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Seasonality in fish assemblage structure in an East African mangrove creek

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The spatial and seasonal structures of fish assemblages in a tropical mangrove tidal creek, Tudor, Kenya, were analysed from monthly survey data, extending from October 2007 to July 2008, and covering the north-east (NEM; October–March) and south-east (SEM; April–July) monsoon seasons. A total of 2 118 individuals, representing 84 species belonging to 49 families, were caught. *Gerres oyena*, *Terapon jarbua* and *Lutjanus fulviflamma* were the dominant species in all seasons. There was within-creek seasonal variability in species abundance and diversity. Overall, the mean density (individuals m^{-2}) was higher during the SEM season (0.368; SE 0.078) than the NEM season (0.255; SE 0.041). The NEM season had significantly more species ($n = 69$) than the SEM season ($n = 63$) ($\chi^2 = 317.891$, $p < 0.0001$). Two-way ANOVA indicated the influence of season and habitat on abundance of some species. The abundance of creek-resident species was significantly influenced by site whereas abundance of creek-dependent and transient species was influenced by interaction between seasons and stations. Bray-Curtis cluster analysis defined two species assemblages, reflecting differences in temporal and spatial use of the creek by the fish species. Correspondence analysis indicated that seasonal fish assemblages were only distinct at the mouth of the creek with less clear seasonal structure in the upper region of the creek.

Keywords: conservation, habitat functions, seasons, species abundance

Introduction

Mangrove tidal creeks and estuarine habitats are highly productive transitional zones that are occupied by a combination of brackish-water and marine species, including many juveniles (Claridge et al. 1986). The fact that they support commercial fisheries and serve important ecological functions as nursery grounds for fish and macro-crustaceans (Blaber 1997) makes it important to examine factors that affect their assemblage structures. Furthermore, variability in community structure may affect ecological services of ocean systems (Worm et al. 2006), including creeks (Lotze et al. 2006). Research on estuarine fish communities is more developed in temperate regions, where salinity has been regarded as a key regulating factor (Haedrich 1983, Potter et al. 1986, Marshall and Elliott 1998, Harris and Cyrus 2000). However, the factors regulating fish community structure of tropical estuarine habitats such as creeks are poorly documented but are thought to be more complex and include a variety of biotic (Barry et al. 1996) and abiotic factors such as salinity, turbidity and habitat structure (Lowe-McConnell 1987, Blaber 1997). The extent to which spatial dimensions in community structure interact with seasonality to influence fish assemblages has received little attention in the Western Indian Ocean, even though it may be significant in structuring estuarine communities.

In Kenya, work on fish communities of tidal creeks is limited mainly to descriptions of species composition (e.g. Little et al. 1988, Kimani et al. 1996, Oyugi 2005) without analysing the structure of fish assemblages and the factors that influence species composition and distribution. This study bridges that gap by describing the fish assemblage structure of Tudor Creek and by examining the influence of monsoon seasonality on the distribution and abundance of fish species within the creek. Tudor is the largest creek in Kenya and is an important artisanal fisheries ground. Our study attempts to provide a baseline for monitoring and management of these systems.

Material and methods

Study area

This study was carried out in Tudor Creek, Mombasa, Kenya (Figure 1). Three seasonal rivers, Kombeni, Tsatu and Mtsapuni, flow into the creek on a seasonal basis (Wakwabi 1993). Freshwater input occurs mainly through surface-water flow from Kombeni River and, to a lesser extent, from Tsatu and Mtsapuni (Norconsult 1975). The offshore currents and the outward ebb currents near the entrance to the creek flow northwards during both the north-east monsoon (NEM) and the south-east monsoon (SEM) seasons. The currents at the entrance channel of the creek behave like a stream reversing in direction with flooding and ebbing tides and hence conditions remain more marine, while the currents are weaker towards the upper regions of the creek (Wakwabi 1993). The Kenyan coast is influenced by both north-easterly and south-easterly monsoon winds (McClanahan 1988). The NEM (October–March) is a period of calm weather, elevated temperatures, high salinities and high phytoplankton production, whereas the SEM

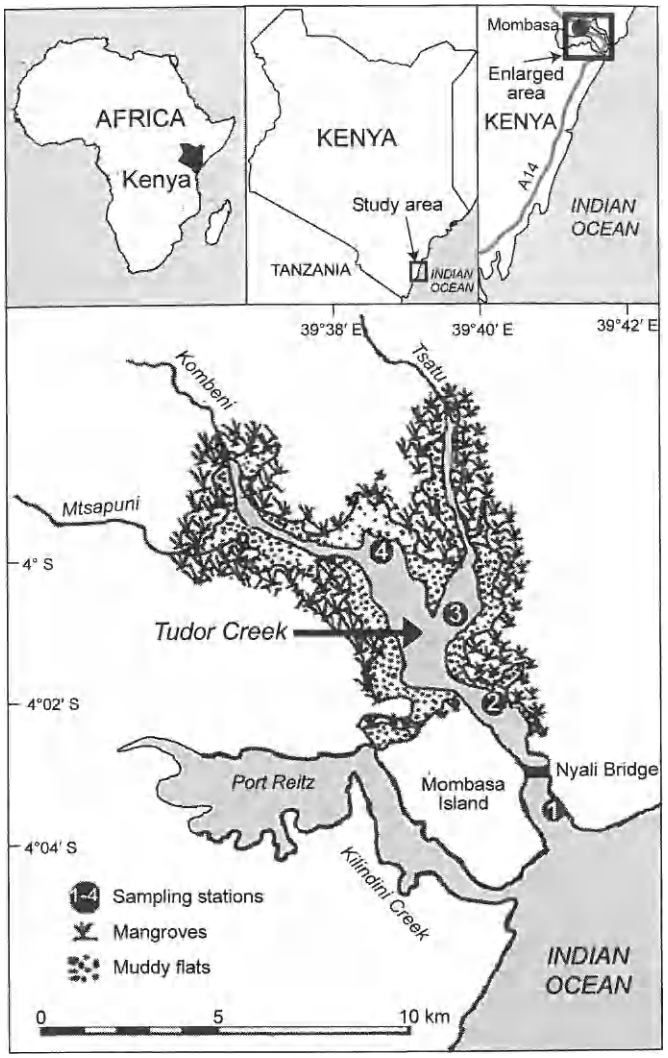

Figure 1: Map of the study area showing Tudor Creek, Kenya, and the sampling stations (1–4) within the creek

(April–July) is characterised by rough seas, fast currents, cool temperatures and low salinities (McClanahan 1988). This seasonality affects chemical and biological processes along the coast. For example, spawning and recruitment of fish and invertebrates to benthic populations predominantly occur during the calm NEM season (Nzioka 1979, Kaunda-Arara and Ntiba 1997).

