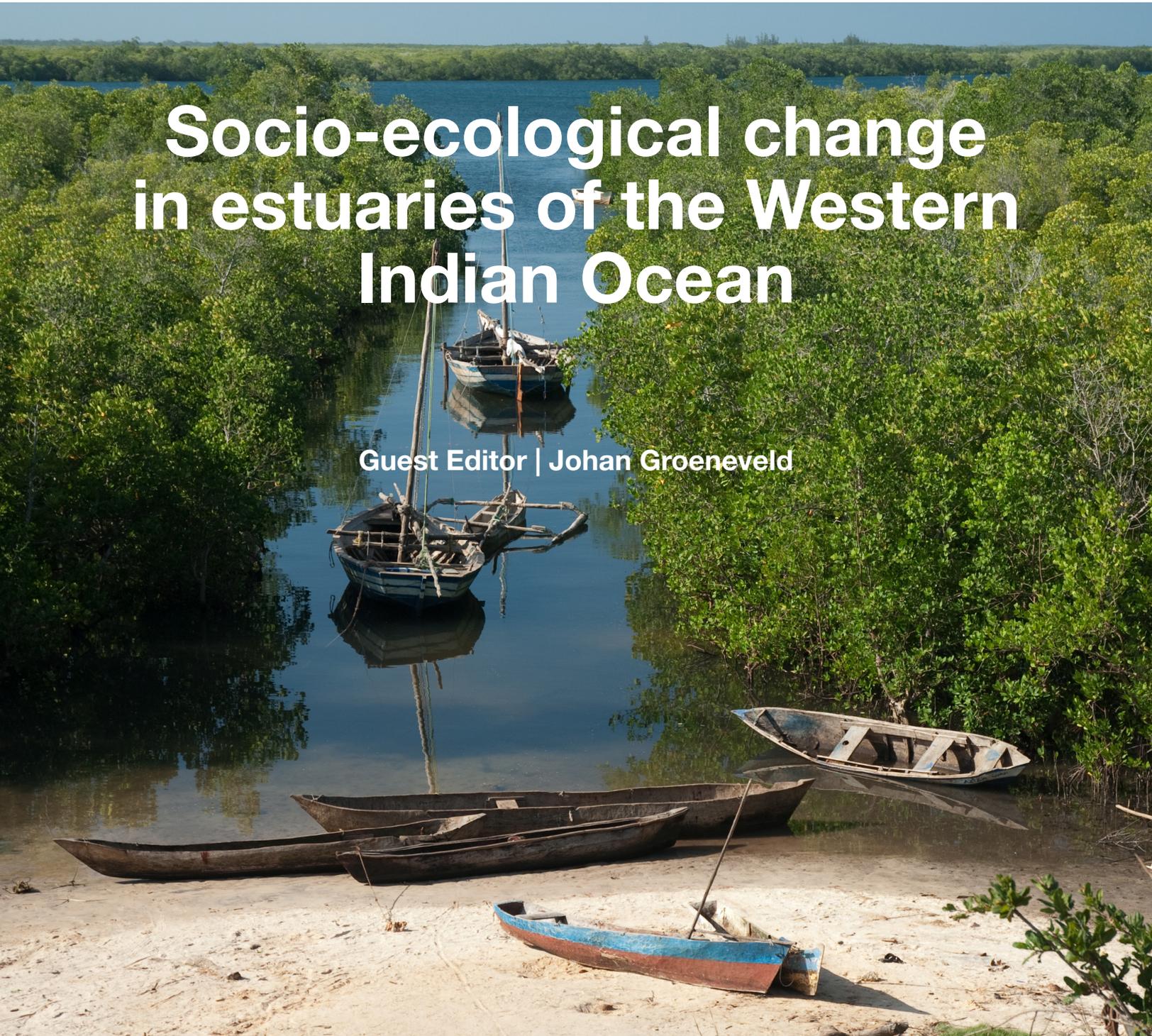


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Socio-ecological change in estuaries of the Western Indian Ocean

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Small-scale fisheries of the Tana Estuary in Kenya

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Abstract

The role of small-scale fisheries in maintaining socio-ecological systems (SES) in the Western Indian Ocean is well-documented, yet few studies have addressed estuarine fisheries in the region. Small-scale fisheries in the Tana Estuary in Kenya are described in this paper, accounting for location along a salinity gradient, seasonality, gear types used, species composition and relative abundance of landings. Monthly shore-based sampling was undertaken at four locations in 2017 – Ungwana Bay near the estuary mouth, lower and mid-estuary, and upper estuary at Ozi village, ~10 km upstream. Fishing gear comprised of seine nets, gillnets, hook-and-line and traditional gear such as self-made traps, sticks and spears operated from the shore (foot fishers), dugout canoes, dhows and fibreglass boats with outboard engines. A total of 12,840 fish and crustacean specimens belonging to 89 species in 45 families were sampled. Landings were dominated by catfishes *Arius africanus* (31 %) and *Clarias gariepinus* (21 %), small pelagic fishes *Pellona ditchela* (10 %) and several sardine species (~5 %), croaker *Otolithes ruber* (10 %), eel catfish *Plotosus limbatus* (6 %), mullet *Mugil cephalus* (4 %) and Nile tilapia *Oreochromis niloticus* (4 %). Multivariate analyses (nMDS and ANOSIM) found that fishing gear ($p < 0.05$) and location ($p = 0.001$) significantly influenced catch composition, but season ($p = 0.146$) was not significant. Traps were used in the upper and mid estuary only and were selective for three catfish species. Seine nets (54 species) and gillnets (40 species) were least selective and used at all four locations. Rarefaction curves indicated that species diversity was higher at the bay and lower estuary than the mid and upper estuary, and that diversity was highest for canoe-gillnet and canoe-encircling net combinations. Catch rates (avg. of 2.3 to 8.4 kg.fisher⁻¹.day⁻¹) depended on gear type and was highest for monofilament gillnets. Catches comprised a broad size range of multiple species, but on average, seine nets selected smaller individuals than traps, gillnets and long lines. The high complexity and organization of the fishery at an estuary-scale makes it a good example of a relatively intact SES suitable for regional comparative analyses.

Keywords: artisanal fishery, species composition, fishing pressure, estuary, Western Indian Ocean

Introduction

Small-scale fisheries in coastal waters, estuaries and surrounding wetlands of the Western Indian Ocean region (WIO) are a vital source of food security and economic activity (van der Elst *et al.*, 2005; Groeneveld, 2015). These fisheries are highly diverse, exploiting multiple species using different types of traditional and modern fishing gear, either from the shore or from small craft, such as dugout canoes and seagoing dhows (Jid-dawi and Ohman, 2002; Samoilys *et al.*, 2011; Munga

et al., 2014a; Fondo *et al.*, 2015; www.wiofish.org). The high socio-economic importance and diversity of WIO fisheries make them difficult to manage using conventional fishery management practices (McClanahan and Mangi, 2004; van der Elst *et al.*, 2005).

Several fisheries studies have focused on Ungwana Bay along the northern Kenya coast. The Tana and Athi-Sabaki estuaries discharge into the bay, thus enriching it with terrigenous sediments, nutrients and

biological material (Kitheka *et al.*, 2005; Kitheka and Mavuti, 2016). Recent studies of Ungwana Bay have focused on shallow water shrimp semi-industrial trawl fisheries (Munga *et al.*, 2012, 2013, 2016); fish bycatch and resource use conflicts (Munga *et al.*, 2014b; Tunje *et al.*, 2016); socio-economics and fishery management systems (Fulanda *et al.*, 2009, 2011; Munga, 2013; Munga *et al.*, 2014a); larval dispersal and recruitment to fisheries (Mkare *et al.*, 2014, 2017); and ecological vulnerability of coastal fishing communities to climate variability (Hamerlynck *et al.*, 2010; Dzoga *et al.*, 2018, 2019, 2020). The above studies focused mainly on the marine environment, with less attention given to fisheries in the enclosed parts of the Tana and Athi-Sabaki estuaries (Mireri, 2010).

Small-scale fishing in the Tana Estuary (defined as the northern-most channel of the Tana River Delta that discharges near Kipini town; Groeneveld *et al.*, 2021) forms an important part of a socio-ecological entity that traditionally includes livestock keeping, flood-recession agriculture and tidal rice cultivation, hunting and gathering, utilization of woody and non-woody forest products and beekeeping (Hamerlynck *et al.*, 2010, 2020; Mwamlavya *et al.*, 2021). The productive delta ecosystems that support traditional livelihoods have remained relatively intact (van Beukering *et al.*, 2015; Duvail *et al.*, 2017). Activities are strongly seasonal, driven by the influence of semi-annual flood pulses in November to December (short rains associated with the northeast [NE] monsoon) and April to May (long rains associated with the southeast [SE] monsoon). Upstream damming and freshwater abstraction in catchments of the Tana River for economic development have disrupted the seasonal timing and volume of freshwater pulses, with impacts on estuarine functioning and dependent socio-ecological systems (SES) (Hamerlynck *et al.*, 2010, 2020; Duvail *et al.*, 2012, 2017; Leauthaud *et al.*, 2013; Kitheka and Mavuti, 2016; Mwaguni *et al.*, 2016; Odhiambo-Ochiewo *et al.*, 2016).

Fishing in the Tana Estuary takes place in the main estuary channel, smaller tributaries, wetland lakes and in nearshore coastal waters (van Beukering *et al.*, 2015). Full-time fishers at Kipini (including seasonal migrants; see Fulanda *et al.*, 2009) fish mainly in Ungwana Bay and the lower Tana Estuary. Munga *et al.* (2014a, 2014b) reported 177 fish species from small-scale fisheries and 223 species from trawl samples in the bay. Ngoro *et al.* (2014) found 20 decapod crustacean species, including 9 portunid crab and 5 penaeid prawn species. The brackish water habitats

and mangrove forests of the Tana Estuary provide vital habitats and nursery grounds for juvenile fish and crustaceans, including those with marine-dependent life history phases (de Freitas, 1998; Mkare *et al.*, 2014). At Ozi village (~10 km upstream from the estuary mouth) part-time fishers set their gear in the oligohaline backwaters and wetlands to catch fish to consume or augment their income from farming (Mwamlavya *et al.*, 2021). The fresh and brackish water of the lower Tana Delta is relatively ichthyo-diverse, with 9 fish families (Mochokidae, Protopteridae, Claroteidae, Schilbeidae, Cichlidae, Alestidae, Clariidae, Mormyridae and Cyprinidae) and at least 48 species (Odhengo *et al.*, 2012).

