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Influence of mangrove deforestation and land use change on trophic organization of fish assemblages in creek systems

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Abstract

The impacts of human related activities on trophic structure of mangrove-associated fish species, was investigated by sampling fish in mangrove creeks. Trophic organization and stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of fish in undisturbed mangrove creeks were compared with clear-cut areas of mangrove and reservoirs for saltworks and fish farms constructed after mangrove clearing. Results showed significantly higher densities, species numbers, diversity (H') and numbers of trophic groups in undisturbed sites compared to disturbed sites. Overall, omnivorous fish comprised the most abundant feeding guild, which dominated in the cleared sites followed in order by the uncleared sites and reservoirs. The zoobenthivores/piscivores was the most diverse group, with the highest species richness in the undisturbed areas. Multivariate analysis showed that assemblage structure of omnivores in the reservoirs was separated from those in uncleared and cleared sites, while zoobenthivores/piscivores differed between uncleared sites and disturbed areas. Stable isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in fish muscles indicated significant diet shifts between undisturbed and disturbed mangrove creek systems, although the effects were species-specific. The findings suggest that mangrove deforestation combined with land-use changes, has a greater impact on the trophic structure of fish in mangrove creeks than mangrove deforestation only.

Keywords: Ecology, Anthropogenic disturbance, Mangroves, Tanzania

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1. Introduction

Mangrove forests are under intense pressure from human-induced activities and are dwindling all over the globe (Valiela *et al.*, 2001; and Manson *et al.*, 2005). The anthropogenic effects on mangroves vary in scale from local modifications such as boardwalk construction to more broad-scale changes as urbanization and total clearing of mangroves for the construction of finfish and shellfish farms (Valiela *et al.*, 2001). It is estimated that activities related to animal mariculture alone are responsible for the increasing losses of mangrove forests globally. For instance, aquaculture accounts for significant loss mangrove areas in the Philippines and Southeast Asia (Primavera *et al.*, 2007). The clearing of mangrove vegetation can have major impacts on both the mangroves themselves and the associated organism communities through reduction or loss of habitat structure, in turn affecting provision of refuge areas, food availability and survival of natural stocks of organisms (Granek and Ruttenberg, 2008). Hence, there have been increasing demand to determine the effects on fish communities to natural and anthropogenic stressors (Greenwood *et al.*, 2006). Moreover, biologists and

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conservationists have been given the task to determine which attributes are important in explaining the extent of changes in fish communities (Elliott *et al.*, 2007).

Many researchers have dealt with fish compositions and their variations in space and time (Ecoutin *et al.*, 2005). In recent time, studies have also dealt with assigning fish species into different ecological groups or guilds (Elliott *et al.*, 2007; and Franco *et al.*, 2008), which represent species grouped by ecological or functional traits with similar influence on ecosystem processes and response to environmental stress. Numerous studies have used the trophic group approach in quantitative analyses of the functions of various marine habitats (Maes *et al.*, 2004; and Nagelkerken and van der Velde, 2004).

The use of biological indicators that take into account the ecological functioning of mangrove ecosystems is becoming a widely accepted method in determining the departure from natural conditions to stages affected by human activities (Whitfield and Elliot, 2002). For instance, indicators based on fish community composition are considered to be useful tools in investigating anthropogenic effects on nearshore coastal areas (Breine *et al.*, 2007). Moreover, it is widely acknowledged that functional attributes of fish organization, species number, abundance and biomass when studied together provide useful information for the understanding and management of anthropogenic impacts in coastal habitats (Elliott *et al.*, 2007). Yet, there is little substantial information characterizing the trophic compositions of fish due to mangrove deforestation for various purposes.

Since the late 1970s, analysis of carbon and nitrogen stable isotopes has been used to investigate the trophic ecology of aquatic systems, and has greatly improved our understanding of trophic structure, resource partitioning, habitat usage and species migration (Vizzini *et al.*, 2002; and Lugendo *et al.*, 2006). In recent time, with the progressive escalation of human pressure on coastal environments and the desire to employ new and more effective environmental indicators, the isotopic approach has been used successfully for assessing and monitoring ecosystem quality (Umezawa *et al.*, 2002; and Vizzini and Mazzola, 2006). For instance, increasing attention has been directed to investigating the environmental impact of anthropogenic input of nutrients and organic matter from sewage and effect of fish farm effluent discharge to adjacent systems (Mazzola and Sará, 2001).

The present study aimed at investigating the effects of human-induced alteration through mangrove deforestation and land-use change on trophic composition of fish in mangrove creeks. Trophic organization in undisturbed mangrove areas was compared with those in cleared mangrove and reservoirs for solar salt production and fish farming constructed after mangrove deforestation. In addition, stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values was investigated in fish samples by comparing the reservoirs and uncleared sites.

2. Materials and methods

2.1. Study sites

This investigation was performed in different sites within mangrove creeks of Makoba Bay and Chwaka Bay in Zanzibar as well as in Bagamoyo, Kunduchi and Mbegani mangrove forests on the Tanzanian mainland (Figure 1) based on three levels of human disturbance (Table 1). Sites regarded as uncleared were situated within a well-developed mangrove forest, mainly utilized for small-scale fishing as well as limited domestic uses for fuel wood. These sites had a bottom substratum composed predominantly of sand and/or mud. The disturbed sites fall into two categories: cleared sites and reservoirs. The first group, cleared sites, consists of two localities, one in Kiongwe creek (Makoba Bay) and another one in Nunge creek (Bagamoyo), which are both lacking mangrove trees as a result of deforestation and since no further modification has been done in the area they are referred in this paper as cleared sites. The cleared sites are affected by prevailing tidal rhythm and receive tidal waters from the lagoon during both neap and spring tides. The bottom substrate is characterized by mud and a low proportion of sand, and supports a significant amount of microalgae, possibly due to exposure and sufficient sunlight. The second group of disturbed sites comprises reservoirs for solar salt production (3 sites) and fish farming (1 site), (Table 1). All reservoirs were originally mangrove areas that were converted into solar salt farms during the 1980s. In 1998 part of the abandoned solar pans in Makoba Bay was transformed to experimental fish culture ponds mostly for farming of milkfish (*Chanos chanos*) and mullet (*Mugil cephalus*). Nevertheless, the remaining part of the mangrove areas, including those affected by solar salt production, are still fringed with mangrove stands such as *Rhizophora mucronata*, *Bruguiera* sp. and *Avicennia* sp. All reservoirs get tidal water by gravitational means from the main creek downstream through the gates. The filling of the reservoirs is estimated to be twice a month every spring tide (Mwandya *et al.*, 2009).