Field sampling

Sampling was done at four stations (1–4) within the creek (Figure 1). The stations were selected to cover the upper, middle and lower regions of the creek and to be sufficiently wide apart to be spatially distinct. Station 1 was near the mouth of the creek on a partially exposed sandy beach with patches of seagrasses; Station 2 was a beach of muddy substrate backed by a fringe of mangroves; Station 3 was at the mouth of a small seasonal channel leading into the creek, which had a muddy substratum with a narrow fringe of mangroves; Station 4, the innermost site, had an exposed beach of sand–muddy substratum. Stations 1 and 2 were 4 km apart, Stations 2 and 3 were 2 km apart and the distance between Stations 3 and 4 was 3 km.

Samples of fish were collected once every month, between October 2007 and July 2008, during high spring tides (normally shortly after the full or new moon). A motorised rubber boat (3 m long) was used to access the stations. Sampling at each station was conducted using a 25 m × 2 m beach seine-net of ¾ inch (19 mm) mesh size. The net was laid perpendicular to the shore and then hauled against the current by four people pulling from the deepest part of the station towards the shore. Each single haul swept an area of approx. 327 m^2 (from knowing the mouth area of the nets and the distance towed). For each replicate sample, all the fish caught were preserved in 5% formalin in the field. In the laboratory, fish were identified to species, counted and measured (standard length to the nearest millimetre). Species identification followed Smith and Heemstra (1991), Randall (1992), Allen (1997) and Lieske and Myers (2001).

At each station, physico-chemical variables investigated included turbidity, temperature, salinity and water depth, which were measured before sampling the fish. Four random replicate measurements of the physico-chemical parameters were taken at different points within the stations. Turbidity was measured using a Secchi disc, surface water temperature (±0.1 °C) was measured using a hand-held mercury-in-glass thermometer and salinity was determined using a refractometer. Water depth at each station was recorded using a portable echo sounder (model SM-5).

Data analysis

Fish numbers for every replicate sample at each station were divided by the area swept to provide an estimate of species density (no. m^{-2}). Prior to statistical analysis, the density data were fourth-root transformed to normalise their distribution (Underwood 1981). The choice of parametric test was made after the data were tested for homogeneity of variances using Levene's test (Shapiro and Wilks 1966). Mean fish density and diversity indices were used to describe and compare fish assemblage structure between stations and seasons. Analysis of variance (ANOVA) test (STATISTICA 6.0) was used to test for differences in mean fish abundance between stations. Tukey HSD test was then applied to partition any observed significant differences between stations (Zar 1996). Two-way ANOVA was used to test the interaction between stations and seasons in affecting abundance of the main species.

Spatial and seasonal patterns in fish assemblage structure were investigated using multivariate correspondence analysis. Species occurring in <2% of the samples were eliminated from the correspondence analysis for easier identification of the patterns of associations. Species mean abundance matrices were computed using Log (x + 1)-transformed density data and subjected to cluster analysis. The species were clustered following the Bray-Curtis similarity index (Clarke and Warwick 1994) based on their abundance following group-average sorting. The multivariate non-metric multidimensional scaling (MDS) technique was used to group stations based on distribution of the most abundant species following Bray-Curtis similarities. PRIMER 6 and CANOCO 3.1 statistical packages were used for the multivariate analyses.

Diversity indices were determined from the Shannon-Wiener diversity index (Shannon and Weaver 1949) and Margalef's species richness index (Margalef 1968) was used to determine species richness. Pielou's index (J') (Pielou 1966) was used to determine species evenness at each station.

A species–rank abundance curve was plotted to visualise species richness and evenness and to further display relative species abundance, a component of biodiversity (Magurran 2004). The curve overcomes the shortcomings of biodiversity indices because they cannot display the relative role different variables played in their calculation (Magurran 2004).

Species were further categorised into bio-ecological groupings depending on their temporal utilisation of the creek during all or part of their life-history stages. The following groupings are modified from Smith and Heemstra (1991) and Albaret (1999):

- Creek residents: permanent residents that spend their entire life (juvenile to adult) within the creek and are highly adapted to estuarine conditions by possessing specialised physiological adaptations
- Creek dependent: opportunists or secondary residents that spend only part of their life in the creek, usually as juveniles, and generally have few physiological adaptations to estuarine conditions
- Transients: often stenothermal and stenohaline species that enter the creek only occasionally, usually when conditions there are very similar to those in the open sea. Transients generally have no specialised adaptations to estuarine conditions
- Rare: occurrence is very sporadic in the creek.

Results

Environmental parameters

The physico-chemical parameters of Tudor Creek during the study period are presented in Table 1. Mean monthly surface temperature varied between 29.74 (SD 0.30) and 28.67 °C (SD 0.36), being highest in February 2008 and lowest in June 2008. The Secchi disc depths ranged between 0.93 m (SD 0.02) in July 2008 and 0.98 m (SD 0.02) in March 2008 and salinity varied slightly between months, ranging between 33.58 (SD 0.15) in November 2007 and 34.08 (SD 0.15) in April 2008. Mean water depth was lowest in January 2008 (1.17 m, SD 0.09) and highest in May 2008 (1.38 m, SD 0.07). The highest and lowest mean temperatures were recorded at Stations 4 and 1 (29.42 °C [SD 0.17] and 28.87 °C [SD 0.21] respectively; Table 2). Mean salinity ranged from 34.00 (SD 0.12) to 33.70 (SD 0.11) at Stations 1 and 4 respectively. The highest mean water depth was recorded at Station 1 (1.38 m, SD 0.02) and lowest at Station 3 (1.23 m, SD 0.04). There was no significant difference in physico-chemical parameters in the creek between months and sampling stations (Tables 1, 2).