Several studies have described the management of Kenyan fisheries (Fondo *et al.*, 2015). Fishing has been an open-access activity for many centuries but increases in human population size and more effective fishing methods have increased fishing pressure leading to localized depletions over the past decades (Botsford *et al.*, 1997; Mansfield, 2011). A top-down governance approach has failed to curb increases in fishing effort. Collaborative fisheries management in which stakeholders and resource users are involved in decision making processes (e.g., Beach Management Units or BMUs) have been active for >20 years but have been plagued by low transparency and accountability, and mismatched priorities between officials and members (Oluoch and Obura, 2008; Kanyange *et al.*, 2014). A deeper understanding of small-scale fisheries in the Tana Estuary and of traditional decision-making is required, so that fisheries management objectives and livelihood priorities can be better aligned. It was hypothesized that local estuary-scale conditions would determine the fishing gear used, and the species composition and relative abundance of landings made by small-scale fishers operating between Ungwana Bay (near-marine) and Ozi village (oligohaline) in the Tana Estuary. Small-scale fisheries are described with emphasis on spatio-temporal trends in species composition and relative abundance of landings and gear selectivity. The new information is useful for detailed socio-ecological assessments of the role of small-scale fisheries in WIO estuaries (see Groeneveld *et al.*, 2021; Santos *et al.*, 2021).

Materials and methods

Study area

The Tana River Delta is roughly triangular in shape, with its apex at Lake Bilisa (north of Garsen town) and its base a 50 km stretch of beach along Ungwana Bay,

stretching from Kipini town in the north-east to Mto Kilifi in the south-west (Mireri, 2010). The delta is a low-lying area bounded by higher land to the east and west and to the south by a dune ridge parallel to the shore, which separates it from the bay. The delta is characterized by fresh- and brackish water lakes and streams, fresh water and saline grasslands and wetlands, and successional stages of forest and woodland on the riverbanks and dune ridges (Mireri, 2010). The delta discharges into the bay through several estuaries that extend inland for up to 10 km, with a mean depth of about 5 m (Scheren *et al.*, 2016). Mangrove forests line the estuary banks and coastal depressions, providing a natural buffer to flooding, vital habitats

river-dominated with a moderate tidal influence and salinity fluctuating between 2 and 10 ppt; lower estuary - enclosed marine transition area with mixed tidal - and river currents, mesohaline water with salinity mostly >10 ppt; and the bay - exposed near-shore marine-dominated waters influenced by tidal currents, waves and floods with salinity fluctuating mainly >20 ppt. The salinity categories were adapted from the classification by Rhoadles *et al.* (1992). The four sampling locations were verified with in-situ salinity measurements using a YSI salinity meter, with readings falling within expected ranges: i.e., 1.2 ± 0.5 ppt (upper); 9.1 ± 0.4 ppt (mid); 12.5 ± 0.7 ppt (lower); and 24.7 ppt (bay).

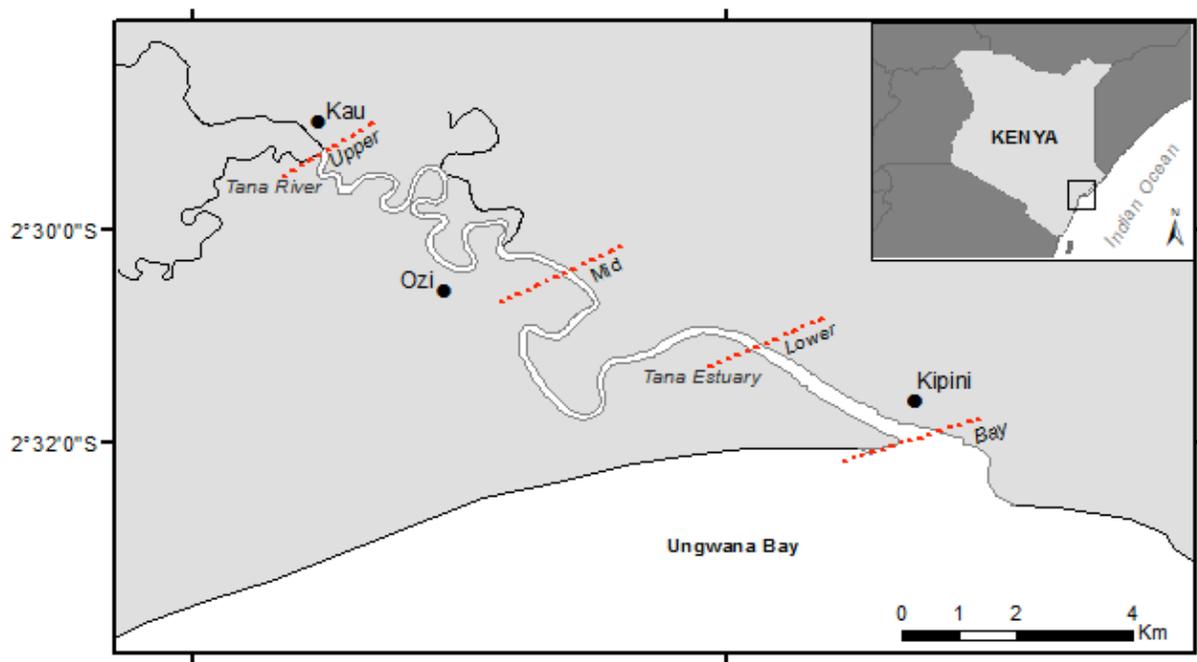


Figure 1. The Tana Estuary in Kenya (see inset) showing the four sampling locations in the bay, lower estuary, mid estuary and upper estuary, separated by dotted red lines. The town at Kipini and villages at Ozi and Kau are also indicated.

for estuarine fish and crustaceans, and a diversity of forest products used by local coastal communities, including wood for building and fuel (Bosire *et al.*, 2016). Information on the geographical setting of the Tana Estuary, ecosystems, socio-ecological importance and drivers of change is summarized by Groeneweld *et al.* (2021).

Four sampling locations were defined (Fig. 1): upper estuary - riverine channels around Ozi with fresh or oligohaline water with <2 ppt salinity; mid estuary - tidal channels and mangroves on both banks,

Data collection

Field sampling surveys to collect detailed fisheries data were conducted between March and December 2017 (incl. 5-day surveys in March and June). The types of fishing gear and craft used, number of fishermen and landings at sites between Kipini and Ozi were investigated. Total landings per fishing craft and gear were weighed to the nearest kilogram (kg) on a weighing balance. For large landings, the catch was first mixed before scooping up a random sub-sample; for small landings the entire catch was sampled. Samples were identified to the lowest possible taxonomic

Table 1. Gear types observed at four locations in the Tana Estuary in Kenya during shore-based sampling in 2017. Sampling locations were Ungwana Bay (bay), lower, mid and upper Tana Estuary between Kipini town and Ozi village. Gear descriptions relied on technical details in Samoilyis *et al.*, (2011). The most abundant families in landings by gear type are shown.

| Gear type | Description of fishing gear | Most abundant families in landings by gear type |
|--|--|---|
| Encircling nets (includes cast nets and seine nets) | Cast nets: Circular nets with weighted edges, monofilament nylon, and 7-30 mm mesh. Deployed from canoe, boat or while wading. Cast over shoal of fish and hauled back. Used in the lower Tana Estuary. | Ariidae, Clupeidae Engraulidae, Sciaenidae |
| | Seine nets: Monofilament nylon, attached to mangrove poles or bars at each end. Small mesh. Deployed on foot by dragging it towards the shore by 1-3 fishers or from a canoe while drifting with one end attached. Sometime set across mangrove channels. 1.8 x 20 m long. Larger multifilament beach seine nets (illegal in Kenya) were not observed. Used at all 4 locations. | Ariidae, Belonidae, Cichlidae, Claridae, Clupeidae, Mugilidae, Sciaenidae, Penaecidae, Palaemonidae, Plotosidae, Pristigasteridae |
| Gillnets (includes mono- and multifilament gillnets) | Stationary gillnets with small floats at the top, weights at the bottom and varying mesh size (2.5 – 12 cm). Deployed from canoe or boat after anchoring 1 end, sometimes across channels, by 2-4 fishers. Set at bottom, mid or surface, depending on target species. Hauled after a few hours. Variable length: 2.5 x 20 m, or up to 50 m. Monofilament nets are lighter and require less maintenance but are illegal in Kenya. Used at all 4 locations. | Ariidae, Cichlidae, Claridae, Clupeidae, Mugilidae, Sciaenidae, Pristigasteridae |
| Handline | Single monofilament nylon line with baited steel hooks, deployed from canoe, boat or shore. Used in the upper and mid Tana Estuary and in Ungwana Bay. | Ariidae, Clupeidae, Monodactylidae, Sciaenidae |
| Longline | Single mainline of monofilament nylon buoyed horizontally, often anchored. Series of short vertical nylon snoods with baited hooks attached at intervals. Deployed from boat. Used at all 4 locations. | Ariidae, Claridae, Sciaenidae, Pristigasteridae |
| Shark net | Demersal gillnet with large mesh. Used in Ungwana Bay. | Ariidae, Carcharhinidae, Sphyrnidae |
| Traditional traps | Traditional traps made locally from poles tied together in a conical shape with entrance at one side. Set in deep areas along the estuary bank using canoes or by foot. Used in the upper and mid estuary. | Ariidae, Claridae, Plotosidae |
| Other gear (spear, harpoon, hooked sticks) | Spears or home-made spearguns; harpoons are wooden poles with or without metallic tip. Used mainly from the shore by foot fishers. Used at all 4 locations. | Claridae, Octopodidae |

level (mostly species level) using available fish identification guides (Smith and Heemstra, 1998; Lieske and Myers, 2001; Anam and Mostarda, 2012). The total length (TL in cm) of selected species (based on abundance and importance to fishers) was measured on a calibrated fish measuring board, and individual weights determined to the nearest gram (g) using a digital weighing balance (Ashton Meyers® 7767).