2.2. Sample collection

Data collection for fish samples was conducted on monthly basis during daytime from January through December (September excluded). A seine net measuring 17 m in length and 2 m in height with a mesh size of

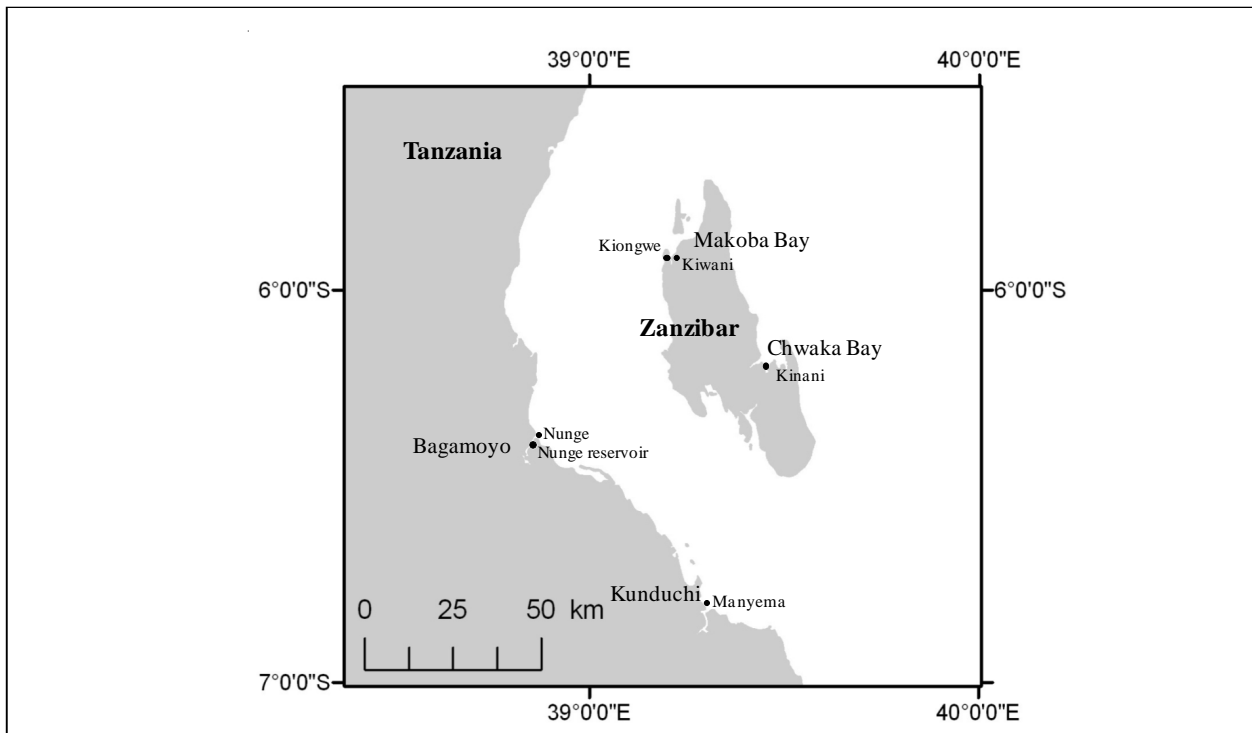


Figure 1: Map of locations of the studied creeks in Zanzibar and along the Tanzanian mainland coast

Bay/Area	Creek/Site	Activities	Status
Makoba	Kiwani	Fishing (hook and lines)	Undisturbed
Chwaka	Mapopwe		
	Kinani		
Bagamoyo	Mbegani		
Makoba	Kiongwe	Occasional fishing	Disturbed
Bagamoyo	Nunge		(mangrove clear-cut)
Kunduchi	Manyema (salt farm 1)	Solar salt production	Disturbed
	Manyema (salt farm 2)		(mangrove clear-cut +
Bagamoyo	Nunge (salt farm 3)	saltworks and fish farm)	
Makoba	Makoba fish farm	Fish pond aquaculture	

1.9 cm was used for collecting fish samples. Two hauls, covering an area of about 170 m² each, were performed at every site once a month (i.e., two hauls at one site each day). Collected fish specimens were kept in ice-boxes prior to be taken to the laboratory. Fish total length was measured to the nearest 0.1 cm. All individuals were counted and identified to the lowest taxonomic level possible according to Smith and Heemstra (1991). Information about feeding guilds (trophic levels) of fish species was obtained using FishBase (Froese and Pauly, 2009), peer-reviewed published articles and field observations. Fish samples for determination of carbon (¹³C) and nitrogen (¹⁵N) stable isotope compositions were collected in from three undisturbed sites and two disturbed salt-producing reservoirs using seine net. Because of uneven spatial distribution of various fish species only three species (i.e., *Mugil cephalus*, *Gerres oyena* and *G. filamentosus*) that had sufficient number of individuals in both undisturbed and disturbed sites were collected. The aim was to investigate if there was a shift in diet caused by mangrove deforestation for solar salt production. Muscle tissues were sampled from 30 individuals of *M. cephalus*, 25 individuals of *G. oyena* and 20 individuals of *G. filamentosus*. Dry muscle samples were grinded after having removed lipids according to Bligh and Dyer (1959). The carbon and nitrogen

isotopic composition was determined using a Fisons element analyzer coupled on-line via a Finnigan ConFlo II, with a Finnigan Delta-S mass spectrometer. Carbon and nitrogen isotope ratios were expressed in the delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) relative to Vienna PDB and atmospheric nitrogen. Samples were analyzed at the Stable Isotope Laboratory at University of California, Davis, USA.

2.3. Data analysis

Differences in fish density, species number and diversity index (H') were first examined in 20 undisturbed control sites (eight downstream, eight in the intermediate area and four upstream) using one-way ANOVAs. In general, the 20 undisturbed sites showed similar results, especially in the uppermost sites. Therefore, as the intention was to compare deforested sites with undisturbed control areas upstream, all further analysis of trophic composition involved four undisturbed and six disturbed sites (two cleared sites, three reservoirs for solar salt farm constructions and one reservoir for fish farming). In order to reduce the risk of bias from large differences in habitat characteristics and water conditions in different reaches within the creek systems (Mwandya *et al.*, 2010), the four undisturbed upstream sites were chosen to limit variability in habitat composition and water depth that resemble the disturbed sites. One-way ANOVAs were used to test for differences in all fish community indices (i.e., density, species number and diversity) and trophic group variables among sites using pooled data of similar disturbance states (i.e., undisturbed sites, cleared sites and reservoirs). Statistical analysis of trophic groups was performed on three functional guilds (i.e., omnivores, zoobenthivores/piscivores and zoobenthivores), chosen since they were relatively common and comprised comparable and sufficient number of individuals at each site ($n > 6$, Figure 2). Homogeneity of variances was tested using Levene's (1960) test, and if necessary data were square root or $\log_{10}(x + 1)$ transformed to achieve the assumptions for equal variances. However, because the densities of all trophic groups and species number of zoobenthivores/piscivores data did not showed homogeneity of variances even after transformation, data were tested using the non-parametric Kruskal-Wallis test. Games-Howell post-hoc test was used for this type