Species distribution

In total, 2 118 fish, belonging to 49 families and 84 species, were caught in the creek (Table 3). The family with the highest number of species was Gobiidae (11 species), contributing 19% of the total number of fish in the creek.

Table 1: Temporal variation in mean (±SE) physico-chemical parameters within Tudor Creek during the study period

Date	Temperature (°C)	Turbidity (m)	Salinity	Depth (m)
Oct. 2007	29.46 ± 0.22	0.94 ± 0.02	33.67 ± 0.14	1.35 ± 0.08
Nov. 2007	29.52 ± 0.30	0.95 ± 0.02	33.58 ± 0.15	1.28 ± 0.07
Dec. 2007	28.99 ± 0.34	0.94 ± 0.03	33.75 ± 0.13	1.19 ± 0.09
Jan. 2008	29.74 ± 0.28	0.97 ± 0.01	34.00 ± 0.28	1.17 ± 0.09
Feb. 2008	29.74 ± 0.30	0.93 ± 0.03	33.82 ± 0.23	1.38 ± 0.06
Mar. 2008	29.46 ± 0.22	0.98 ± 0.02	33.94 ± 0.19	1.30 ± 0.06
Apr. 2008	28.71 ± 0.31	0.93 ± 0.03	34.08 ± 0.15	1.26 ± 0.06
May 2008	28.86 ± 0.21	0.94 ± 0.02	33.87 ± 0.14	1.38 ± 0.07
Jun. 2008	28.67 ± 0.36	0.93 ± 0.03	33.69 ± 0.14	1.25 ± 0.07
Jul. 2008	28.73 ± 0.17	0.93 ± 0.02	33.75 ± 0.13	1.29 ± 0.07
ANOVA: F	1.96	0.77	0.92	1.00
p	0.06	0.65	0.51	0.44

Table 2: Spatial variation in mean (±SE) physico-chemical parameters within Tudor Creek, during the study period

Station	Temperature (°C)	Turbidity (m)	Salinity	Depth (m)
1	28.87 ± 0.21	0.98 ± 0.01	34.00 ± 0.12	1.38 ± 0.03
2	29.08 ± 0.18	0.93 ± 0.02	33.77 ± 0.11	1.28 ± 0.04
3	29.08 ± 0.17	0.95 ± 0.01	33.73 ± 0.09	1.23 ± 0.04
4	29.42 ± 0.17	0.93 ± 0.02	33.70 ± 0.11	1.24 ± 0.06
ANOVA: F	1.50	1.82	1.55	2.28
p	0.22	0.15	0.20	0.08

Teraponidae and Gerreidae were represented by two and one species respectively, contributing almost equally in terms of numerical abundance (~10%). Lutjanidae and Apogonidae were represented by two and three species respectively and contributed 9.1% and 7.5% respectively of the total numerical abundance of species in the creek (Table 3). Totals of 53, 46, 44 and 51 species were sampled from Stations 1, 2, 3 and 4 respectively. The species with the highest mean catch rate and numerical abundance in the creek were *Gerres oyena*, *Terapon jarbua* and *Lutjanus fulviflamma* (Table 3). During the NEM season, the most abundant species were *Siganus canaliculatus*, *L. fulviflamma* and *Aeoliscus punctulatus*, whereas *T. jarbua*, *G. oyena* and *Apogon cyanosoma* dominated during the SEM season (Table 3). The number of species in the creek differed significantly between the NEM (n = 69) and SEM (n = 63) seasons (χ^2 = 317.891, $p < 0.0001$). However, there was no significant difference in the overall mean density of fish (no. m^{-2}) between seasons (NEM = 921, SEM = 1 197; $t = -1.328$, $p = 0.186$).

Density and diversity

The overall mean fish density (no. m^{-2}) was 0.34 (SE 0.01), 0.39 (SE 0.03), 0.34 (SE 0.01) and 0.31 (SE 0.01) at Stations 1, 2, 3 and 4 respectively (Table 4). The mean fish density was significantly different between stations ($p < 0.05$). Tukey's HSD test partitioned the between-stations density variations to differences between Stations 4 and 1 and Stations 4 and 2.

The highest and lowest mean Shannon-Wiener diversity indices (H') were recorded at Stations 2 (1.96, SE 0.12)

Table 3: Mean fish density of beach-seined fish species at Tudor Creek, during the north-east monsoon (NEM) and south-east monsoon (SEM) seasons. SE denotes standard error of the mean. T = transient, CD = creek dependent, CR = creek resident, R = rare species; dashes denote absence of data