Trophic levels (rankings of how many steps a species is above primary producers at the base of the food web) of captured fish were obtained from FishBase (Froese and Pauly, 2019), where a mean trophic level per family has been determined from fish diet composition. The diet composition of fish depends on food availability which varies between locations – hence the trophic levels obtained from FishBase were indicative only. Trophic level 1 comprises primary producers (plants and algae that make their own food, mainly through photosynthesis), level 2 are herbivores, level 3 are secondary consumers (carnivores that eat herbivores) and level 4 are tertiary consumers (carnivores that eat other carnivores). In this study, the mean trophic levels of landings were calculated based on numerically weighted contributions of all species caught per gear and location, respectively.

Data analysis

Data were stratified by season (SE monsoon between April and September; NE monsoon between October

and March), sampling locality (bay, lower-, mid- and upper estuary), gear type and fishing craft used to catch sampled fish. Fishing gear were described based on field observations and grouped into categories for encircling nets, gillnets, hook-and-line, and traditional gears (Table 1). Additional information on gear types, including mesh size, construction material and method of deployment was obtained from Samoily *et al.* (2011).

The number of individuals per species was used to calculate the relative abundance in landings (%) using the following formula:

$$\text{Relative abundance (\%)} = \frac{\text{Number of individuals of species 'A' in location 'S'}}{\text{Total number of individuals of all species in location 'S'}} \times 100$$

Catch composition by gear, location and season was investigated using a multivariate non-Metric Multidimensional Scaling (nMDS) technique and 1-way Analysis of Similarity (ANOSIM). Differences in catch composition were confirmed using 1-way SIMPER analysis to ascertain which species contributed most to the dissimilarity. Both ANOSIM and SIMPER analyses were based on Bray-Curtis similarity using PRIMER statistical software version 6 (Clarke *et al.*, 2014).

To standardize for non-uniform sampling and sample sizes, rarefaction curves (Sanders, 1968) were used to determine the expected number of species per sample across combinations of gear type and fishing location. Catch rates were calculated as $\text{kg.fisher}^{-1}.\text{day}^{-1}$ for each

Table 2. Proportional distribution of fish sampled per location and gear type in the Tana Estuary in Kenya during shore-based sampling in 2017. Locations were: bay (mudbanks in Ungwana Bay near the estuary mouth); lower-, mid-, and upper estuary.

| Gear | Sampling location | | | | |
|---|-------------------|-------|------|-------|----------|
| | Bay | Lower | Mid | Upper | Combined |
| Castnet | | 1.00 | | | <0.01 |
| Gillnet | 0.90 | 0.10 | | | 0.10 |
| Handline | 0.98 | | 0.01 | 0.01 | 0.01 |
| Longline | 0.76 | 0.05 | 0.17 | 0.02 | 0.10 |
| Monofilament gillnet | 0.77 | 0.04 | 0.05 | 0.14 | 0.28 |
| Seine | 0.32 | 0.02 | 0.28 | 0.38 | 0.31 |
| Sharknet | 1.00 | | | | <0.01 |
| Spear/stick | 0.07 | | 0.18 | 0.75 | 0.01 |
| Traditional trap | | | 0.35 | 0.65 | 0.18 |
| Proportion of gear sampled per location | 0.49 | 0.03 | 0.18 | 0.29 | 1 |

gear, by dividing the total weight of catch landed by the number of associated fishers. Differences in catch rates were compared using 1-way ANOVA, followed by a post hoc pair-wise comparison using the Tukey Honest Significant Difference (HSD) test. Homogeneity of variance was tested with Levene's test (Levene, 1960).

Results

Descriptive analysis

Fishing craft were dugout canoes (constructed from a single log approx. 4 m long with flat bottom for stability, with or without outriggers); dhows (mean length of 5 m, constructed from timber planks and with a flat bottom, pointed bow and round or pointed stern, propelled by triangular sail); and fibreglass boats with outboard engines of varying size. Foot fishers accessed shallow fishing grounds by foot. Dugout canoes without outriggers were observed at all four locations, but those with an outrigger for stability were observed mainly in the lower estuary and bay. Dhows were also used in the lower estuary and bay. A single sample was obtained from a fibreglass boat fishing in the lower estuary. Foot fishers were present at all four locations. Some 85 % of 12,840 sampled fish were obtained from dugout canoes, 13 % from foot fishers, and 2 % from dhows and fibreglass boats combined.

By gear, samples originated from seine nets (31 % by number), monofilament gillnets (28 %), traditional

traps (18 %), multifilament gillnets (10 %) and long lines (10 %) (Table 2). Samples from cast nets, shark nets, hand lines, spears and hooked sticks combined made up the remaining 3 %. Samples from traditional traps were available for the mid and upper estuary only, whereas samples from seine nets were relatively evenly spread between the bay, upper and mid estuary (28-38 % per location). Samples from multifilament gillnets originated from the bay and lower estuary only; samples from monofilament gillnets originated predominantly from the bay (77 %), with smaller proportions captured at the other three locations (4 – 14 %). The bulk of samples from long lines originated from the bay (76 %), with lower percentages from the three enclosed locations. Overall, sampling effort between locations was uneven, dominated by the bay (49 %) and upper estuary (29 %), and with lower representation from the mid (18 %) and lower estuary (3 %) (Table 2).

A total of 12,840 specimens belonging to 89 species in 45 families were sampled (see Appendix 1 for full list) of which 58 species comprised of <10 specimens each. The African sea catfish *Arius africanus* made up the bulk of all sampled fish (31 % of all samples combined; Fig. 2), followed by freshwater African catfish *Clarias gariepinus* (21 %). Both catfish species are benthopelagic and inhabit tropical and subtropical climates (www.fishbase.org). Tigertooth croaker *Otolithes ruber* (10 %)

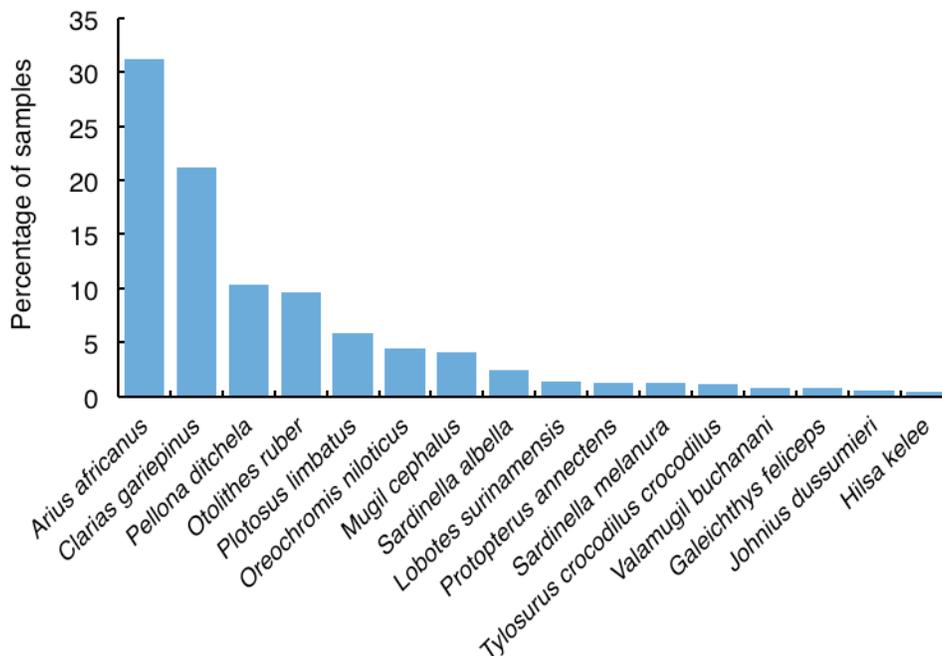


Figure 2. Observed relative abundance of fish in landings of small-scale fishers in the Tana Estuary in Kenya during shore-based sampling of landings in 2017.

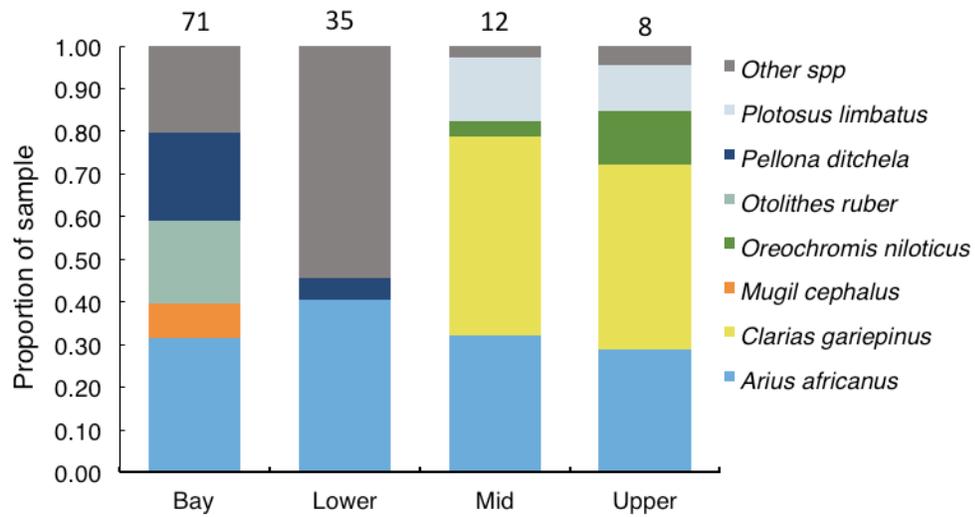


Figure 3. Proportional abundance of key species in landings of small-scale fishers at four sampled locations in the Tana Estuary in Kenya during shore-based sampling of landings in 2017. Species with < 5 % representation in landings were grouped as Other spp. The total number of species observed per location is shown above the bars.

was also a common benthopelagic species in landings. Small pelagic species were mostly Indian pellona *Pellona ditchela* (10 %) and several sardine species (~5 %). Other common species in samples were Darkfin eel catfish *Plotosus limbatus* (5 %), Nile tilapia *Oreochromis niloticus* (5 %) and Flathead grey mullet *Mugil cephalus* (4 %). Crustaceans were not well-represented in samples, i.e., shrimps *Penaeus indicus*, *P. monodon* and *Metapenaeus monoceros*, mud crab *Scylla serrata*, freshwater crayfish *Macrobrachium* spp. and spiny lobster *Panulirus ornatus*.

