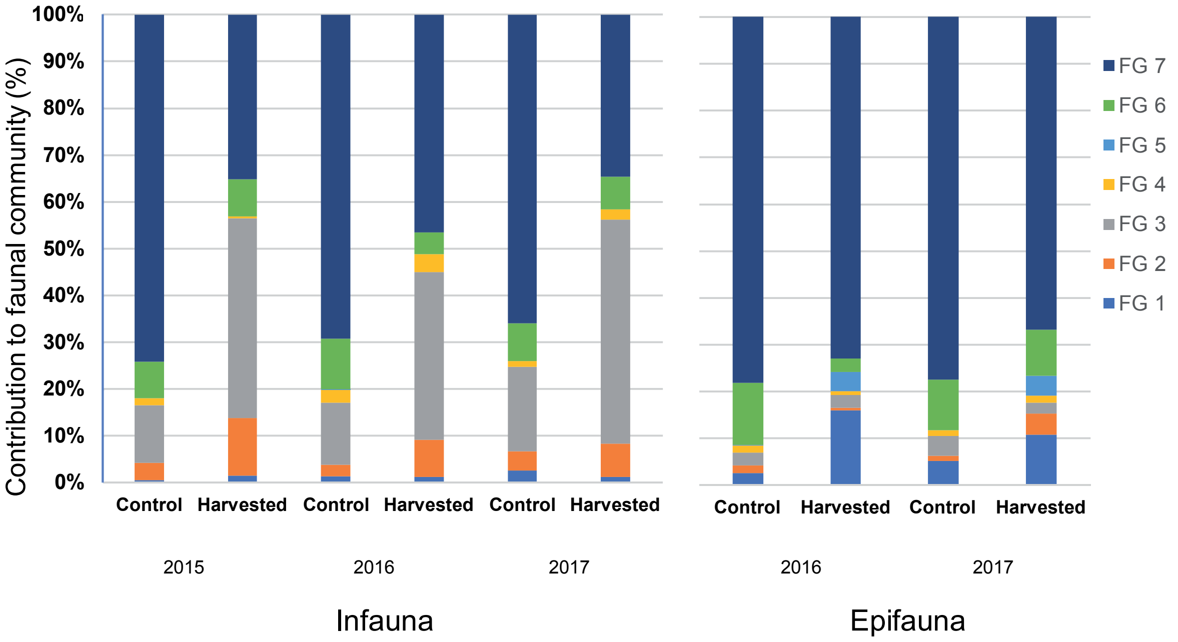

Figure 4. Proportion of infauna and epifauna attributed to each of the seven functional groups based on mean abundance values, separated per treatment and year. Functional group numbers are in accordance with Table 3.

Table 7. Mean abundance and contribution to dissimilarity (SIMPER analysis) of fourth root transformed macrofaunal taxa averaged between control and harvested plots. Taxa are ranked in order of their contribution (%) to the average Bray-Curtis dissimilarity between both treatments. A cut-off at 45.5% of dissimilarity was applied to the list of taxa.

Taxa	Group Control Av. Abundance	Group Harvested Av. Abundance	Contribution %
Apseudomorpha	5.36	0.99	4.92
Ostracoda	5.11	0.76	4.90
Amphipoda	9.35	5.85	3.93
Asellota	3.04	0.00	3.40
Buccinoidea	3.01	0.18	3.19
Echinodermata	3.00	0.18	3.18
Apseudomorpha (hermit)	3.33	0.77	3.05
Isopoda (other)	3.16	0.62	2.88
Leptostraca	2.93	0.62	2.88
Anthuroidea	2.69	0.31	2.64
Nereididae	2.83	0.62	2.46
Diogenidae	2.46	0.57	2.15
Ampharetidae	2.12	1.12	2.15
Tanaidomorpha	4.22	2.42	2.13
Sabellidae	1.87	0.3	2.00
Cirratulidae	2.01	1	1.95
Hesionidae	2.53	0.46	1.92

The removal of aboveground seagrass biomass led to alterations in relative abundance of functional groups (Fig. 4). The observed pattern of change differs between epifauna and infauna groups. Within infauna, lower abundance of functional group 7 was recorded for harvested plots (45%) compared to control plots (70%). In contrast, functional groups 2 and 3 showed higher abundances in harvested (50%) than in control (25%) plots. Functional groups 1, 4, 5 and 6 exhibited similar relative abundances for both treatments. For epifauna, functional groups 1 and 5 increased in relative abundance in harvested plots by 10% and 4%, respectively. Functional group 7 declined in relative abundance as a result of the treatment, while functional groups 2, 3 and 4 stayed unaffected. Treatment had a significant effect ($p = 0.001$) on the relative abundance of functional groups, while time had no effect ($p = 1$) (Table 5).

Discussion

The present study on the experimental removal of seagrass canopy in Gazi Bay revealed major changes in the structure and functional identity of seagrass associated macrofauna communities.

The results of this study showed that seagrass canopy facilitates a high fauna density and diversity. Their loss subsequent to the first harvest led to a severe disturbance of benthic communities. After three years of seagrass removal, the decline in the abundance of epifauna taxa was the most evident, followed by the slightly less affected infauna community. This decline is in line with results from previous studies obtained under laboratory conditions (Reed and Hovel 2006, Herkül and Kotta 2009, Gartner et al. 2010). This change in abundance and taxon richness could be related to the strong dependence of infauna on seagrass as habitat, food and protection from predation (Orth et al. 1984, Bologna and Heck 1999, Sirota and Hovel 2006). However, it is not known which of those factors acted as main driver of infauna loss after a relatively short time of disturbance. The impact of the loss of seagrass aboveground biomass on infauna was immediate and its abundance, community structure and functional group composition did not significantly differ in time. After the first harvest, infauna abundance stabilised in disturbed plots within only one month. The same process was observed for epifauna abundance between 2016 and 2017. This stabilisation could be the result of a quick recolonization of the barren area by new macrofauna communities, highlighted by the nMDS and PERMANOVA. The reduction of habitat quality, due to seagrass leaf removal, is described in the literature as the main driver of this macrofauna community shift (Bourque et al. 2015). All taxa contributing up to 50% of dissimilarity between treatment groups were more abundant in control than harvested groups. These taxa exhibit a variety of feeding modes and behaviours, e.g., the predatory snails from the family Buccinoidea and the deposit feeding polychaetes from the family Cirratulidae. The importance of seagrass as feeding ground is assumed to be directly linked to this high diversity in associated fauna feeding strategies (Orth et al. 1984, Lee et al. 2001, Paula et al. 2001).