Taxon	Bio-ecological group	Total no.	% of total	Fish density (no. m^{-2})			
				NEM	SE	SEM	SE
Acropomatidae							
Acropoma japonica	R	1	0.05	0.019	0.019	–	–
Ambassidae							
Ambassis natalensis	CD	8	0.39	0.058	0.042	0.145	0.145
Apogonidae							
Apogon cyanosoma	T	148	6.97	0.986	0.418	2.811	2.076
Apogon nigripes	T	10	0.47	0.039	0.027	0.231	0.230
Apogon nigrofasciatus	T	1	0.05	0.019	0.019	–	–
Atherinidae							
Atherinomorus lacunosus	CD	36	1.69	0.387	0.347	0.464	0.320
Belonidae							
Tylosurus acus	T	2	0.09	–	–	0.261	0.174
Blenniidae							
Petroscirtes breviceps	T	34	1.60	0.309	0.206	0.754	0.361
Bothidae							
Bothus mancus	T	1	0.05	0.193	0.088	0.145	0.070
Canthigasteridae							
Canthigaster bennetti	T	1	0.05	0.039	0.039	0.029	0.029
Carangidae							
Caranx ignobilis	T	38	1.79	0.599	0.315	0.202	0.146
Caranx melampygus	T	10	0.47	0.193	0.174	–	–
Trachinotus baillonii	T	70	3.30	0.367	0.216	1.478	0.868
Trachinotus blochii	T	48	2.26	0.213	0.158	1.073	0.444
Centriscidae							
Aeoliscus punctulatus	R	102	4.80	1.971	1.089	–	–
Chanidae							
Chanos chanos	CD	1	0.05	0.019	0.019	–	–
Cichlidae							
Oreochromis mossambicus	R	2	0.09	0.058	0.042	–	–
Clupeidae							
Sardinella gibbosa	T	54	2.55	0.387	0.241	0.986	0.583
Cynoglossidae							
Paraplagusia bilineata	T	1	0.05	0.019	0.019	–	–
Engraulidae							
Stolephorus commersonii	T	7	0.34	0.083	0.031	0.026	0.026
Ephippidae							
Platax orbicularis	CD	1	0.05	0.019	0.019	–	–
Platax pinnatus	CD	3	0.14	0.058	0.042	–	–
Platax teira	CD	2	0.09	0.039	0.027	0.087	0.087
Fistularlidae							
Fistularia petimba	T	11	0.52	0.193	0.088	0.029	0.029
Gerreidae							
Gerres oyena	CD	204	9.60	1.024	0.301	4.377	2.672
Gobiidae							
Acentrogobius audax	CR	6	0.28	0.116	0.08	–	–
Amblygobius spp.	CR	1	0.05	0.019	0.019	–	–
Callogobius maculipinnis	CR	8	0.38	–	–	0.087	0.063
Favonigobius melanobranchus	CR	96	4.53	0.541	0.251	1.971	0.799
Favonigobius reichei	CR	19	0.89	0.213	0.128	0.232	0.127
Gobius albimaculatus	CR	15	0.72	0.058	0.042	0.261	0.179
Oligolepis keiensis	CR	43	2.04	0.831	0.579	–	–
Oxyurichthys ophthalmonema	CR	114	5.37	1.333	0.385	1.305	0.391
Oxyurichthys papuensis	CR	70	3.51	0.831	0.218	0.783	0.583
Yongeichthys nebulosus	CR	28	1.33	0.367	0.142	0.261	0.158
Goby spp.	CR	2	0.09	0.039	0.039	–	–
Haemulidae							
Plectorhinchus gaterinus	T	6	0.26	0.116	0.073	–	–
Plectorhinchus gibbosus	T	2	0.09	–	–	0.029	0.029
Plectorhinchus plagiodesmus	T	3	0.14	0.058	0.032	–	–

Table 3: (cont.)

Taxon	Bio-ecological group	Total no.	% of total	Fish density (no. m^{-2})			
				NEM	SE	SEM	SE
Hemiramphidae							
Hemiramphus far	T	10	0.47	0.174	0.092	0.029	0.029
Labridae							
Cheilio inermis	T	1	0.05	0.019	0.019	–	–
Halichoeres iridis	T	1	0.05	0.019	0.019	–	–
Halichoeres scapularis	T	1	0.05	0.019	0.019	–	–
Leptoscarus vaigiensis	T	11	0.52	0.155	0.082	0.058	0.040
Novaculichthys macrolepidotus	T	1	0.05	0.019	0.019	–	–
Leiognathidae							
Leiognathus equula	T	35	1.66	0.232	0.118	0.667	0.393
Secutor insidiator	CD	4	0.19	0.058	0.058	0.029	0.029
Lethrinidae							
Lethrinus harak	CD	2	0.09	0.039	0.039	–	–
Lethrinus lentjan	CD	2	0.09	0.039	0.039	–	–
Lethrinus mahsena	CD	3	0.14	0.019	0.019	0.058	0.058
Lethrinus nebulosus	CD	2	0.09	0.019	0.019	0.029	0.029
Lethrinus variegatus	CD	22	1.05	0.019	0.019	0.609	0.548
Lethrinus spp.	CD	7	0.34	0.135	0.052	–	–
Lobotidae							
Lobotes surinamensis	T	6	0.28	0.135	0.086	0.029	0.029
Lutjanidae							
Lutjanus fulviflamma	CD	190	8.97	2.029	0.752	2.464	1.012
Lutjanus sanguineus	CD	3	0.14	0.019	0.019	–	–
Monacanthidae							
Paramonacanthus frenatus	T	27	1.27	0.271	0.150	0.377	0.190
Monodactylidae							
Monodactylus argenteus	CD	42	1.98	0.657	0.389	0.232	0.112
Mugilidae							
Valamugil seheli	CD	32	1.51	0.019	0.019	0.899	0.748
Mullidae							
Parupeneus barberinus	CD	1	0.05	0.019	0.019	–	–
Upeneus sulphureus	CD	1	0.05	0.019	0.019	–	–
Nemipteridae							
Scolopsis ghanam	T	2	0.09	0.039	0.039	–	–
Ostraciidae							
Lactoria cornutus	R	3	0.014	0.039	0.027	0.029	0.029
Percophidae							
Bembrop scaudimacula	CD	1	0.05	0.019	0.019	–	–
Bembrop splatyrhynchus	CD	3	0.14	–	–	0.029	0.029
Platycephalidae							
Papilloculiceps longiceps	CD	1	0.05	0.019	0.019	–	–
Plotosidae							
Plotosus lineatus	T	40	1.81	1.044	0.722	–	–
Polynemidae							
Polydactylus sextarius	CD	7	0.33	–	–	0.029	0.029
Polynemus plebeius	CD	3	0.14	0.039	0.039	0.058	0.058
Pomacentridae							
Abudefduf sexfasciatus	CD	6	0.28	–	–	0.087	0.087
Pomadasydae							
Pomadasys spp.	R	1	0.05	0.019	0.019	–	–
Scorpaenidae							
Scorpaena mossambica	T	1	0.05	–	–	0.029	0.029
Siganidae							
Siganus canaliculatus	CD	117	5.54	2.261	1.102	–	–
Sillaginidae							
Sillago sihama	CD	7	0.33	0.039	0.039	0.145	0.070
Soleidae							
Pegusa nasuta	R	6	0.28	–	–	0.116	0.090
Solenostomidae							
Solenostomus cyanopterus	R	1	0.05	0.019	0.019	–	–
Sphyraenidae							
Sphyraena jello	CD	35	1.66	0.560	0.195	0.174	0.083

Table 3: (*cont.*)