The euryhaline catfish species *A. africanus* was abundant in landings at all four sampling locations (29 - 41 % of fish landed per location; Fig. 3). The freshwater species *Clarias gariepinus* made up the bulk of sampled landings in the upper (43 %) and mid estuary (46 %) but was absent from the more brackish waters of the lower estuary and bay. Similarly, freshwater species *O. niloticus* and *P. limbatus* were common in landings in the mid (4 % and 15 %, respectively) and upper estuary (13 % and 11 %) but scarce in the lower estuary and bay. The anadromous small pelagic fish *P. ditchela* appeared in samples in the bay (21 %) and lower estuary (5 %) only,

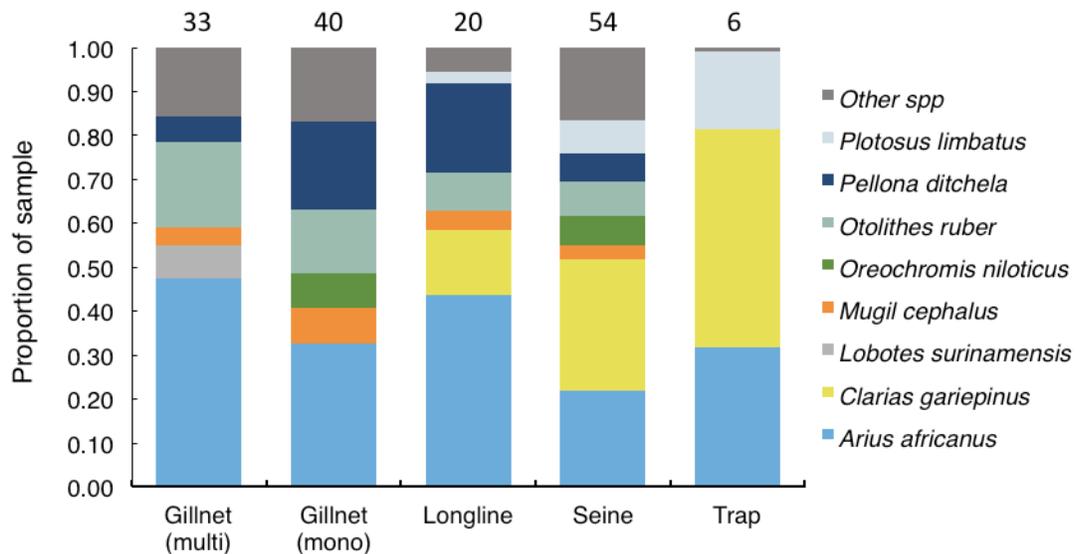


Figure 4. Proportional abundance of key species in landings of small-scale fishers using five gear types in the Tana Estuary in Kenya during shore-based sampling of landings in 2017. Species with < 5 % representation in landings were grouped as Other spp. The total number of species per gear type is shown above the bars.

and catadromous mullet *M. cephalus* made up 8 % of landings in the bay. *Otolithes ruber*, an amphidromous species, made up 19 % of landings at the bay location. The number of sampled species decreased sharply between the bay (71 species recorded) and upper estuary locations (8 species).

Traditional traps were highly selective gear and caught only three species in noteworthy quantities, *C. gariepinus* (50 % of all landings caught by traps), *A. africanus* (32 %) and *P. limbatus* (18 %) (Fig. 4). The high selectivity of traps can partly be explained by their use in the upper and mid estuary locations only, where species

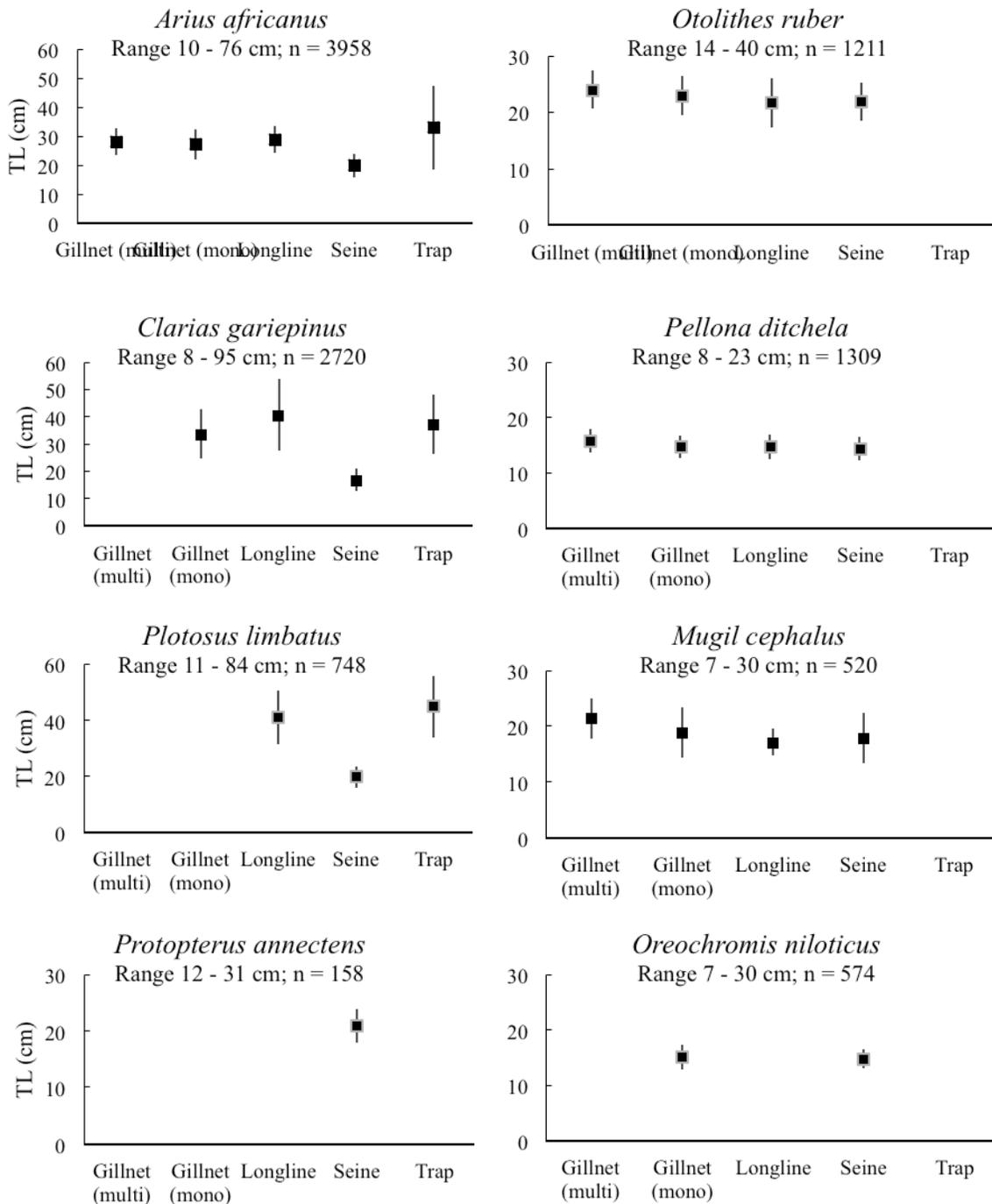


Figure 5. The mean size (Total Length \pm SD cm) of selected fish species caught per gear type by small-scale fishers in the Tana Estuary in Kenya during shore-based sampling of landings in 2017. Observed size ranges and sample sizes (n) are shown. Data of fish caught by cast nets, shark nets, hand lines and spears / sticks were excluded because of small samples.

diversity was much lower than in the bay and lower estuary. Seine nets (54 species recorded from landings) and monofilament gillnets (40 species) were unselective gears used at all four locations. Seine nets caught a mixture of freshwater, estuarine and marine species, and they also caught a mixture of small pelagic, benthopelagic and demersal species. Monofilament gillnets were similarly unselective, although few *C. gariepinus* or *P. limbatus*, both abundant in samples from seine net and trap catches, were caught by gillnets. Multifilament gillnets were unselective for marine and brackish water species occurring in the bay and lower estuary locations, and they were not used in the mid and upper estuary. *Arius africanus* made up a large proportion of landings made by all five gear types, particularly multifilament gillnets (47 % of sampled landings) and long lines (44 %).

Gear types selected fish of different sizes, but size-selectivity also depended on gear-species interactions (Fig. 5). The largest *A. africanus* were caught in traps (mean TL of 33.1 ± 14.3 cm) and the smallest in seine nets (19.9 ± 4.3 cm), whereas multi- and monofilament gill nets and long lines caught intermediate sizes with TL of between 27.1 and 28.9 cm. Large *C. gariepinus* were caught by long lines (40.5 ± 13.2 cm) and traps (36.9 ± 10.9 cm) but seine nets caught only small ones (16.6 ± 4.1 cm). Size selectivity by gear was less obvious for *M. cephalus*, *O. ruber* and *P. ditchela*, where multi- and monofilament gillnets, long lines and seine nets caught similar-sized fish, and traps caught none. *Oreochromis niloticus* caught by monofilament gillnets were

similar in size to those caught by seine nets (means of 15 ± 2 cm in both cases), but they were not caught by any other gear. Seine nets caught small *P. limbatus* (19.8 ± 3.8 cm) compared to long lines (40.9 ± 9.6 cm) and traps (45.0 ± 10.1 cm), but they were absent from gillnet catches. *P. annectens* were caught in seine nets only (21.0 ± 3.0 cm).