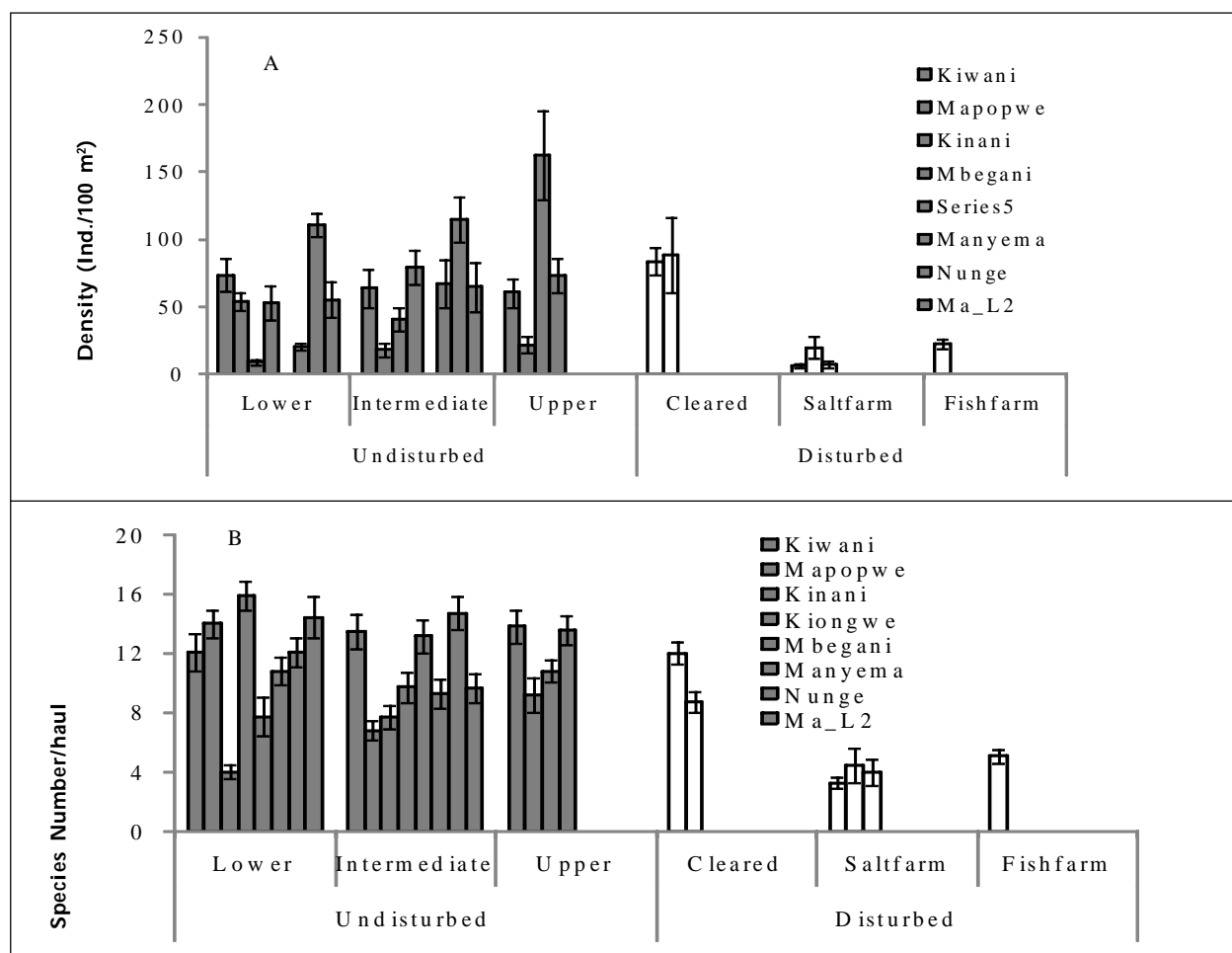


Figure 2: Mean (± SE) of (A) Density (B) Species number and (C) Diversity (H') of fish in undisturbed sites (grey bars) in different parts (lower, intermediate and upper) of the creeks and in disturbed sites (white bars) at the upper parts of various creek systems

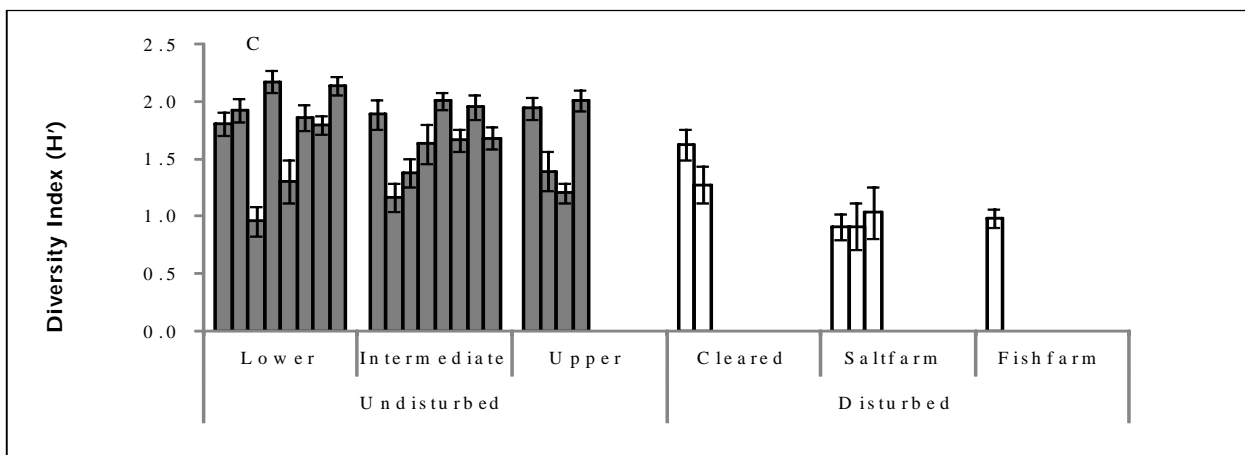


Figure 2 (Cont.)

of data (Field, 2000), while Hochberg’s GT2 was used as a post-hoc test for data which met homogeneity of variances. Multivariate analyses of functional group data were achieved with ANOSIM (analysis of similarities) and SIMPER (similarity of percentages) using the PRIMER 6 software package (Clarke and Warwick, 1994). The multivariate analyses were performed using pooled data of fish densities of the three trophic groups (i.e., omnivores, zoobenthivores/piscivores and zoobenthivores) from similar sites. To reduce the influence of the dominant species, data were square root-transformed. Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between undisturbed and disturbed sites was achieved using one-way ANOVAs. Comparisons of stable isotope signatures were made between sites of the same creek and those in other creeks for each fish species separately. Because of unbalanced sample sizes, a Hochberg’s GT2 was applied as a post-hoc test for data which showed homogeneity of variances (Field, 2000).

3. Results

3.1. Fish species number, density and diversity

In general, densities, species number, and diversity (H') of fish were lowest in the reservoirs based on pooled data (Figure 2). Species number showed significant differences among uncleared sites, cleared sites and reservoirs. In terms of diversity, the reservoirs differed significantly from the uncleared and cleared sites (Games-Howell test, $p < 0.001$), while there were no differences between the uncleared and cleared sites themselves.

3.2. Composition of trophic groups

A total of seven feeding groups of fish were encountered during the whole sampling period (Figure 3 and Table 2), with the highest number being recorded at the uncleared sites (ranging from four to seven groups in

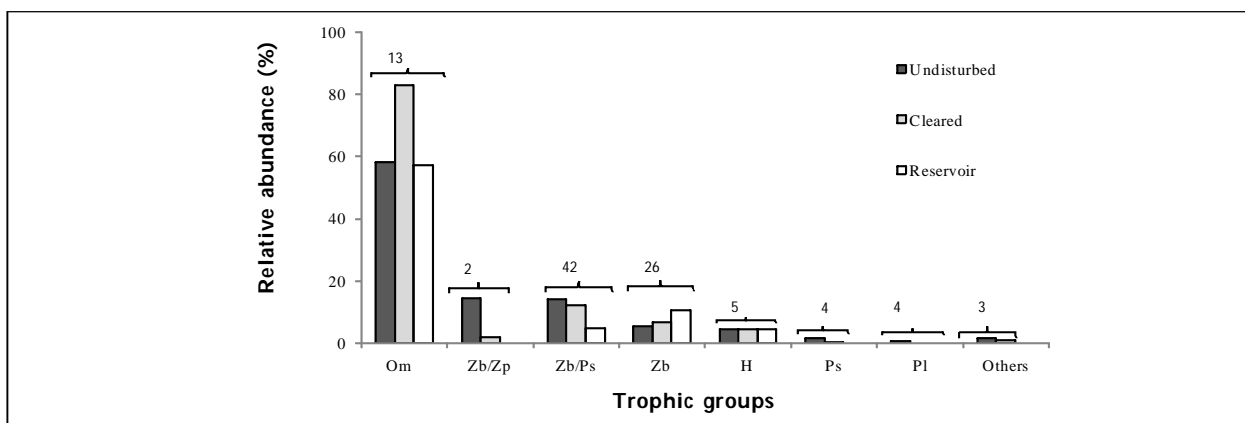


Figure 3: Overall relative proportions in abundance of various feeding guilds in mangrove creek systems subjected to deforestation, cleared only and reservoirs for salt and fish farms along the coastline of Tanzania

Note: Om = omnivores; H = herbivores; Zb = zoobenthivores Zp = zooplanktivores; Ps = piscivores; Pl = planktivores; and others = unidentified; Species number for each category are shown on top.