Taxon	Bio-ecological group	Total no.	% of total	Fish density (no. m^{-2})			
				NEM	SE	SEM	SE
Syngnathidae							
Syngnathoides biaculeatus	T	1	0.05	0.019	0.019	–	–
Synodontidae							
Saurida undosquamis	T	37	1.74	0.135	0.059	0.87	0.429
Teraponidae							
Pelates quadrilineatus	T	12	0.56	0.406	0.293	0.232	0.180
Terapon jarbua	CD	200	9.39	0.329	0.194	5.305	2.144
Tetraodontidae							
Arothron immaculatus	T	13	0.61	0.174	0.096	0.208	0.028
Chelonodon laticeps	CD	4	0.19	0.058	0.042	0.029	0.029
Zenarchopteridae							
Zenarchopterus dispar	R	4	0.19	–	–	0.289	0.289
Total/mean		2 118	100	0.255	0.041	0.368	0.078

Table 4: Variation (±SE) of mean density, Shannon's diversity index (*H'*), Margalef's richness index (*D*) and Pielou's evenness index (*J'*) between stations in Tudor Creek

Index	Station 1	Station 2	Station 3	Station 4	*F*	*p*
Fish mean density (no. m^{-2})	0.34 ± 0.01	0.39 ± 0.03	0.34 ± 0.01	0.31 ± 0.01	4.17	0.007
Shannon's diversity index (*H'*)	1.69 ± 0.10	1.96 ± 0.12	1.79 ± 0.12	1.92 ± 0.13	0.67	0.58
Margalef's richness index (*D*)	2.48 ± 0.27	2.95 ± 0.28	2.53 ± 0.23	2.70 ± 0.26	3.47	0.36
Pielou's evenness index (*J'*)	0.75 ± 0.04	0.79 ± 0.04	0.78 ± 0.04	0.89 ± 0.02	1.11	0.03

and 1 (1.69, SE 0.10) respectively (Table 4). Margalef's species richness index (*D*) followed the same trend as *H'*, with high and low *D* values at Stations 2 and 1 respectively. However, the evenness index (*J'*) was highest at Station 4 (0.89, SE 0.02) and lowest at Station 1 (0.75, SE 0.04) (Table 3). *H'* and *D* indices did not differ significantly between stations, but *J'* differed significantly between stations (Table 4). On a temporal scale, *D* ranged between 2.15 and 3.19 in March and July 2008 respectively (Figure 2). Generally, *D* values increased during the NEM but decreased during the SEM season. Values of *H'* ranged from 1.99 to 2.11 between June and March 2008 respectively; however, *J'* remained nearly constant over time, ranging between 0.8 and 0.9 (Figure 2). Stations 4 and 1 were the most diverse (34 and 32 species ranked respectively), whereas Station 3 was the least diverse compared to the other stations (29 species ranked) (Figure 3). The slope of the curves showed that species composition was more even (number of individuals equitably distributed among species) at Stations 4 and 2, whereas Stations 3 and 1 had the lowest evenness, indicating unequal distribution of individuals per species as the higher ranked species had more individuals than the lower ranked ones.

The mean total catch for the common fish species within the creek varied among stations and within season ($p < 0.05$, Table 5). The abundance of *Oxyurichthys ophthalmonema* and *Yongeichthys nebulosus* (creek-resident species) varied significantly between stations but not with seasons, whereas the abundance of *Oxyurichthys papuensis* (a creek-resident species) varied significantly between stations and seasons (Table 5). The distribution of the transient *Saurida undosquamis* and creek-dependent *T. jarbua* species was more influenced by season than by

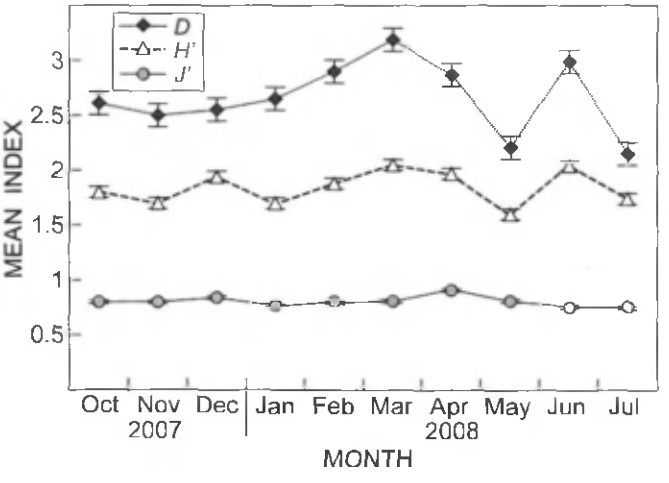

Figure 2: Temporal variation in mean Shannon-Wiener diversity (*H'*), Margalef's species richness (*D*) and Pielou's evenness (*J'*) indices for fish assemblages within Tudor Creek. Error bars denote SE

station location. The abundance of the creek-dependent *G. oyena* and the transients (*Trachinotus baillonii* and *Leiognathus equula*) were influenced by both station location and season (Table 5), indicating synergistic effects of both these factors in determining distribution of some species in the creek.

Assemblage structure

The Bray-Curtis cluster analysis defined two main groups among the most abundant species in the creek (Figure 4). The grouping appears to represent the temporal and spatial