The change in the structure of associated macrofauna communities in harvested plots was mainly characterized by the significant decline of a few taxa parallel to the increase of several taxonomic groups. In particular, a decrease in small crustaceans was observed, in combination with increases in opportunistic (e.g., Nematoda, Nemertea, Platyhelminthes, Capitellidae and Syllidae) and tube dwelling or burrowing taxa (e.g., Capitellidae, Terebellidae and Orbiniidae/Paraonidae) (Kalejta and Hockey 1991, Rosenberg et al. 2001, Campos and Burgos 2015). The removal of seagrass leaves dramatically lowered the habitat complexity, therefore facilitating the occurrence of opportunistic species with broader habitat requirements (Airoldi et al. 2008). The observed increase in burrowing activity, presumably related to Caliannassid shrimp (Githaiga et al. 2019), could have prevented an effective recolonization of the barren areas by seagrass. Burrowing shrimp are considered ecosystem engineers and can rework impressive amounts of sediment in the intertidal and subtidal regions (Kneer et al. 2013). In general, seagrasses are assumed to be dominant ecosystem engineers, but disturbances as applied in this experiment, could have favoured the colonization by burrowing shrimp, initiating the competitive exclusion of seagrasses (Castorani, 2014). However, the relationship between seagrass and burrowing shrimp varies depending on the considered zone within the intertidal. At the upper tidal level, seagrasses benefit from tidal pools created by burrowing shrimp, since they retain water during low tide (Kneer et al. 2013). In the present study, the harvest of seagrass (in the mid intertidal) led to potentially less productive and less resilient macrofaunal communities, as the overall taxon richness declined and variability increased (Edgar 1990, Hemminga and Duarte 2000).

Seagrass leaf removal also had effects on the functional composition of the related communities. As seagrass meadows provide shelter for associated fauna, their loss most likely increased the predation pressure in the harvested plots (Orth et al. 1984). As a matter of fact, small organisms were the most affected, and showed a severe decline in both infauna and epifauna communities (functional group 7, Fig. 4). In general, the changes in functional groups were more pronounced within the infauna, potentially linked to the presence of Caliannassid shrimps, which are able to modify the sediment characteristics by their burrowing activity and therefore modulate the overall habitat (Berkenbusch et al. 2007). Large tube dwelling and burrowing polychaetes and crustaceans, deposit feeders and grazers (functional groups 1, 2 and 3, Fig. 4), representing the 5 taxa exclusively found in harvested plots, seemed to benefit from seagrass harvest. This might be related to the loss of seagrass rhizomes; a sharp decline in belowground seagrass biomass (roots and rhizomes) was recorded one year after removing the leaves, in 2016, but belowground biomass declined further in 2017 (Fig. 3). The loss of belowground seagrass biomass would have allowed large burrowing and tube-building organisms to move more efficiently in the sediment and thereby lowering the likelihood of encountering predators (Skilleter 1994, Leopardas et al. 2014). The increased abundance of deposit feeders and grazers when seagrass canopy is removed, is likely the result of increased bioturbation. Since the availability of organic material fragments in less stable sediment can provide an important food source for deposit feeders and grazers (Stoner et al. 1980).

The observed changes in functional composition can result in alterations in ecosystem functioning. The increased proportion of burrowing macrofauna might be directly linked to the magnitude of bioturbation in the ecosystem, particularly associated to the Caliannassid shrimp (Suchanek and Colin 1986, Thomson et al. 2018). Simultaneously, sediment transport away from the meadow is promoted by the loss of structuring roots and rhizomes, which is expected to result in lower carbon storage in the sediment (Berkenbusch et al. 2007, Airoldi et al. 2008, Blackburn and Orth 2013). This has been confirmed by the results described in Githaiga et al (2019), with a mean carbon loss of 2.21 Mg C ha^{-1} in the top 5 cm of the sediment, as a result of seagrass canopy removal, and a potential additional loss of 2.54 Mg C ha^{-1} due to erosion of the sediment over an 18 months period. In addition, increased sediment loads in the water column can also hamper recovery of seagrass meadows from a disturbance through, among others, light limitation and the lack of stable sediment for seagrass ramets and/or seed settlement (Orth et al. 2006, Maxwell et al. 2017). Hence, within our study, the loss of seagrass canopy initiated a transition towards less diverse communities dominated by bioturbating fauna, with important consequences on the sediment stability and associated carbon storage.

Conclusion

In a long-term approach we demonstrated the effects of losses in seagrass cover on biotic and abiotic habitat characteristics. The structure and functional identity of associated macrofauna communities changed immediately after the disturbance and showed no recover until the end of the study. We suggest that changes in functional groups and the alteration of associated bioturbation processes prevented the effective recolonization by seagrasses. The establishment of bioturbators has the potential to lower the resilience and productivity of the ecosystem, enhancing the release of organic carbon from the sediment.

Authors' contributions: C.C. and A.F. contributed equally to this article.

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