Table 2: Fish species from mangrove creeks along the coastline of Tanzania separated into trophic groups based on FishBase (Froese and Pauly, 2009) and field observations. Feeding guilds: (H) herbivores, (PI) planktivores, (Zb) zoobenthivores, (Ps) piscivores, (Zpl) zooplanktivores, and (Om) omnivores, Sites: (U) uncleared, (C) cleared, (RS) reservoir for saltfarms and (RF) reservoir for fish farm

Family/Species	Trophic Group	Sites	Family/Species	Trophic Group	Sites
Acanthuridae			Hemiramphidae		
<i>Acanthurus blochii</i>	H	U,C,RF	<i>Hyporhamphus improvisus</i>	Zb	U,RS
<i>Acanthurus mata</i>	PI	U	Leiognathidae		
Ambassidae			<i>Leiognathus eguulus</i>	Zb/Ps	U,C
<i>Ambassis gymnocephalus</i>	Zb/Ps	U,C,RS	<i>Leiognathus elongatus</i>	Zb	U,C
<i>Ambassis natalensis</i>	Zb	U,C,RF	<i>Leiognathus fasciatus</i>	Zb/Ps	U
Antennariidae			<i>Gaza minuta</i>	Zb/Ps	U
<i>Antennarius pictus</i>	Zb/Ps	U	Lethrinidae		
Apogonidae			<i>Lethrinus mineatus</i>	Zb/Ps	U
<i>Apogon lateralis</i>	Zp/Zb	U,C	<i>Lethrinus nebulosus</i>	Zb/Ps	U
<i>Sphaeramia orbicularis</i>	Zb	U	<i>Lethrinus variegatus</i>	Zb	RS
Atherinidae			<i>Lethrinus genivittatus</i>	Zb/Ps	U
<i>Atherina afra</i>	Zb/Ps	U	<i>Lethrinus harak</i>	Zb/Ps	U
<i>Atherinomorus duodecimalis</i>	Zb/Ps	U	Lutjanidae		
Belonidae			<i>Lutjanus arbacularis</i>	Zb/Ps	RF
<i>Strongylura leiura</i>	Zb/Ps	U,RS	<i>Lutjanus argentimaculatus</i>	Zb/Ps	U,C,RF
<i>Tylosurus crocodilus crocodilus</i>	Ps	C,RS	<i>Lutjanus ehrenbergii</i>	Zb/Ps	U,C
Carangidae			<i>Lutjanus fluviflamma</i>	Zb/Ps	U,RF
<i>Alectis indicus</i>	Zb/Ps	U,C	<i>Lutjanus monostigma</i>	Zb/Ps	U,RS
<i>Caranx papuensis</i>	Zb/Ps	U,C	<i>Lethrinus rubrioperalatus</i>	Zb/Ps	RS
<i>Caranx heberi</i>	Zb/Ps	U,C,RS	Monodactylidae		
<i>Caranx ignobilis</i>	Zb/Ps	U,C	<i>Monodactylus argenteus</i>	Om	U,C,RS
<i>Caranx sexfasciatus</i>	Zb/Ps	U,RS	Mugilidae		
<i>Scomberoides lysan</i>	Zb/Ps	U	<i>Liza macrolepis</i>	Om	U,C,RS,RF
<i>Trachinotus blochii</i>	Zb	U,C	<i>Mugil cephalus</i>	Om	U,C,RS,RF
Chanidae			Mugilidae spp.	Om	U,C,RS,RF
<i>Chanos chanos</i>	Om	U,C,RS,RF	Mullidae		
Cichlidae			<i>Mulloidichthys flavolineatus</i>	Zb	U
<i>Oreochromis mossambicus</i>	Om	U,C,RS	<i>Parupeneus macronemus</i>	Zb	U
Clupeidae			<i>Parupeneus barberinus</i>	Zb	U
<i>Sardinella gibbosa</i>	Zb	U	<i>Parupeneus cinnabarinus</i>	Zb	U
Dactylopteridae			<i>Upeneus tragula</i>	Zb	U

Table 2 (Cont.)

Family/Species	Trophic Group	Sites	Family/Species	Trophic Group	Sites
<i>Dactyloptera peterseni</i>	Zb	U	Serranidae		
Elopidae			<i>Epinephelus malabaricus</i>	Zb/Ps	U
<i>Elops machnata</i>	Zb/Ps	C,RS	<i>Epinephelus merra</i>	Zb/Ps	U
Engraulidae			<i>Epinephelus tukula</i>	Zb/Ps	U
<i>Stolephorus indicus</i>	Zb/Ps	U	Siganidae		
<i>Thryssa baelama</i>	Zb/Ps	U,RF	<i>Siganus canaliculatus</i>	H	U,C,RS
Ephippidae			<i>Siganus sutor</i>	H	U,C
<i>Platax arabularis</i>	Om	U,C,RS,RF	Sillaginidae		
<i>Platax teira</i>	Om	U,RS,RF	<i>Sillago sihama</i>	Zb	U,C,RS
Fistularidae			Sparidae		
<i>Fistularia petimba</i>	Ps	U	<i>Acanthopagras berda</i>	Zb/ps	RS
Gerreidae			Sphyraenidae		
<i>Gerres acinaces</i>	Zb	U,C	<i>Sphyraena baraccuda</i>	Zb/Ps	U,C
<i>Gerres filamentus</i>	Zb	U,C,RS,RF	<i>Sphyraena chrysotaenia</i>	Zb/Ps	U
<i>Gerres oyena</i>	Zb/Ps	U,C,RS,RF	<i>Sphyraena flavicauda</i>	Zb/Ps	U
Gobiidae			<i>Sphyraena forsteri</i>	Zb/Ps	U
<i>Acentrogobius audax</i>	Zb	C	<i>Sphyraena jello</i>	Zb/Ps	U
<i>Amblygobius albimaculatus</i>	H	U,CRS	<i>Sphyraena obtusata</i>	Ps	U
<i>Arothron hispidus</i>	Om	U,C,RS	<i>Sphyraena putnamiae</i>	Zb/Ps	U,C
<i>Arothron immaculatus</i>	Om	U,RS	Syngnathidae		
<i>Bathygobius cotticeps</i>	Zb	U,C,RS	<i>Hippichthys spicifer</i>	?	U,C
<i>Bathygobius fuscus</i>	Zb	C,RS	Synodontidae		
<i>Faronigobius reichei</i>	Om	C,RS	<i>Synodus variegatus</i>	Ps	U,RS
<i>Glossogobius callidus</i>	Zb	U,C	Teraponidae		
<i>Gobiidae sp</i>	?	C	<i>Terapon jarbua</i>	Om	U,C,RS
<i>Oxyurichthys ophthalmonema</i>	Zb/Ps	U,C,RS	<i>Pelates quadrilineatus</i>	Zp/Zb	U,C,RS
<i>Oxyurichthys papuensis</i>	Zb/Ps	U,C	<i>Terapon theraps</i>	Zb/Ps	U,C
<i>Psammogobius knysaensis</i>	Zb	U	Tetraodontidae		
<i>Yongeichthys nebulosus</i>	Zb	U,C,RS	<i>Arothron immaculatus</i>	Om	RF
Haemulidae			<i>Arothron stellatus</i>	Zb	U,RS
<i>Pomadasys kaakan</i>	Zb	U,C	<i>Canthigaster bennetti</i>	Zb	U
<i>Plenctorhynchus plagiodesmus</i>	Zb/Ps	U	<i>Chelonodon laticeps</i>	Zb	U
Kyphosidae			<i>Unknown</i>	?	U,C
<i>Kyphosus cinerascens</i>	H	RS			