Catch rates by fishing location indicated higher fishing intensity in the bay, mid and upper estuary than in the lower estuary (Fig. 6). Monofilament nets, long lines and seine nets were recorded at all four fishing locations, traps only in the mid and upper estuary, and multifilament gillnets only in the bay. Overall catch rates kg.fisher⁻¹.day⁻¹ differed significantly between gear types (1-way ANOVA: df = 4; f = 23.737; p = 0.001). Post hoc pair-wise comparison using the Tukey HSD test confirmed catch rates of multifilament gillnets differed significantly from those of monofilament gillnets, traps and seine nets (p < 0.01 in all cases) while monofilament gillnets differed significantly from traps and seine nets (p < 0.01 in both cases). Catch rates of long lines differed significantly from those of traps and seine nets (p < 0.01 in both cases). Average catch rates were highest for monofilament gillnets (8.4 ± 0.6 kg) followed by long lines (6.6 ± 0.4 kg) and seine nets (4.1 ± 0.5 kg). Multifilament gillnets and traps recorded lower catch rates of 3.1 ± 0.4 and 2.3 ± 0.5 kg, respectively.

Trophic levels (weighted average) of catches made by multifilament gillnets were highest (4.08) followed by traps (3.79), spears and long lines (3.73). Monofilament

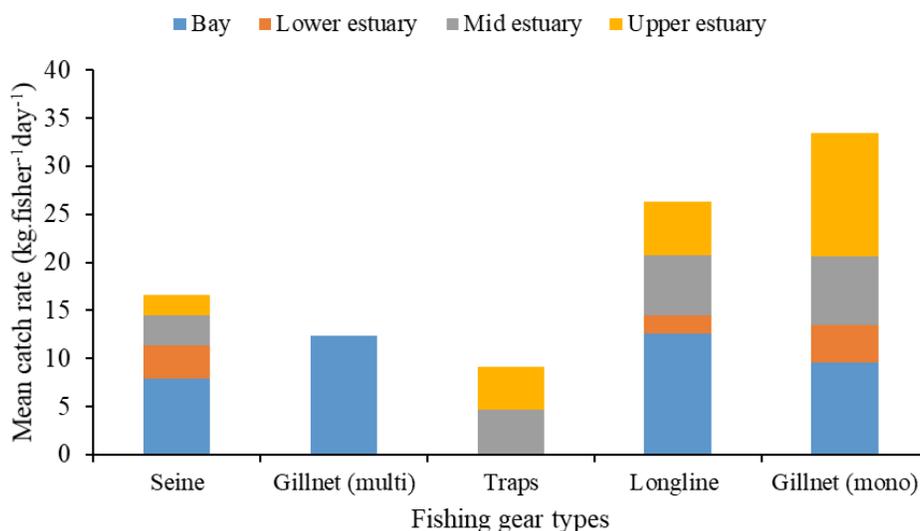


Figure 6. Mean catch rate (kg.fisher⁻¹.day⁻¹) per gear type and fishing location during shore-based sampling of landings and fishing effort in the Tana Estuary in Kenya in 2017.

gillnets (3.49) and seine nets (3.55) caught fish at lower trophic levels. By fishing location, the trophic level of catches was marginally lower in the bay and lower estuary (3.58 and 3.44, respectively) than in the mid and upper estuary (3.72 and 3.57). In general, traps and long lines caught more carnivores whereas gill nets and seine nets caught a mixture of herbivorous, omnivorous and carnivorous fish species.

Multivariate analysis

Results of nMDS plots showed no distinct seasonal pattern in species composition of sampled landings (stress value of 0.11) (Fig. 7A). Results of 1-way ANOSIM confirmed no significant difference in catch composition between seasons ($p = 0.146$). The 20 most abundant species were observed in both NE and SE monsoon seasons, except for *Moolgarda seheli* (NE monsoon only), *Liza vaigiensis*, *P. annectens* and *Acanthopagrus berda* (SE monsoon only).

The nMDS plots could differentiate landings across sampling locations (Fig. 7B; ANOSIM; $R = 0.42$; $p = 0.001$), but no pairwise difference could be found between landings from the mid and upper estuary

($p > 0.05$; Appendix 2). Species that contributed most to dissimilarities between sampling locations in 1-way SIMPER analyses were more abundant *P. ditchella* and *O. ruber* in the bay compared to abundant *Thryssa vitrirostris*, *Macrobrachium* spp. and *O. niloticus* in the lower estuary, and more abundant *P. ditchella*, *O. ruber*, *L. surinamensis*, *S. melanura* and *S. albella* in the bay compared to *C. gariepinus*, *P. limbatus* and *O. niloticus* in the mid and upper estuary (Appendix 2). The dissimilarity between the lower and mid estuary was attributed to more *T. vitrirostris*, *Johnius dussumieri*, *Macrobrachium* spp., *L. surinamensis* and *P. ditchella* in the lower estuary compared to *C. gariepinus* and *P. limbatus* in mid estuary. The same species contributed most to the dissimilarity between lower and upper estuaries (Appendix 2).

The nMDS plots could differentiate landings among gear types, most clearly between traditional gears (traps, spears / sticks) and the rest of the gears (Fig. 7C). Pairwise differences in landing composition were found between encircling nets (combined seine and cast nets) and gillnets (combined multi- and monofilament gillnets), long lines and traditional gears, respectively ($p = 0.001$ in all cases) (Appendix

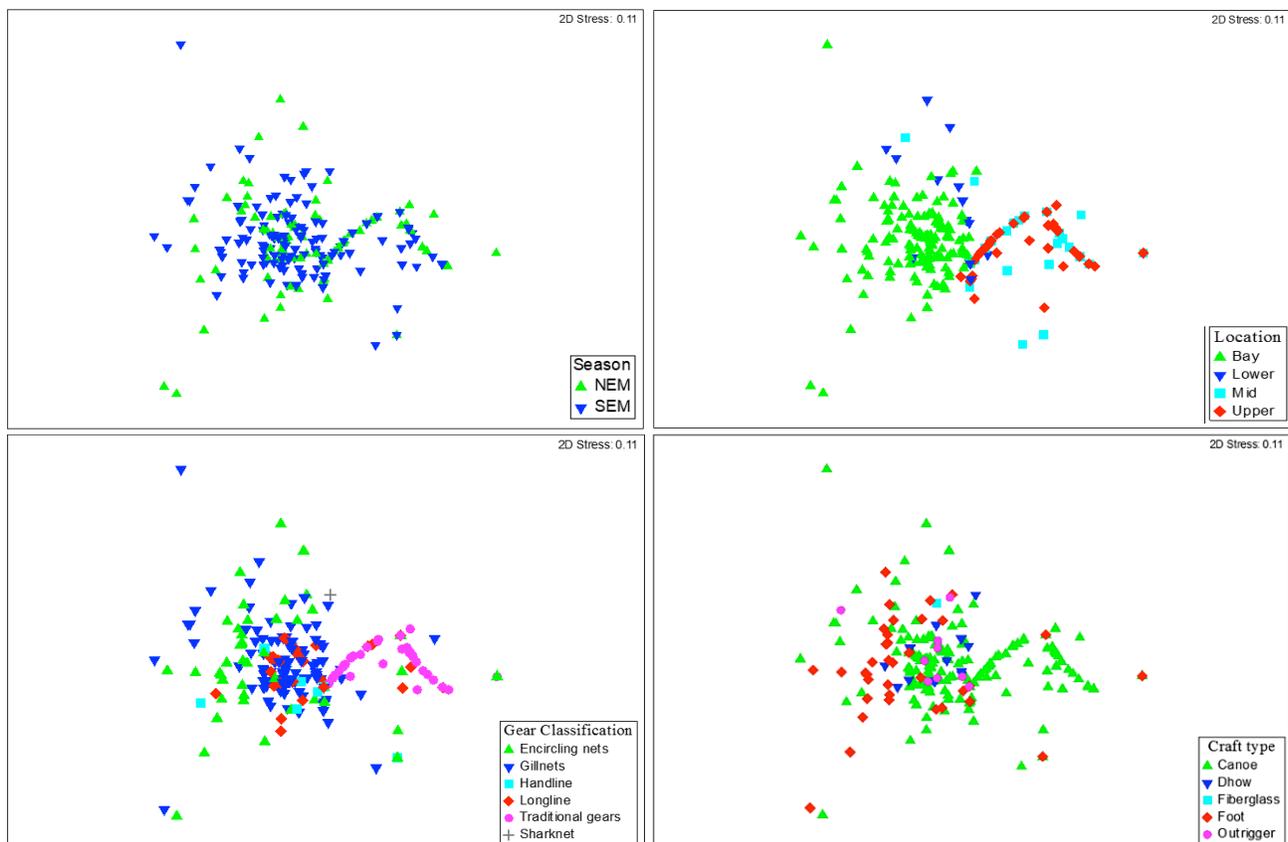


Figure 7. Non-metric MDS plots showing the composition of catches by (A) season; (B) location; (C) gear type; and (D) fishing craft type in the Tana Estuary in Kenya determined from shore-based sampling of landings and fishing effort in 2017. 24

2). The landings composition of gillnets differed from traditional gears and long lines, respectively, and hand lines differed from long lines ($p = 0.001$ in all cases). Species that contributed most to dissimilarities between gears in 1-way SIMPER analyses were abundant *C. gariepinus* and *P. limbatus* in encircling nets versus *A. africanus* and *Lobotes surinamensis* in gillnets; abundant *O. niloticus*, *T. crocodilus* and *S. albella* in encircling nets compared to *A. africanus* in long lines; abundant *P. ditchela*, *O. ruber*, *O. niloticus*, *T. crocodilus*, *S. albella* and *S. melanura* in encircling nets compared to *C. gariepinus* and *P. limbatus* in traditional gears; abundant *O. ruber*, *P. ditchela*, *L. surinamensis*, *M. cephalus*, *O. niloticus*, *G. feliceps* and *S. albella* in gillnets compared to *C. gariepinus* and *P. limbatus* in traditional gears; abundant *O. niloticus*, *S. albella*, and *M. seheli* in hand lines compared to *P. ditchela* and *C. gariepinus* in long lines; and abundant *A. africanus*, *P. ditchela*, *O. ruber* associated with long line catches compared to *C. gariepinus* and *P. limbatus* caught with traditional gears.