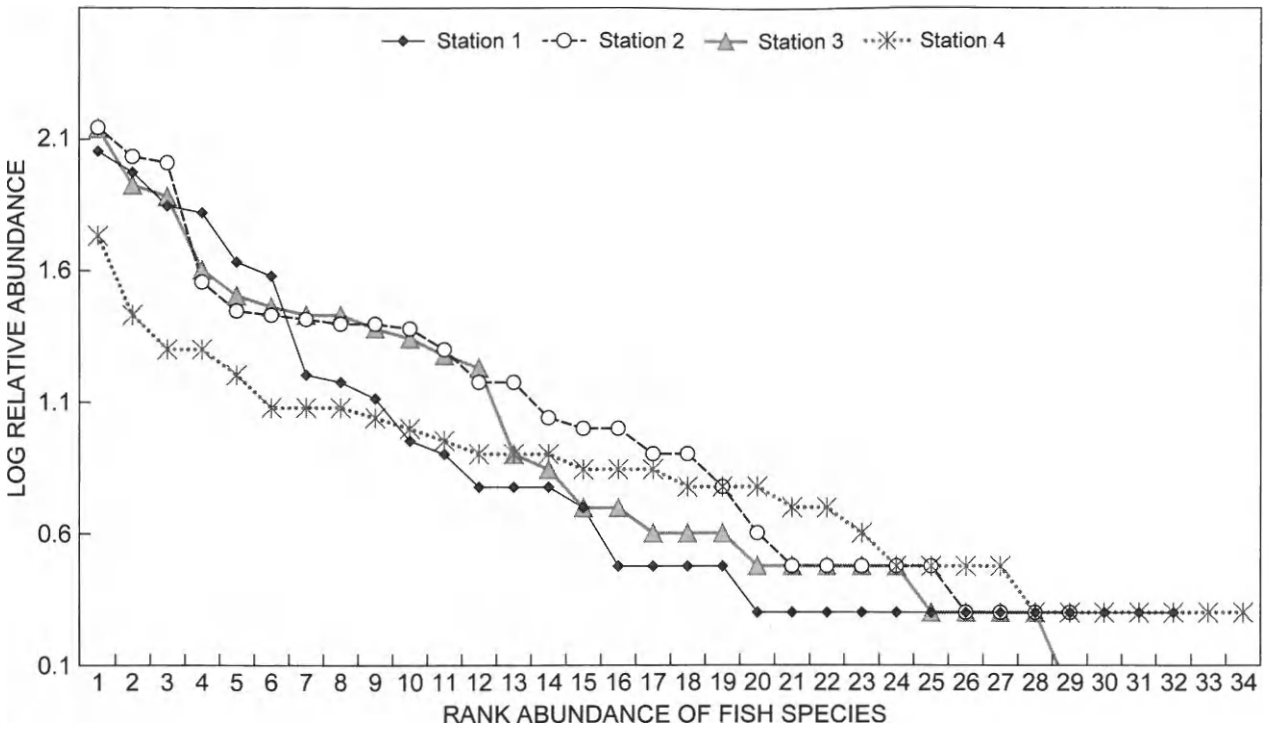

Figure 3: Species–rank abundance curves derived from total fish collections from the four stations sampled within Tudor Creek

Table 5: Two-way ANOVA results on the influence of site, season, and interaction effects between site and season on the mean density (no. m^{-2}) of the common fish species within Tudor Creek

Species	Site			Season			Site × Season		
	MS	df	*F*	MS	df	*F*	MS	df	*F*
Atherinomorus lacunosus	0.209	3	1.043	0.011	1	0.054	0.047	3	0.235
Caranx ignobilis	0.110	3	0.507	0.499	1	2.308	0.372	3	1.721
Favonigobius melanobranchus	0.793	3	2.459	1.408	1	4.368	0.304	3	0.943
Gerres oyena	0.595	3	1.856	0.804	1	2.508	1.557	3	4.857*
Leiognathus equula	0.487	3	2.671	0.013	1	0.069	0.618	3	3.388*
Lutjanus fulviflamma	2.703	3	11.586*	0.001	1	0.004	0.396	3	1.698
Monodactylus argenteus	0.278	3	1.183*	0.050	1	0.214	0.261	3	1.109
Oxyurichthys opthalmonema	1.816	3	6.047*	0.003	1	0.011	0.175	3	0.582
Oxyurichthys papuensis	1.542	3	8.172*	1.043	1	5.527*	0.139	3	0.737
Petroscirtes breviceps	0.113	3	0.465	0.838	1	3.444	0.008	3	0.035
Sardinella gibbosa	10.265	3	4.085*	3.446	1	1.371	2.377	3	0.946
Saurida undosquamis	0.421	3	2.155	1.150	1	5.890*	0.307	3	1.575
Sphyraena jello	0.864	3	5.188*	0.279	1	1.675	0.309	3	1.856
Terapon jarbua	0.071	3	0.154	3.023	1	6.618*	0.509	3	1.097
Trachinotus baillonii	1.272	3	9.406*	0.304	1	2.251	1.531	3	11.323*
Yongeichthys nebulosus	0.675	3	3.687*	0.095	1	0.519	0.044	3	0.239
Total/mean	25.241	3	5.212*	48.278	1	9.969*	8.053	3	1.663

* Significant at $\alpha = 0.05$

use of the creek by the fish. Group 1 was represented by a mix of bio-ecological groupings including transient species *Caranx ignobilis*, *L. equula*, *A. cyanosoma*, *Petroscirtes breviceps* and *S. undosquamis*; creek-resident species *O. ophthalmonema*, *O. papuensis*, *Y. nebulosus* and *Favonigobius melanobranchus*; and creek-dependent species *L. fulviflamma*, *G. oyena* and *T. jarbua*. Members of Group 1 were mostly from Stations 2 and 3. Group 2 was exclusively composed of transient species *T. baillonii*, *Trachinotus blochii*, *S. canaliculatus* and *Sardinella gibbosa*, principally from Station 1. The multidimensional scaling (MDS) analysis further clustered the four stations into three main groups (2 and 3, 1, and 4) based on the distribution of the abundant species (Figure 5). Stations 2 and 3, which had similar habitats of muddy substrate backed by a fringe of mangroves, showed closer similarity in species composition, consisting of those in Group 1 (Figure 4).

The results of correspondence analysis showed that only the fish assemblage at Station 1 formed a distinct seasonal structure from the other stations (Figure 6). During the NEM