the particular sites), whilst the reservoirs had the lowest (four groups) (Figure 3). For the relative number of species belonging to different feeding guilds, zoobenthivores/piscivores were the most diverse group (44% of all species) followed by zoobenthivores (27%) and omnivores (14%). In terms of relative abundance, 66% of all fishes collected were omnivores (particularly detritivores), and as much as 44% of this group were found in the uncleared areas of mangrove creeks. Other abundant groups were those composed of zoobenthivores (i.e., zoobenthivores/piscivores, zoobenthivores/zooplanktivores/and zoobenthivores). The least abundant groups were herbivores, piscivores and planktivores.

The abundant trophic groups at the various sites showed patterns related with the habitat composition and the level of mangrove disturbance (i.e., clearing only or clearing followed by construction of reservoir) (Figure 4). Densities, species number and diversity (H') of omnivores were higher at the cleared and undisturbed

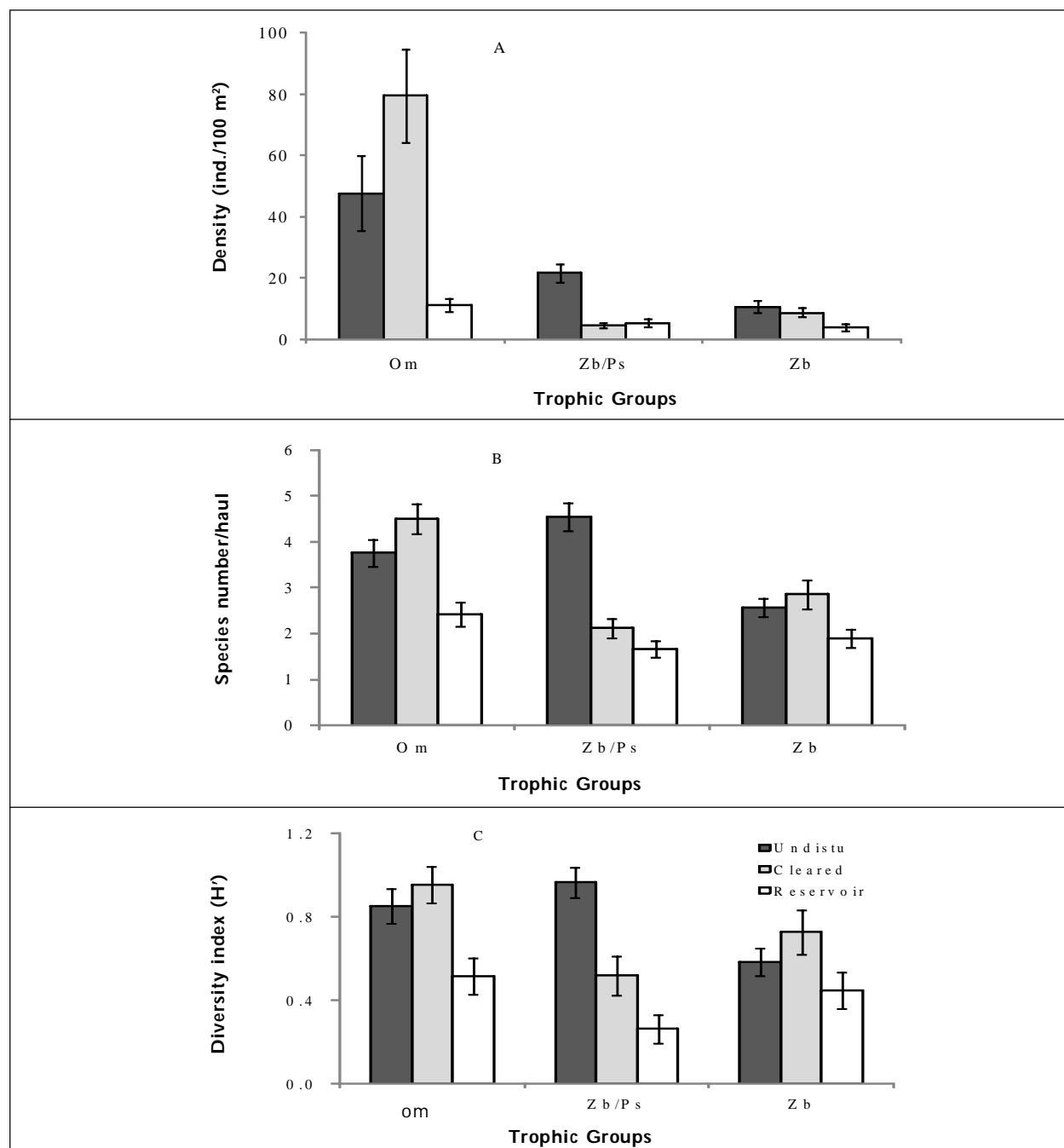


Figure 4: Mean (\pm SE) of density (A), Species number (B) and Diversity (C) of different trophic groups collected from undisturbed (black bars) cleared-only (grey bars) and reservoirs (white bars) in mangrove creeks along the coastline of Tanzania

Note: Om = omnivores; Zb/Ps = zoobenthivores/piscivores; and Zb = zoobenthivores; Note the use of different ordinate scales.

sites compared to the reservoirs (Figure 4 and Table 3). Zoobenthivores/piscivores were more abundant and had higher species richness in the undisturbed sites than in cleared sites and the reservoirs. Species number and diversity in cleared sites were higher compared to the reservoirs (Figure 4b and c, and Table 3). The densities and species number of zoobenthivores were found to be higher in undisturbed and cleared sites compared to the reservoirs, but species number did not vary significantly between undisturbed sites and the reservoirs (Table 3). The herbivores had higher fish densities in the uncleared and cleared sites compared to the reservoirs. However, differences in herbivore density and densities of the three other groups (i.e., zoobenthivores/planktivores, planktivores and piscivores) were not tested statistically due to low sample sizes.