The nMDS plots could differentiate landings originating from various fishing craft types (Fig. 7D). Landings originating from dugout canoes (incl. those with outrigger) and foot fishers were dispersed, but those made from dhows were clustered closely. The ANOSIM indicated a significant difference in the landings composition between the fishing crafts ($R = 0.133$; $p = 0.001$).

Rarefaction curves based on craft-gear combinations across fishing locations indicated higher diversity in landings originating from canoe-gillnet and canoe-encircling net combinations in the bay and lower estuary (3.5 to 7 species expected) compared to canoe-traditional gear (also canoe-gillnet, and canoe-encircling net combinations) in the mid- and upper estuary (<3 species) (Figure 8). A medium-high diversity of landings made by the foot fisher-encircling net combination in the bay (>4 species) suggests that overall, location had a greater influence on landings diversity than craft-gear combinations. The canoe-long line combination was an exception, with low diversity in the bay (~2 species), suggesting that long lines were more selective than other gears used in the bay.

Discussion

The use of the multivariate non-metric multidimensional technique was appropriate in the analysis of a multigear and multispecies fishery. The results confirmed that the small-scale fishery in the Tana Estuary is typical of tropical coastal fisheries, in which multiple species are caught with diverse fishing gears (van der Elst

et al., 2005). The fishery operates along a salinity gradient between the upper Tana Estuary and Ungwana Bay, resulting in mixed landings of freshwater (dominated by *C. gariepinus*, *O. niloticus*, *P. limbatus*), brackish water (*A. africanus*, *M. cephalus*) and marine species (*P. ditchela*, *Sardinella albella*). The diversity of landings was further enhanced because multiple gear types (encircling nets, gillnets, hook-and-line and traditional traps) were used to access different habitats, and therefore exploit several distinct fish assemblages. As a result, landings comprised of a mixture of small pelagic, benthopelagic and demersal fish species, ranging from herbivores (several sardine species) to medium-sized and large predatory fishes, including sharks.

Key assumptions made during the study were that shore-based sampling of landings would reflect the species / size composition of catches made by fishers; that samples would include all landed species in proportion to their numerical abundance in the fishery; that seasonality in catch composition would be adequately represented by a monthly sampling protocol spanning a single year; and that the timing and water volume of the annual flooding regime in 2017, when sampling took place, followed a typical annual pattern. The assumptions were only partially met in most cases, with implications for the interpretation of results.

Small-scale fishers retain nearly all catches made, irrespective of species and size (Mangi and Roberts, 2006), and therefore shore-based sampling of landings was considered representative of the catch. Landings were processed in several different ways (sun-dried, smoked, fried and fresh; pers. obs. JCG) for local consumption and sale at fish markets (see also Wamukota, 2009). The scarcity of crustaceans (Penaeidae, Palaemonidae, Portunidae) in the data suggests that this taxon was undersampled, thus breaching the assumption of proportionality in samples. Ungwana Bay is well-known for penaeid prawn fisheries (Munga *et al.*, 2013, 2014b, 2016) and it is unlikely that so few prawns would have been present in landings. Under-sampling of prawns and other crustaceans is plausibly explained by selective sampling of finfish during field-work, and by more rapid processing of prawn landings by fishers and buyers to maintain their quality for established markets, thus precluding representative sampling at landing sites.

The absence of a significant seasonal effect in our study contradicts the finding of Munga *et al.*, (2013), that species richness and diversity of landings in

Ungwana Bay increased during the NE monsoon season, when sea conditions are favorable for fishing. Undersampling of prawns, a seasonally abundant taxon, may have obscured the seasonal trend in the current study (see above). Alternatively, the absence of observed seasonality in this study potentially reflects year-round fishing in the enclosed (sheltered) part of the estuary, compared to strongly seasonal fishing in the bay observed by Munga *et al.* (2013), exacerbated by seasonal movements of migrant fishers that fish mainly in nearshore waters (Fulanda *et al.*, 2009).

The flooding regime during the sampling period in 2017 was anomalous, because the March-May long rains began late across most of Kenya, and Tana River County received only 25 to 50 % of normal rainfall (Government of Kenya, 2017). Lower flood levels in 2017 would have reduced land available for flood-recession agriculture, thus increasing the reliance of farmers on fishing (see Mwamlavya *et al.*, 2021). Flexibility in time

spent on farming and fishing, as an adaptive livelihood strategy to cope with inter-annual flood variability, is well established in the highly dynamic deltaic systems of the WIO (Duvail *et al.*, 2017; Hamerlynck *et al.*, 2020). In this study, increased fishing effort in the mid and upper estuary by communities that predominantly farm may have obscured typical seasonal trends in the species diversity of fish landings.

Negi and Mamgain (2013) found that fish communities in riverine and estuarine systems follow a pattern of increasing species richness, diversity and abundance from upstream to downstream. The same pattern was observed by Odhengo *et al.*, (2012) in the Lower Tana River Delta, with higher species richness in the lower delta and estuary compared to further upstream in the river. The current study showed a clear gradient in the number of species recorded per location, increasing sharply from the upper (8 spp) and mid estuary (12 spp) to the lower estuary (35 spp) and

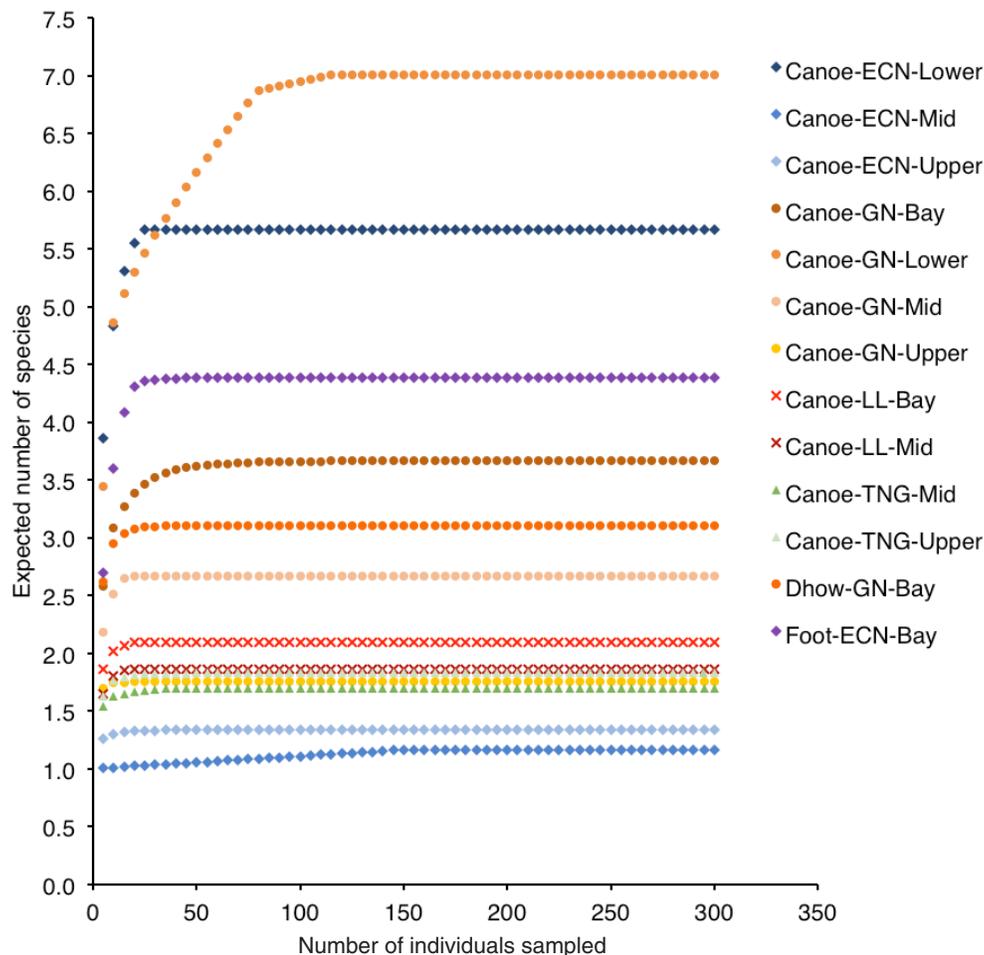


Figure 8. Rarefaction curves indicating the expected total number of species caught by craft-gear combination categories at four locations in the Tana Estuary in Kenya, determined from shore-based sampling of landings and fishing effort in 2017.

bay (71 spp) (Fig. 3). The gradient was not affected by combinations of fishing gear and craft used by fishers, as demonstrated by rarefaction curves in which the expected number of species were consistently greater in the bay and lower estuary compared to upstream locations, irrespective of the gear-craft combinations tested (Fig. 8). Higher biological productivity in brackish water and the presence of estuary-dependent marine species can explain the enhanced species richness in the bay and lower estuary. In contrast, the mid and upper estuary were dominated by a small number of freshwater species.

Factors that influenced the choice of gear were affordability, whether it can be constructed from local materials and easily repaired when damaged (e.g., traps used by part-time fishers in the upper estuary; Mwamlavya *et al.*, 2021), number of fishers required to operate the gear (e.g., 8-15 fishers for large seine nets; Samoilys *et al.*, 2011), gear propulsion by foot, dugout canoe or dhow (Munga *et al.*, 2014a), physical environment (open bay, intertidal or narrow backwater channels) and target assemblage (small pelagic fishes, benthopelagic or demersal fish or invertebrates). Monofilament gillnets are light and easy to transport with canoes and deploy in estuaries and they recorded the highest catch rates in the fishery. The gillnet-canoe combination was popular among fishers in this study, in agreement with Munga *et al.* (2014a). Traditional traps are made locally and cheaply and set in channels to target mainly catfishes (*A. africanus*, *C. gariepinus* and *P. limbatus*). These species are also targeted by spanning monofilament gillnets across narrow channels, or with seine nets along estuary banks.