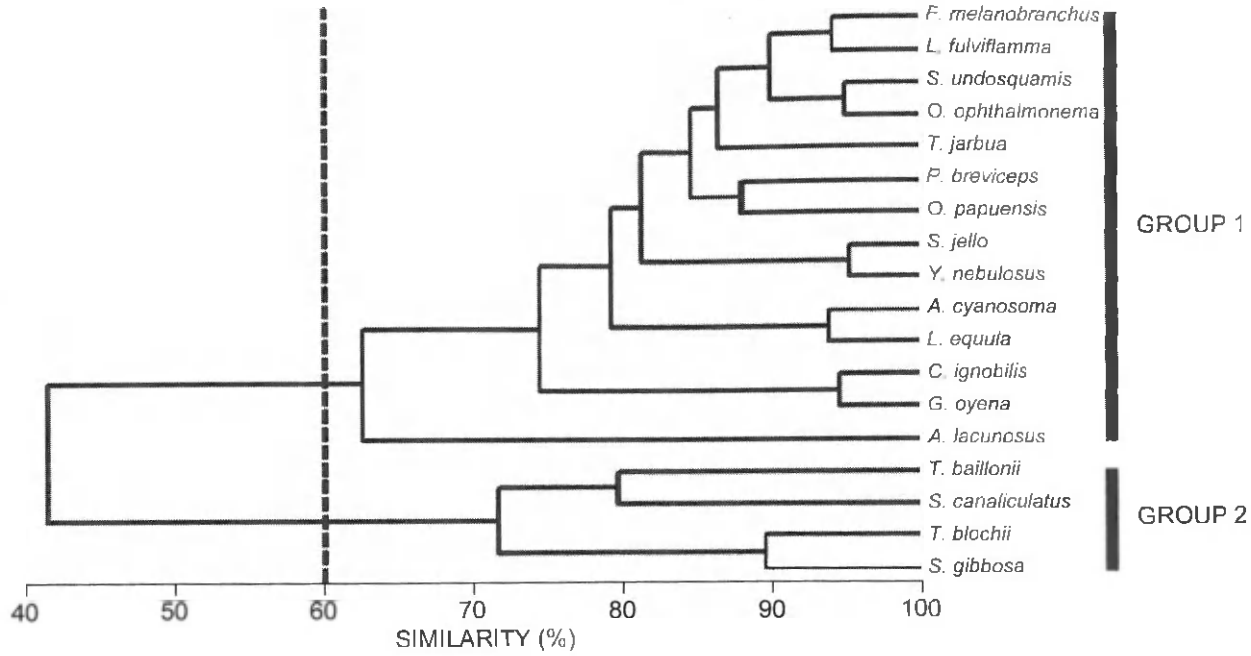

Figure 4: A correlation dendrogram for species based on Bray-Curtis similarities of the most abundant species sampled within Tudor Creek

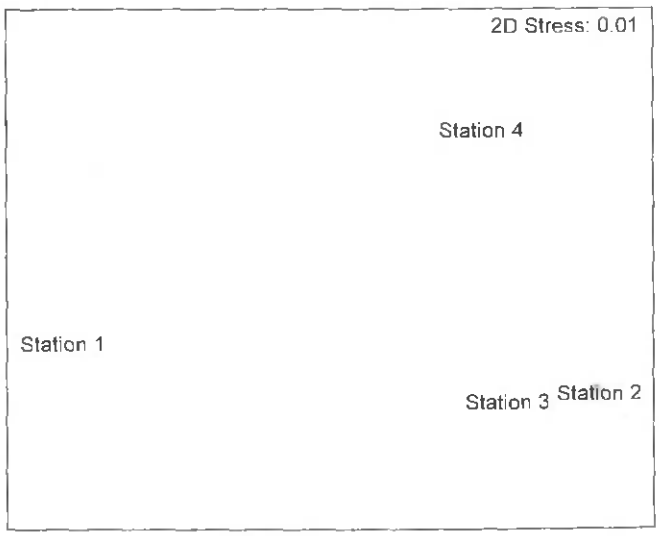

Figure 5: *MDS ordination plot based on* Bray-Curtis similarities of the most abundant species at stations within Tudor Creek

season, Station 1 was dominated by *S. canaliculatus*, *G. oyena* and *C. ignobilis*, whereas *Sardinella gibbosa* and *T. baillonii* dominated this station during the SEM season (Figure 6). Fish assemblages were poorly separated between the seasons at Station 4; however, NEM season appeared to be dominated by *P. breviceps*, *L. equula* and *Atherinomorus lacunosus* in this station (Figure 6). The fish assemblage structure of Station 4 was distinct from that of Stations 2 and 3 only during the SEM season. Fish assemblage structure at Stations 2 and 3 was indistinct between the two seasons and consisted of *F. melanobranchus*, *Y. nebulosus*, *T. jarbua* and *L. fulviflamma* (Figure 6).

Discussion

The biodiversity found at Tudor Creek is typical of tidal creeks and tropical estuarine communities, where a small number of species contribute a large proportion of the fish community (Little et al. 1988, Kimani et al. 1996, Vidy 2000, Rueda and Defeo 2003). The fish assemblages within the creek differed considerably between stations and monsoon seasons. The families Siganidae, Carangidae and Clupeidae dominated the oceanic station at the mouth of the creek, whereas Gerreidae, Teraponidae, Gobiidae and Lutjanidae were most dominant in the more inland stations in the creek. Little et al. (1988) found a similar distribution during an earlier study in Tudor Creek; however, we found an inland shift in the distribution of Gerreidae which was not reported in this earlier study. It is likely that anthropogenic and climatic influences have affected distribution of fish in Tudor Creek, as has been observed in other similar systems (Lotze et al. 2006). Whereas Gobiidae, Gerreidae, Teraponidae, Lutjanidae and Apogonidae were found to dominate Tudor Creek, Leiognathidae, Syngnathidae, Gerreidae, Atherinidae and other groups have been reported to dominate other tidal creeks in Kenya (Kimani et al. 1996, Oyugi 2005) and elsewhere (Blaber and Milton 1990), indicating biogeographic variation in factors affecting community structure. The presence of a diversity of substrate types, including mangrove fringed sections, could explain the high species diversity within Tudor Creek. However, because of differences in sampling techniques and effort, it is difficult to compare species diversity and abundance between different habitats studied.

The fish assemblage structure seemed to correspond to both habitat variability within the creek and to seasonality. Fish composition at the oceanic station was affected