Table 3: Results of *Post hoc* comparison tests of density, species number and diversity of trophic groups among sites subject to different human activities in mangrove creeks

Trophic Group	Undisturbed vs Undisturbed vs Cleared vs			
	Variable	Cleared	Reservoir	Reservoir
Omnivores	Density	0.246	0.013	0.001
	Species number	0.289	0.003	<0.001
	Diversity (<i>H'</i>)	0.830	0.016	0.008
Zoobenthivore/ Piscivores	Density	<0.001	<0.001	<0.001
	Species number	<0.001	<0.001	<0.001
	Diversity (<i>H'</i>)	<0.001	<0.001	<0.001
Zoobenthivores	Density	0.748	0.013	0.031
	Species number	1.000	0.084	0.026
	Diversity (<i>H'</i>)	0.730	0.637	0.097

3.3. Multivariate patterns

Multivariate analysis based on density data showed variations in fish assemblage structure of omnivores and zoobenthivores/piscivores among sites with different human influences (one-way ANOSIM; omnivores: Global $R = 0.146$, $p = 0.004$, zoobenthivores/piscivores: Global $R = 0.361$; $p = 0.001$), while no separation was found for zoobenthivores (Global $R = 0.068$, $p = 0.016$). Pairwise comparisons showed that the assemblage structure of omnivorous fish in uncleared and cleared sites differed significantly from those found in reservoirs, but did not vary between the uncleared and cleared sites (Table 4). Fish assemblage structures of zoobenthivores/piscivores in the uncleared sites differed from the cleared sites and reservoirs (Table 4). SIMPER analysis showed that *Gerres oyena* and *Pelates quadrilineatus* were those species that contributed most (about 15-35%) to

Table 4: Summary of one-way ANOSIM (*R*) of three common trophic groups found in all areas of the creek systems subject to different human activities

Habitat Status	Trophic Groups		
	Om	Zb/Ps	Zb
Undisturbed vs. Cleared	-0.042 ns	0.426**	0.085 ns
Undisturbed vs. Reservoir	0.237 **	0.432**	0.080 ns
Cleared vs. Reservoir	0.305**	0.059 ns	0.032 ns

Note: ** = significant at $p < 0.01$, and ns = not significant at $p < 0.05$.

dissimilarities between uncleared and disturbed sites (cleared sites and reservoirs) in the group zoobenthivores/piscivores. *Elopse machnata* which was abundant in the reservoirs for salt farms contributed 37% to the differences, while *Lutjanus argentimaculatus*, abundant in the fish farm reservoir, contributed 44% to the separation in zoobenthivores/piscivores. For omnivores, the detritivorous species *Chanos chanos*, *Mugil cephalus* and *Mugilidae* sp., which were relatively abundant in uncleared and cleared sites, contributed 20-40% to the differences in assemblage structure.

3.4. Environmental variables

Generally, deforested areas of mangrove creeks had higher mean salinity values (47-55) and water temperature (ranged 35-36 °C) compared to the values (35-36 and 29-30 °C, respectively) in undisturbed areas fringed by mangrove forest.

3.5. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of fish muscle tissues

The ranges in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the muscle tissues of fish collected from mangrove creeks in the order of disturbed (reservoirs) and undisturbed areas for the different fish species were 4.31 ‰ to 7.99 ‰ and -16.19 ‰ to -21.26 ‰ for *M. cephalus*, 6.37 ‰ to 9.65 ‰ and -16.03 ‰ to -20.75 ‰ for *G. Oyena*, and 8.19 ‰ to 8.93 ‰ and -12.13 ‰ to -21.24 ‰ for *G. filamentosus* (Figure 5). Part of the differences between the reservoir and undisturbed

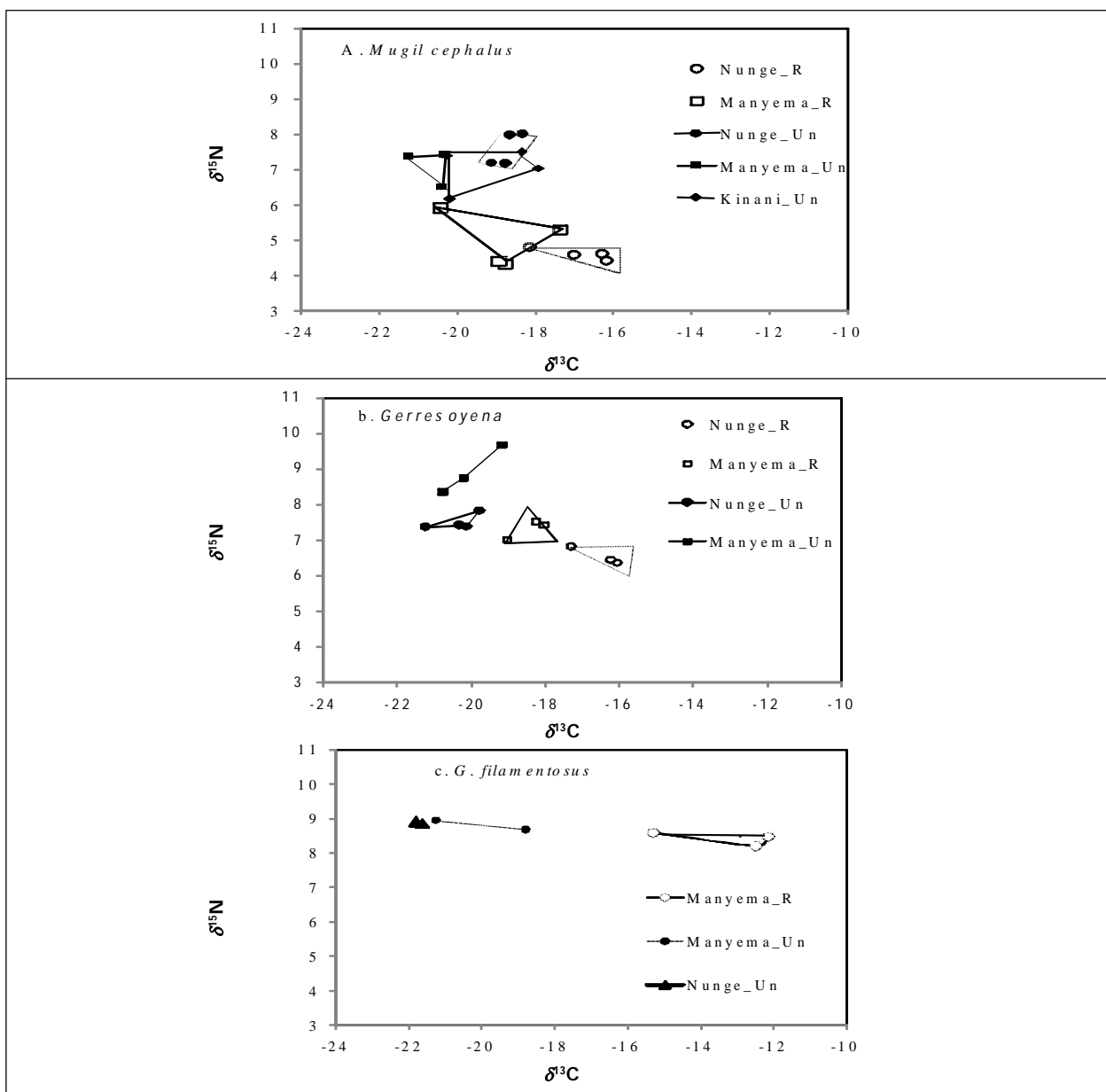


Figure 5: Patterns of stable isotope of ^{13}C and ^{15}N values in muscle tissues of fish from undisturbed (Un) sites (filled symbols) and disturbed sites (R = reservoir) (open symbols) in different mangrove creeks

sites could be attributed to salinity effect. The high-saline areas of the reservoirs showed significant increases in $\delta^{13}\text{C}$ values for all three species when compared to the undisturbed sites, while only one species showed a change (decrease) in $\delta^{15}\text{N}$ (Figure 6).