Salinity is the dominant factor influencing the distribution of fish species in estuaries (Barletta *et al.*, 2005). The salinity profile of the Tana Estuary is influenced by tides and seasonal freshwater inflow (Kitheka and Mavuti, 2016). Droughts and floods are regular occurrences in Kenya (listed chronologically by Mwaguni *et al.*, 2016), implying that the salinity profile of the Tana Estuary is highly variable. Fishes that are stenohaline, for example *C. gariepinus* that tolerate only low salinity levels up to 2.2 ppt (Brummett, 2008) may undertake lateral migrations, upstream to escape increasing salinity during dry periods, or downstream when the river is in flood. The species composition of landings at any location in the estuary is therefore inherently inconsistent, depending on flood or drought mediated salinity profiles. The results of this study, particularly the species selection by location, should be seen in this light.

In conclusion, the small-scale fishery in the Tana Estuary has a multi-species character and relies on multiple gear types to access different habitats in the estuary. Species composition correlated well with the location of landing sites in the estuary, along a salinity gradient. Seine nets were used throughout the estuary, captured the highest number of species among gear types, and caught smaller individuals of some abundant species (*A. africanus*, *C. gariepinus* and *P. limbatus*) than other gears. Gillnets (mono- and multifilament) also captured a high number of species, mainly in the bay. Traditional traps were used in the upper and mid estuary and caught mainly catfish species. The high complexity and apparent organization of the fishery at estuary-scale makes it a good example of a relatively intact socio-ecological system (SES) in the WIO region, suitable for regional comparative analyses within a theoretical SES framework (Berkes *et al.*, 2014; Santos *et al.*, 2021).

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Appendices

Appendix 1. List of all fish species sampled, including their guild and trophic level (www.fishbase.org) per location (Bay, Upper, Mid and Lower estuary) in the Tana Estuary in Kenya in 2017. (Y=Present, N=Absent)

| No. | Species name | Guild | Trophic level | Bay | Lower | Mid | Upper |
|-----|--|------------|---------------|-----|-------|-----|-------|
| 1 | <i>Arius africanus</i> | Estuarine | 3.8 | Y | Y | Y | Y |
| 2 | <i>Clarias gariepinus</i> | Freshwater | 3.76 | N | N | Y | Y |
| 3 | <i>Pellona ditchela</i> | Estuarine | 3.95 | Y | Y | N | N |
| 4 | <i>Otolithes ruber</i> | Estuarine | 3.6 | Y | N | N | N |
| 5 | <i>Plotosus limbatus</i> | Freshwater | 3.91 | N | N | Y | Y |
| 6 | <i>Oreochromis niloticus</i> | Freshwater | 2 | N | Y | Y | Y |
| 7 | <i>Mugil cephalus</i> | Estuarine | 2.48 | Y | Y | Y | N |
| 8 | <i>Sardinella albella</i> | Estuarine | 2.62 | Y | N | N | N |
| 9 | <i>Lobotes surinamensis</i> | Estuarine | 4.04 | Y | Y | N | N |
| 10 | <i>Protopterus annectens</i> | Estuarine | 3.83 | N | N | N | Y |
| 11 | <i>Sardinella melanura</i> | Estuarine | 2.84 | Y | N | N | N |
| 12 | <i>Tylosurus crocodilus crocodilus</i> | Estuarine | 4.43 | Y | N | N | N |
| 13 | <i>Valamugil buchanani</i> | Estuarine | 2.22 | Y | Y | N | N |
| 14 | <i>Galeichthys feliceps</i> | Estuarine | 3.75 | Y | N | N | N |
| 15 | <i>Johnius dussumieri</i> | Estuarine | 4.09 | Y | Y | N | N |
| 16 | <i>Hilsa kelee</i> | Estuarine | 2.85 | Y | Y | N | N |
| 17 | <i>Moolgarda seheli</i> | Estuarine | 2.32 | Y | N | N | N |
| 18 | <i>Liza vaigiensis</i> | Estuarine | 2.18 | Y | N | N | N |
| 19 | <i>Thryssa vitrirostris</i> | Estuarine | 3.31 | Y | Y | N | N |
| 20 | <i>Acanthopagrus berda</i> | Estuarine | 3.5 | Y | N | Y | N |
| 21 | <i>Lutjanus fulviflamma</i> | Estuarine | 3.79 | Y | N | N | N |
| 22 | <i>Sardinella gibbosa</i> | Estuarine | 2.85 | Y | N | N | N |
| 23 | <i>Macrobrachium sp.</i> | Estuarine | | N | Y | N | N |
| 24 | <i>Pomadasys opercularis</i> | Estuarine | 3.53 | Y | N | N | N |
| 25 | <i>Nemipterus randalli</i> | Estuarine | 3.5 | N | Y | N | N |
| 26 | <i>Sphyrna lewini</i> | Estuarine | 4.08 | Y | N | N | N |
| 27 | <i>Trachinotus botla</i> | Estuarine | 3.21 | Y | Y | N | N |
| 28 | <i>Carcharhinus leucas</i> | Estuarine | 4.31 | Y | N | N | N |

| No. | Species name | Guild | Trophic level | Bay | Lower | Mid | Upper |
|-----|----------------------------------|-----------|---------------|-----|-------|-----|-------|
| 29 | <i>Carcharhinus amblyrhincos</i> | Estuarine | 4.11 | Y | Y | N | N |
| 30 | <i>Lutjanus rivulatus</i> | Estuarine | 4.13 | Y | N | Y | N |
| 31 | <i>Megalops cyprinoides</i> | Estuarine | 3.48 | N | N | Y | N |
| 32 | <i>Gerres filamentosus</i> | Estuarine | 3.34 | Y | N | N | N |
| 33 | <i>Lethrinus nebulosus</i> | Estuarine | 3.76 | Y | N | Y | N |
| 34 | <i>Amphilius jacksonii</i> | Riverine | 2.96 | N | N | Y | Y |
| 35 | <i>Euthynnus affinis</i> | Estuarine | 4.13 | Y | N | N | N |
| 36 | <i>Penaeus indicus</i> | Estuarine | 3.32 | Y | Y | N | N |
| 37 | <i>Plotosus japonicus</i> | Estuarine | 3.66 | N | Y | N | N |
| 38 | <i>Gazza minuta</i> | Estuarine | 4.19 | Y | Y | N | N |
| 39 | <i>Carcharhinus plumbeus</i> | Estuarine | 4.49 | Y | Y | N | N |
| 40 | <i>Epinephelus tauvina</i> | Estuarine | 4.13 | Y | N | N | N |
| 41 | <i>Terapon jarbua</i> | Estuarine | 3.93 | Y | N | N | N |
| 42 | <i>Lutjanus argentimaculatus</i> | Estuarine | 3.58 | N | Y | N | N |
| 43 | <i>Octopus vulgaris</i> | Estuarine | 3.74 | Y | N | N | N |
| 44 | <i>Oreochromis hunteri</i> | Estuarine | 2 | N | Y | N | N |
| 45 | <i>Penaeus monodon</i> | Estuarine | 3.36 | N | Y | N | N |
| 46 | <i>Scylla serrata</i> | Estuarine | 3.17 | Y | Y | N | N |
| 47 | <i>Pardiglanis tarabinii</i> | Riverine | 3.47 | N | N | N | Y |
| 48 | <i>Pomadasy maculatus</i> | Estuarine | 4.04 | Y | N | N | N |
| 49 | <i>Sardinella neglecta</i> | Estuarine | 2 | Y | N | N | N |
| 50 | <i>Ambassis natalensis</i> | Estuarine | 3.42 | Y | Y | N | N |
| 51 | <i>Caranx ignobilis</i> | Estuarine | 4.22 | N | Y | N | N |
| 52 | <i>Carcharhinus melanopterus</i> | Estuarine | 3.94 | Y | N | N | N |
| 53 | <i>Chirocentrus dorab</i> | Estuarine | 4.2 | Y | N | N | N |
| 54 | <i>Leiognathus equulus</i> | Estuarine | 3.01 | Y | Y | N | N |
| 55 | <i>Metapenaeus monoceros</i> | Estuarine | 3.35 | N | Y | N | N |
| 56 | <i>Nematopalaemon tenuipes</i> | Estuarine | 3.15 | N | Y | N | N |
| 57 | <i>Sillago sihama</i> | Estuarine | 3.33 | Y | N | N | N |
| 58 | <i>Epinephelus coioides</i> | Estuarine | 4 | Y | Y | N | N |
| 59 | <i>Epinephelus malabaricus</i> | Riverine | 4.16 | N | N | Y | N |
| 60 | <i>Leiognathus berbis</i> | Estuarine | 3.31 | N | Y | N | N |