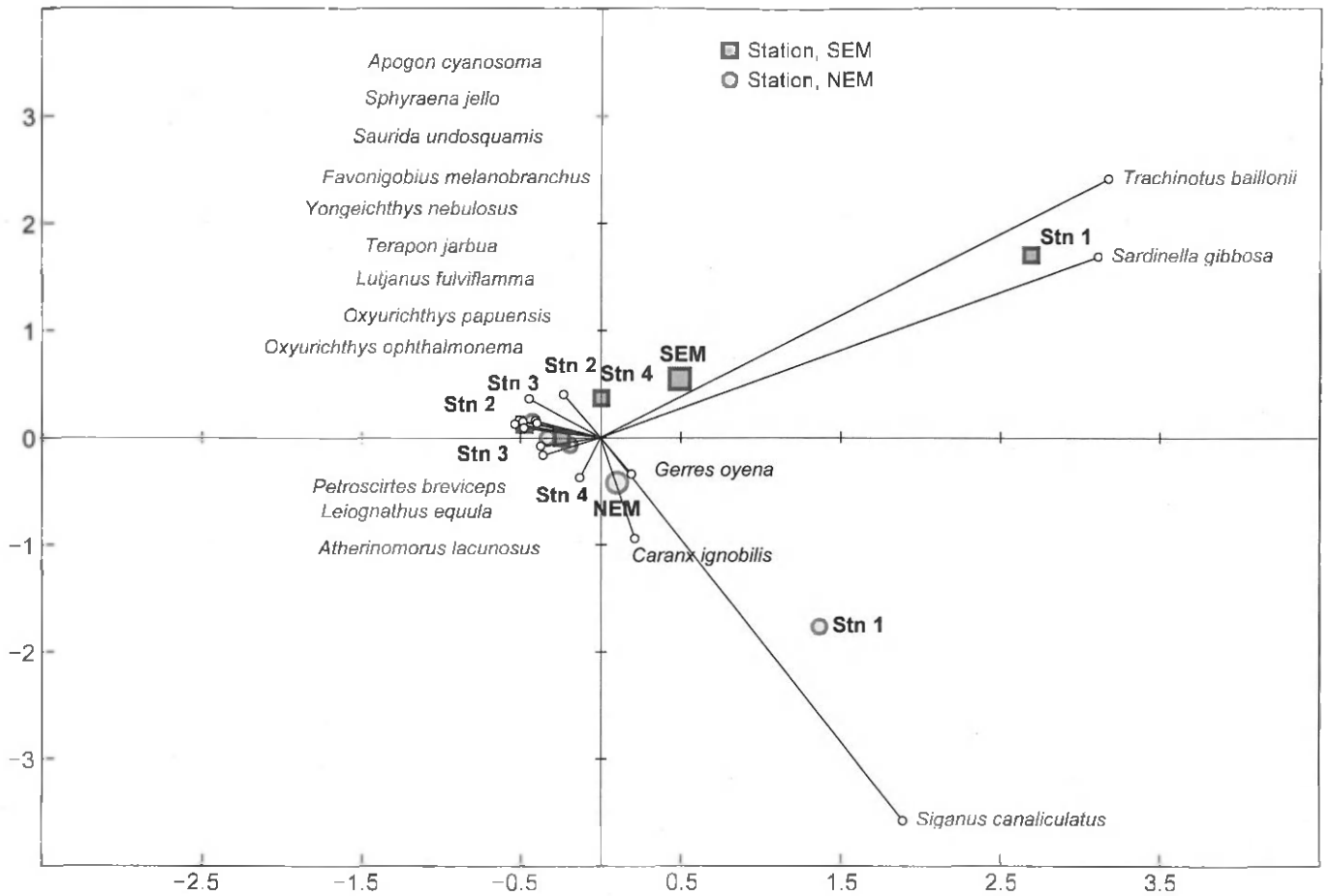

Figure 6: Multivariate correspondence analysis of the association of fish species with stations and seasons at Tudor Creek, for species with catch rates >2%

more by season than those in the upper region of the creek. On the contrary, Little et al. (1988) reported similarity of assemblage structure between stations in the creek. Other studies have documented the influence of salinity variations in structuring estuarine populations (Spach et al. 2004, Sanja et al. 2005); however, lack of significant seasonal variation in salinity in Tudor Creek indicates that other factors (e.g. hydrodynamics, productivity and biological interreactions) were involved in influencing fish distribution and abundance. Site and seasonal factors seem to interact with species behaviour in influencing distribution and abundance of fish species in the creek. The distribution of transient and creek-dependent species (e.g. *G. oyena*, *T. baillonii* and *L. equula*) was significantly affected by both station and season (see also Nagelkerken et al. 2001). However, the abundance of the creek-resident species (e.g. *O. ophthalmonema*, *Y. nebulosus* and *O. papuensis*) was more affected by station within the creek than seasonality. Similar distribution patterns that are not seasonal have been reported for creek-resident species elsewhere (Blaber and Milton 1990), perhaps reflecting evolutionary acclimatisation of species to seasonal influences within creeks.

In the present study, ecological diversity indices showed little spatial variability, and variation in species evenness is likely related to differences in habitat quality within the creek (Gratwicke and Speight 2005). Furthermore, the dominance of some families (e.g. Siganidae, Lutjanidae and Gerreidae) at stations likely affected the species diversity within the creek, as implied by the species rank abundance curves. The high species evenness and diversity in the inland stations was likely associated with the structural complexity caused by mangroves at these stations. Within-creek variation in diversity and evenness appears to characterise many mangrove tidal creeks and estuarine habitats (Allen 1982, Robertson and Duke 1987). The higher values in the ecological diversity indices observed during the NEM season concur with those reported in an earlier study in Tudor Creek (Little et al. 1988). Seasonal changes in species diversity within the creek are likely caused by movement of fish between the creek and offshore areas (Day 1974). The calm conditions and high productivity during the NEM season (McClanahan 1988, Obura 2001) likely contributed to species movement into the creek during that period.

Our study has shown evidence of changes in fish community structure in the creek since the earlier investigation by Little et al. (1988). Species evenness in the creek has decreased and species richness has reduced since the earlier study. However, we found the creek still has a high

diversity of fish, more than 80 species, which is comparable to other tropical mangrove tidal creeks (Blaber 2000). High species evenness occurred on mangrove-lined sections of the creek (Stations 2 and 4). The fish assemblage at the more oceanic station seemed to form a more distinct seasonal structure than at the other inland stations. Also different species dominated the stations during different seasons. The creek also serves as an important habitat for Gobiidae and provides a favourable habitat to the creek-dependent (e.g. Lutjanidae, Gerreidae, Teraponidae and Apogonidae) and transient fish groups (e.g. Carangidae, Hemiramphidae, Chanidae and Leiognathidae).

Our results underscore the need for continuous monitoring of these systems in order to determine whether they are able to sustain their ecological and economic niche in the face of escalating anthropogenic and climate change influences (Blaber 1997, Lotze et al. 2006). Investigations on the anthropogenic impacts and long-term climate change effects on the structure and function of creek communities are required. We have shown that salinity gradients may not be important in structuring creek communities in systems with weak runoff, but seasonality and habitat heterogeneity likely play important roles in structuring bio-ecological fish groups in East African creek systems.

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