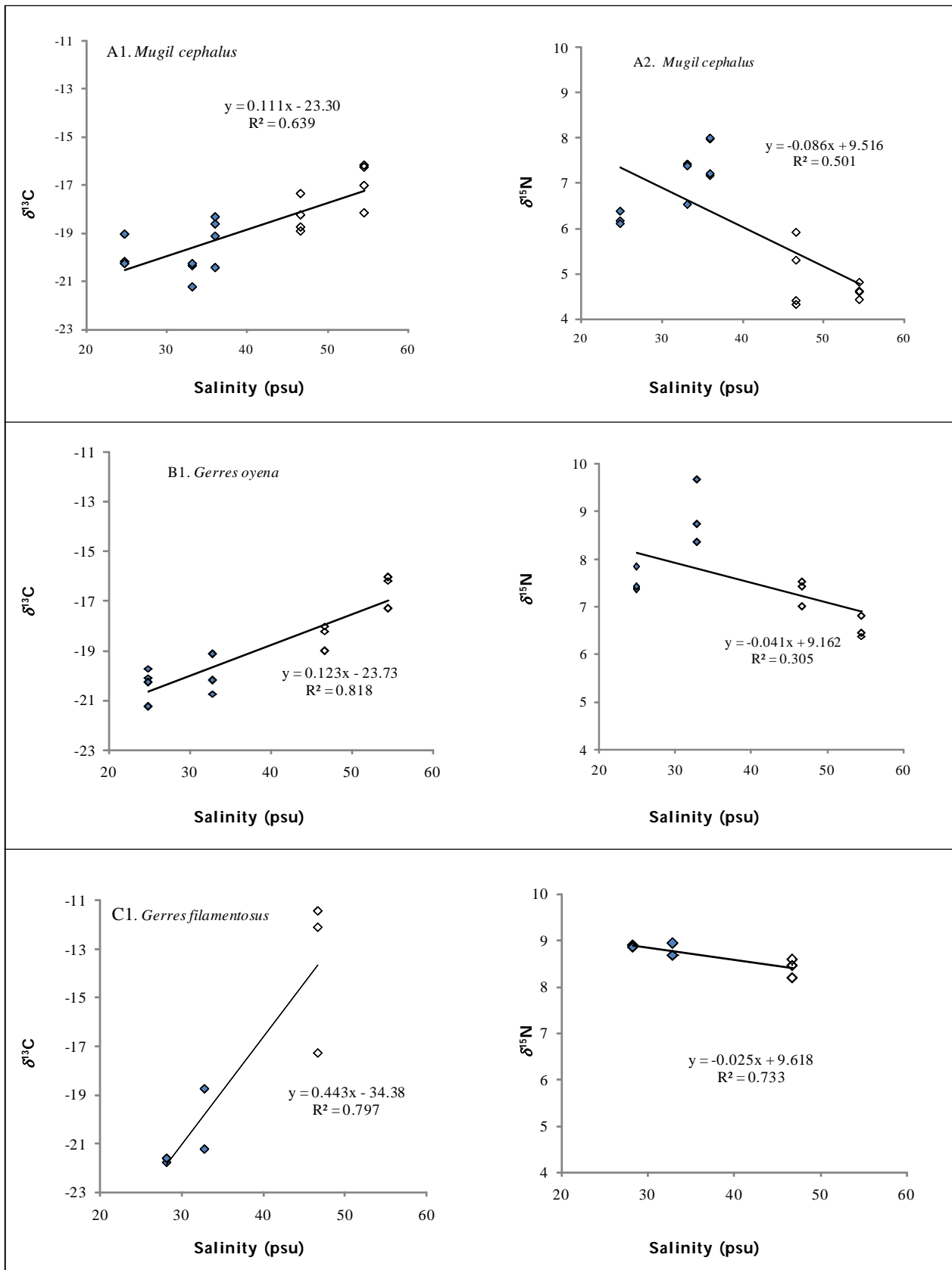


Figure 6: Relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and salinity in muscle tissue of *M. Cephalus* (A), *G. Ogena* (B) and *G. Filamentos* (C). Undisturbed sites (filled symbols) and disturbed sites (open symbols)

The omnivorous *M. cephalus* caught from disturbed sites showed a significant decrease in $\delta^{15}\text{N}$ of almost one trophic level (about 2.5%) but no change in $\delta^{13}\text{C}$ values (Figure 7; and Table 5). *Gerres oyena* showed changes in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between the disturbed and undisturbed sites (Table 5). For *G. filamentosus* on the other hand, there was no change in $\delta^{15}\text{N}$ but a strong shift of about 6% in $\delta^{13}\text{C}$ between disturbed and undisturbed sites (Figure 7; and Table 5).

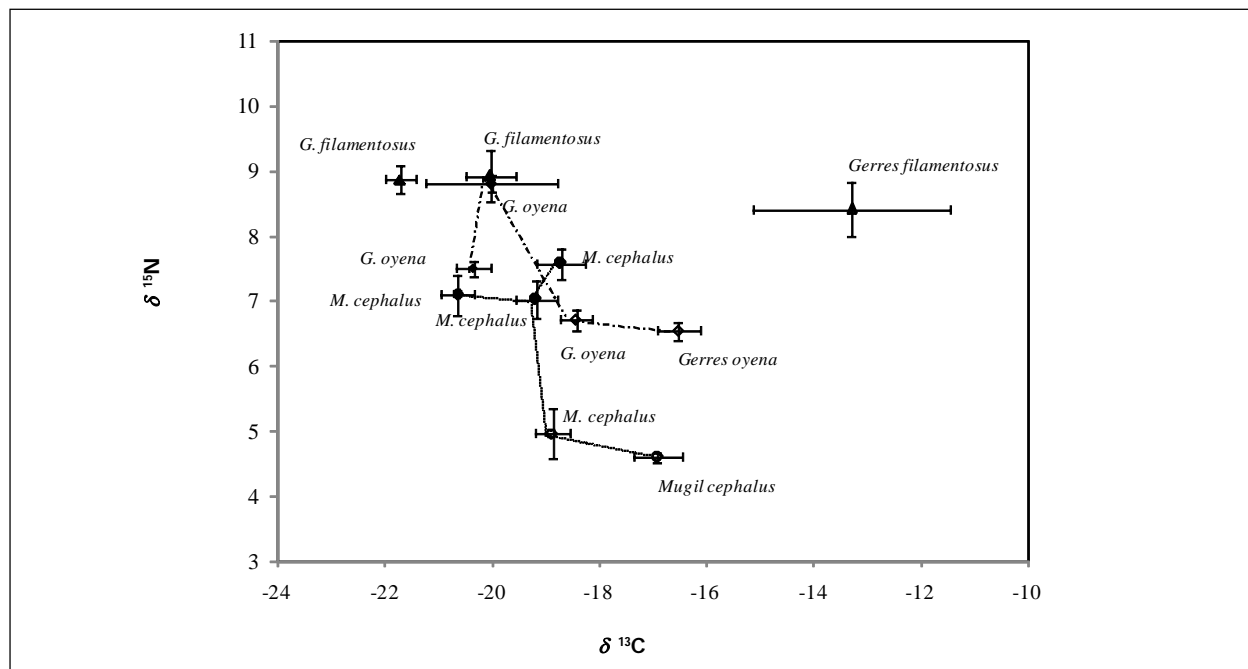


Figure 7: Average (\pm SE) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle tissues of *M. cephalus*, *G. oyena* and *G. filamentosus* collected from undisturbed (closed symbols) and disturbed (open symbols) creek sites