| No. | Species name | Guild | Trophic level | Bay | Lower | Mid | Upper |
|-----|--------------------------------------|-----------|---------------|-----|-------|-----|-------|
| 61 | <i>Panulirus ornatus</i> | Estuarine | 3.74 | Y | N | N | N |
| 62 | <i>Plectorhinchus flavomaculatus</i> | Estuarine | 3.99 | Y | N | N | N |
| 63 | <i>Scomberoides commersonianus</i> | Estuarine | 4.36 | Y | N | N | N |
| 64 | <i>Sphyræna obtusata</i> | Estuarine | 4.5 | Y | N | N | N |
| 65 | <i>Aprion virescens</i> | Estuarine | 4.28 | Y | N | N | N |
| 66 | <i>Carangoides ferdau</i> | Estuarine | 4.31 | Y | N | N | N |
| 67 | <i>Caranx heberi</i> | Estuarine | 3.7 | N | Y | N | N |
| 68 | <i>Carcharhinus macloiti</i> | Estuarine | 4.22 | Y | N | N | N |
| 69 | <i>Cociella crocodillus</i> | Estuarine | 3.86 | N | Y | N | N |
| 70 | <i>Drepane longimana</i> | Estuarine | 3.5 | Y | N | N | N |
| 71 | <i>Elops machnata</i> | Estuarine | 3.97 | Y | N | N | N |
| 72 | <i>Elops saurus</i> | Estuarine | 3.49 | Y | N | N | N |
| 73 | <i>Epinephelus areolatus</i> | Estuarine | 3.74 | Y | N | N | N |
| 74 | <i>Gerres oyena</i> | Estuarine | 2.72 | Y | N | N | N |
| 75 | <i>Himantura gerrardi</i> | Estuarine | 3.73 | Y | N | N | N |
| 76 | <i>Johnius amblycephalus</i> | Estuarine | 3.81 | Y | N | N | N |
| 77 | <i>Leiognathus dussumieri</i> | Estuarine | 3.22 | Y | N | N | N |
| 78 | <i>Liza melineptera</i> | Estuarine | 2.32 | Y | N | N | N |
| 79 | <i>Loxodon macrorhinus</i> | Estuarine | 3.95 | Y | N | N | N |
| 80 | <i>Marsupenaeus japonicus</i> | Estuarine | 3.2 | Y | N | N | N |
| 81 | <i>Plectorhinchus chubbi</i> | Estuarine | 3.86 | Y | N | N | N |
| 82 | <i>Sardinella longiceps</i> | Estuarine | 2.41 | N | Y | N | N |
| 83 | <i>Schilbe uranoscopus</i> | Riverine | 3.53 | N | N | N | Y |
| 84 | <i>Scomberoides lysan</i> | Estuarine | 4.04 | Y | N | N | N |
| 85 | <i>Scomberomorus commerson</i> | Estuarine | 4.36 | Y | N | N | N |
| 86 | <i>Secutor insidiator</i> | Estuarine | 2.84 | Y | N | N | N |
| 87 | <i>Squalus megalops</i> | Estuarine | 4.34 | Y | N | N | N |
| 88 | <i>Stolephorus indicus</i> | Estuarine | 3.33 | N | Y | N | N |
| 89 | <i>Trachinotus bailloni</i> | Estuarine | 3.21 | Y | Y | N | N |

Appendix 2a. Pair-wise comparison tests showing significant differences in species composition of landings by location ($p < 0.05$, bold and italic) in the Tana Estuary in Kenya during shore-based sampling in 2017.

| Fishing location comparisons | R-Statistic | P-Value | Possible Permutations | Actual permutations |
|------------------------------|-------------|---------------------|-----------------------|---------------------|
| Bay, Lower | 0.226 | <i>0.003</i> | Very large | 999 |
| Bay, Mid | 0.57 | <i>0.001</i> | Very large | 999 |
| Bay, Upper | 0.469 | <i>0.001</i> | Very large | 999 |
| Lower, Mid | 0.409 | <i>0.001</i> | Very large | 999 |
| Lower, Upper | 0.426 | <i>0.001</i> | Very large | 999 |
| Mid, Upper | 0.014 | 0.221 | Very large | 999 |

Appendix 2b. One-way SIMPER Analysis: Species contributing to the dissimilarity in terms of abundance (%) between locations (bay versus lower) with an average dissimilarity of 86.6 %; bold numbers being species that were most abundant in one season compared to the other season.

| Species | Bay | Lower | Average Dissimilarity (%) | Contribution (%) |
|------------------------------|-----------------------|-----------------------|---------------------------|------------------|
| | Average Abundance (%) | Average Abundance (%) | | |
| <i>Arius africanus</i> | 41.38 | 45.98 | 19.91 | 27.15 |
| <i>Pellona ditchela</i> | 16.23 | 3.25 | 8.30 | 11.31 |
| <i>Otolithes ruber</i> | 14.72 | 0.15 | 7.36 | 10.04 |
| <i>Thryssa vitrirostris</i> | 0.49 | 6.68 | 3.41 | 4.65 |
| <i>Lobotes surinamensis</i> | 4.05 | 3.73 | 3.39 | 4.63 |
| <i>Mugil cephalus</i> | 4.38 | 2.50 | 3.09 | 4.21 |
| <i>Johnius dussumieri</i> | 1.18 | 5.14 | 2.95 | 4.03 |
| <i>Macrobrachium sp.</i> | 0.08 | 4.46 | 2.26 | 3.08 |
| <i>Oreochromis niloticus</i> | 0.00 | 4.31 | 2.15 | 2.94 |
| <i>Sardinella melanura</i> | 3.43 | 0.00 | 1.71 | 2.34 |

Appendix 2c. One-way SIMPER Analysis: Species contributing to the dissimilarity in terms of abundance (%) between locations (bay versus mid) with an average dissimilarity of 88.68 %; bold numbers being species that were most abundant in one season compared to the other season.

| Species | Bay | Mid | Average Dissimilarity (%) | Contribution (%) |
|------------------------------|-----------------------|-----------------------|---------------------------|------------------|
| | Average Abundance (%) | Average Abundance (%) | | |
| <i>Clarias gariepinus</i> | 0.00 | 51.08 | 25.54 | 28.80 |
| <i>Arius africanus</i> | 41.38 | 21.26 | 20.10 | 22.67 |
| <i>Pellona ditchela</i> | 16.23 | 0.00 | 8.11 | 9.15 |
| <i>Otolithes ruber</i> | 14.72 | 0.00 | 7.36 | 8.30 |
| <i>Plotosus limbatus</i> | 0.00 | 10.86 | 5.43 | 6.12 |
| <i>Oreochromis niloticus</i> | 0.00 | 9.51 | 4.76 | 5.36 |
| <i>Mugil cephalus</i> | 4.38 | 2.33 | 3.25 | 3.67 |
| <i>Lobotes surinamensis</i> | 4.05 | 0.00 | 2.02 | 2.28 |
| <i>Sardinella melanura</i> | 3.43 | 0.00 | 1.71 | 1.93 |
| <i>Sardinella albella</i> | 3.16 | 0.00 | 1.58 | 1.78 |

Appendix 2d. One-way SIMPER Analysis: Species contributing to the dissimilarity in terms of abundance (%) between locations (bay versus upper) with an average dissimilarity of 84.40 %; bold numbers being species that were most abundant in one season compared to the other season.

| Species | Bay | Upper | Average Dissimilarity (%) | Contribution (%) |
|------------------------------|-----------------------|-----------------------|---------------------------|------------------|
| | Average Abundance (%) | Average Abundance (%) | | |
| <i>Clarias gariepinus</i> | 0.00 | 50.79 | 25.40 | 30.09 |
| <i>Arius africanus</i> | 41.38 | 29.49 | 19.84 | 23.50 |
| <i>Pellona ditchela</i> | 16.23 | 0.00 | 8.11 | 9.61 |
| <i>Otolithes ruber</i> | 14.72 | 0.00 | 7.36 | 8.72 |
| <i>Plotosus limbatus</i> | 0.00 | 11.70 | 5.85 | 6.93 |
| <i>Oreochromis niloticus</i> | 0.00 | 6.34 | 3.17 | 3.76 |
| <i>Mugil cephalus</i> | 4.38 | 0.00 | 2.19 | 2.59 |
| <i>Lobotes surinamensis</i> | 4.05 | 0.00 | 2.02 | 2.40 |
| <i>Sardinella melanura</i> | 3.43 | 0.00 | 1.71 | 2.03 |
| <i>Sardinella albella</i> | 3.16 | 0.00 | 1.58 | 1.87 |

Appendix 2e. One-way SIMPER Analysis: Species contributing to the dissimilarity in terms of abundance (%) between locations (lower versus mid) with an average dissimilarity of 86.82 %; bold numbers being species that were most abundant in one season compared to the other season.

| Species | Lower | Mid | Average Dissimilarity (%) | Contribution (%) |
|------------------------------|-----------------------|-----------------------|---------------------------|------------------|
| | Average Abundance (%) | Average Abundance (%) | | |
| <i>Clarias gariepinus</i> | 1.40 | 51.08 | 25.23 | 29.06 |
| <i>Arius africanus</i> | 45.98 | 21.26 | 22.16 | 25.52 |
| <i>Oreochromis niloticus</i> | 4.31 | 9.51 | 6.26 | 7.22 |
| <i>Plotosus limbatus</i> | 0.00 | 10.86 | 5.43 | 6.25 |
| <i>Thryssa vitrirostris</i> | 6.68 | 0.00 | 3.34 | 3.85 |
| <i>Johnius dussumieri</i> | 5.14 | 0.00 | 2.57 | 2.96 |
| <i>Mugil cephalus</i> | 2.50 | 2.33 | 2.35 | 2.71 |
| <i>Macrobrachium sp.</i> | 4.46 | 0.00 | 2.23 | 2.57 |
| <i>Lobotes surinamensis</i> | 3.73 | 0.00 | 1.86 | 2.15 |
| <i>Pellona ditchela</i> | 3.25 | 0.00 | 1.63 | 1.87 |

Appendix 2f. One-way SIMPER Analysis: Species contributing to the dissimilarity in terms of abundance (%) between locations (lower versus upper) with an average dissimilarity of 82.58 %; bold numbers being species that were most abundant in one season compared to the other season.

| Species | Lower | Upper | Average Dissimilarity (%) | Contribution (%) |
|------------------------------|-----------------------|-----------------------|---------------------------|------------------|
| | Average Abundance (%) | Average Abundance (%) | | |
| <i>Clarias gariepinus</i> | 1.40 | 50.79 | 25.05 | 30.33 |
| <i>Arius africanus</i> | 45.98 | 29.49 | 21.86 | 26.48 |
| <i>Plotosus limbatus</i> | 0.00 | 11.70 | 5.85 | 7.08 |
| <i>Oreochromis niloticus</i> | 4.31 | 6.34 | 4.83 | 5.84 |
| <i>Thryssa vitrirostris</i> | 6.68 | 0.00 | 3.34 | 4.05 |
| <i>Johnius dussumieri</i> | 5.14 | 0.00 | 2.57 | 3.11 |
| <i>Macrobrachium sp.</i> | 4.46 | 0.00 | 2.23 | 2.70 |
| <i>Lobotes surinamensis</i> | 3.73 | 0.00 | 1.86 | 2.26 |
| <i>Pellona ditchela</i> | 3.25 | 0.00 | 1.63 | 1.97 |
| <i>Mugil cephalus</i> | 2.50 | 0.00 | 1.25 | 1.51 |