Table 5: Results of *Post hoc* comparison tests of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of muscle tissues of different fish species caught from various sites in mangrove creeks. Und = undisturbed (no mangrove clearing) and Dis = disturbed sites (reservoirs for solar salt farms made after mangrove clear-cut)

Site Comparison		<i>M. cephalus</i>		<i>G. oyena</i>		<i>G. filamentosus</i>	
		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Nunge	Und vs. Dis	<0.001	ns	<0.05	<0.001		
Manyema	Und vs. Dis	<0.01	ns	<0.01	ns	ns	<0.05
Nunge vs Manyema	Und vs. Und	ns	ns	ns	ns	ns	ns
Nunge vs Manyema	Dis vs. Dis	ns	ns	ns	<0.05		
Nunge vs Manyema	Und vs. Dis	<0.001	ns	<0.01	<0.05	ns	<0.01
Nunge vs Manyema	Dis vs. Und	<0.001	<0.01	<0.001	<0.001		
Kinani vs Nunge	Und vs. Und	ns	ns				
Kinani vs Manyema	Und vs. Und	ns	ns				
Kinani vs Nunge	Und vs. Dis	<0.001	<0.05				
Kinani vs Manyema	Und vs. Dis	<0.001	<0.05				

Note: ns = not significant at $p < 0.05$.

4. Discussion

The findings showed that trophic organization of fish differed between disturbed and undisturbed mangrove creeks, but also that there were differences between different types of disturbance, i.e., cleared sites and reservoirs, suggesting that the extent and severity of disturbance may be important in predicting fish assemblage compositions of mangrove creek systems.

The lower number of fish encountered in the disturbed sites (reservoirs as well as cleared sites) compared to the undisturbed sites could be explained by reduced food availability and loss of refuge areas, as has been observed in other disturbed mangrove systems (Primavera *et al.*, 2007). In Tanzania inundated mangrove creeks systems are regularly used as recruitment areas for juvenile fish during low tide (Lugendo *et al.*, 2007; and Mwandya *et al.*, 2009). In general, distribution patterns are species- and site-specific (Mwandya *et al.*, 2009). Such patterns may be a strategy to reduce the intra- and interspecific competition (for food or space) which enhance recruitment. Juvenile fishes are assumed to be associated to mangrove habitats because of better feeding conditions, optimal growth and refuge availability (Cocheret de la Morinière *et al.*, 2004). The relative importance of the various factors affecting juvenile distribution may vary depending on fish species (Selleslagh and Amara, 2008) although most often multiple factors influence fish assemblages (Nagelkerken *et al.*, 2008). This study showed that food abundance particularly in the reservoirs may be affected by loss of hard substratum provided by trunks, prop-roots and pneumatophores for attachments of prey items (Nagelkerken *et al.*, 2008). This could partly explain the lower abundance and species number of invertebrates- and fish-feeders in the reservoirs compared to the cleared and undisturbed sites.

Habitat transformations may change the patterns of resource availability by creating heterogeneous environments constituting a mosaic of optimal and sub-optimal habitats (Krebs *et al.*, 2007; and Primavera *et al.*, 2007). In this study, the effects of mangrove deforestation followed by changes in land-uses on fish assemblages and trophic composition extended beyond the loss of plant canopies and habitat structure provided by mangroves. In addition to reduced habitat complexity in the reservoirs, the water flow is restricted and only a certain amount is allowed to pass through the gates. The abiotic and biotic consequences of limited water supply and habitat loss were extreme with higher salinity and water temperature, changes in bottom substrate grain size from mud/sandflats to soft mudflats, and flourishing of benthic microflora (Mwandya *et al.*, 2009). High salinity and water temperature that characterized the reservoirs may restrict less tolerant species to thrive there due to physiological impacts including lower growth and survival of fish due to increasing energy costs (Wuenschel *et al.*, 2004; and Valentine-Rose *et al.*, 2007). Another important aspect following the construction of reservoirs was that the gates function as physical barriers restricting the movement and migration by fish. Thus, it is likely that a combination of changes in water conditions and denied access to the reservoirs might have had impacts on fish community structure and trophic organization.

Therefore the higher abundance of omnivorous fish in the reservoirs could be explained by the presence of preferable food from benthic communities as well as their ability to proliferate under high salinity and water temperature. Among the most dominant omnivores in the present study were *Chanos chanos* and *Mugil cephalus*, which can proliferate in a broader range of benthic habitats, than invertebrate—and fish feeders. Similarly to this findings, Öhman *et al.* (1997) found high abundance of omnivores in disturbed reef systems, although the fish assemblages in their study were dominated by other species. The results support the hypothesis that fish may respond in different ways to habitat suitability, which can vary significantly at local scale or due to human-induced changes (Selleslagh and Amara, 2008).

The present study indicates little variability in carbon and nitrogen signatures in undisturbed sites. However, muscle tissues of fish from deforested solar salt pond reservoirs were generally depleted of ^{13}C and ^{15}N isotopes, although the level of isotope ratios varied depended on fish species and creeks concerned. Individuals of *Mugil cephalus* collected from deforested sites had significantly lower ^{15}N values than individuals collected in forested sites, but no significant variations in ^{13}C values. This indicates a dietary shift from an omnivorous diet to a diet common for herbivores or planktivores. *Gerres oyena* is classified as a piscivore or a zoobenthivore but the lower values of both ^{13}C and ^{15}N in the samples from disturbed creeks indicate a change from a fish diet to more benthos. However, *G. filamentosus* had comparable ^{15}N values in undisturbed and disturbed sites but a strong shift in ^{13}C , with higher values in disturbed sites. This could be related to the extreme values of salinity in the disturbed creeks. Plants under such conditions will be under physiological stress which will have great effects on ^{13}C values (Wei *et al.*, 2008). These findings show that undisturbed and disturbed sites have different food webs and that the three species adopt different feeding strategies as a

response to available food. Hence, the results of ^{13}C and ^{15}N values, trophic composition and fish assemblage composition together provide a better understanding of the negative impacts of mangrove deforestation followed by construction of solar salt ponds and/or fish farms.

The results revealed negative impacts of mangrove deforestation and land-use change on densities, species numbers, diversity and trophic organization of fish as supported by differences between disturbed and undisturbed sites. In the process of future development and expansion of economic activities within mangrove forests along the coastline of Tanzania, an increased demand for new and pristine mangrove areas is expected. Because of these foreseeable demands and the negative outcome on fish communities, future development activities such as fish farming and saltworks should be restricted to already degraded areas, in order to preserve the remaining mangrove forest.

Conclusion

The findings revealed that a combination of mangrove deforestation and construction of solar salt farms and fish farms negatively affected fish assemblages and functional groups. Based on the negative impact of mangrove deforestations and land-use changes, more impacts are expected with the current increase in demand of mangrove areas for other economic activities to meet exuberating demands associated with global increase in human population. However, salt production and fish farming are important economic activities, which can help to improve the livelihood of coastal people if coastal resource managers and planners set up zonings to ensure that these activities do not jeopardize the ecological and community roles of mangrove ecosystems at an alarming level.

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