

Trophic redundancy among fishes in an East African nearshore seagrass community inferred from stable-isotope analysis

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Stable-isotope analysis supplemented with stomach contents data from published sources was used to quantify the trophic niches, trophic niche overlaps and potential trophic redundancy for the most commonly caught fish species from an East African nearshore seagrass community. This assessment is an important first step in quantifying food-web structure in a region subject to intense fishing activities. Nearshore food webs were driven by at least two isotopically distinct trophic pathways, algal and seagrass, with a greater proportion of the sampled species feeding within the seagrass food web (57%) compared with the algal food web (33%). There was considerable isotopic niche overlap among species (92% of species overlapped with at least one other species). Narrow isotopic niche widths of most (83%) species sampled, low isotopic similarity (only 23% of species exhibited no differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and low predicted trophic redundancy among fishes most commonly caught by fishermen (15%), however, suggest that adjustments to resource management concerning harvesting and gear selectivity may be needed for the persistence of artisanal fishing in northern Tanzania. More detailed trophic studies paired with information on spatio-temporal variation in fish abundance, especially for heavily targeted species, will assist in the development and implementation of management strategies to maintain coastal food-web integrity.

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Key words: $\delta^{13}\text{C}$; $\delta^{15}\text{N}$; artisanal fisheries; Bagamoyo; Indian Ocean; teleosts.

INTRODUCTION

Overfishing and habitat degradation can greatly affect the structure and stability of food webs within coastal ecosystems, putting them at risk, especially in the face of global environmental change (Jackson *et al.*, 2001; Kennish, 2002; Short *et al.*, 2011). Seagrass ecosystems are particularly vulnerable and changes in water quality and community assemblages threaten the essential ecological functions they offer, including providing habitat for fishes and invertebrates, serving as major carbon sinks and protecting shorelines from erosion (Duarte, 2000; Hemminga & Duarte, 2000; Orth *et al.*, 2006; Barbier *et al.*, 2011). Protection of these habitats is a priority for maintaining ecosystem services, including subsistence fisheries (Short & Neckles, 1999;

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Erfteimeijer & Lewis, 2006; Worm *et al.*, 2006). Balancing ecosystem protection and economic stability, however, make managing coastal ecosystems and fisheries challenging, especially in developing nations where overfishing and habitat degradation may have the most immediate and far-reaching effects because of economic reliance on coastal resources (Carbone & Accordi, 2000; de Boer *et al.*, 2001; Gullström *et al.*, 2002).

Along the coast of Tanzania, most fisheries occur in inshore waters, are artisanal or subsistence and target a broad range of species from multiple habitats, including estuaries, coral reefs and seagrass meadows (Gullström *et al.*, 2002; van der Elst *et al.*, 2005). Artisanal and subsistence fisheries in Tanzania involve the majority of the coastal population, whose survival depends on marine resources (de Graaf & Garibaldi, 2014). Fishing in Tanzania, however, often employs destructive gears (dynamite and beach seines), causing habitat degradation and potential unsustainable declines of fish stocks (McClanahan *et al.*, 1999). Improved management of coastal waters is recognized as an urgent need, but financial constraints limit both enforcement and scientific monitoring (van der Elst *et al.*, 2005). Little is known about the ecology and trophic interactions of fish communities associated with seagrass beds in Tanzania and more broadly in East Africa (but see Gullström *et al.*, 2002; Lugendo *et al.*, 2006; Abrantes *et al.*, 2014). As such, understanding trophic structure in this region is important for gaining insights into the possible ecological resilience of these ecosystems and making informed management decisions (but see Gamfeldt *et al.*, 2008).

Ecosystem stability often stems from the maintenance of food-web structure (reviewed by Thompson *et al.*, 2012). One mechanism that aids in maintaining food webs is trophic redundancy, in which species occupy similar trophic niches and perform similar functional roles (Walker, 1992). In the event of ecological disturbance and subsequent species declines, ecosystems where redundancy is high may not result in the loss of connectivity within and across trophic levels, preserving important ecological roles within the ecosystem (Naeem, 1998; Peterson *et al.*, 1998; Rastetter *et al.*, 1999; Borrvall *et al.*, 2000; Downing *et al.*, 2012). Within fish communities, trophic redundancy varies geographically and among habitats. Ross (1986) reviewed stomach contents data and found that about one third of fishes exhibited trophic overlap/redundancy (at least 60% overlap in prey taxa) across all ecosystems, with lower trophic overlap in marine waters (31%) than freshwater ecosystems (44%). While this estimate of redundancy is simplistic and all studies reviewed did not consider factors such as prey size, foraging habitat location and temporal period of foraging, which are important to consider when quantifying redundancy, this estimate provides an important step for better understanding trophic structure beyond local patterns.

Stable-isotope analysis enables the investigation of trophic interactions among communities and can be used to gain insights into the potential for trophic overlap and functional redundancy in food webs (Post, 2002; Newsome *et al.*, 2007; Layman *et al.*, 2012). For example, stable isotopes have enabled investigations of niche partitioning and overlap among fish communities in seagrass ecosystems in the Atlantic (Chasar *et al.*, 2005; Douglas *et al.*, 2011), Pacific (Vonk *et al.*, 2008) and Indian Oceans (Nyunja *et al.*, 2009; Abrantes *et al.*, 2014) and the Caribbean Sea (Fry *et al.*, 1982; Nagelkerken *et al.*, 2006; Mendoza-Carranza *et al.*, 2010), with relatively high frequency of isotopic niche overlap in each region. Stable-isotope analysis is also useful in remote locations where stomach-content analysis may be less manageable. Stable isotopes, however, do not provide the taxonomic resolution of diet data from

stomach-content analysis and multiple trophic pathways can lead to individuals or species having similar stable-isotope values despite different diets. Species with similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggest feeding within similar food web(s) at similar trophic levels, but may be isotopically similar without being trophically redundant (Martinez del Rio *et al.*, 2009). Consequently, pairing stable-isotope data with stomach contents provides a more comprehensive view of species trophic interactions than employing only one method. Here, stable carbon and nitrogen isotope analysis paired with diet data from published sources was used (Table I) to investigate the trophic interactions of the most abundant teleost fishes within a large and highly exploited seagrass ecosystem off the coast of northern Tanzania and to investigate the potential for trophic redundancy among these fishes within the food web.

MATERIALS AND METHODS

STUDY SITE AND SAMPLE COLLECTION

Teleosts and primary producers were sampled along the coast of Bagamoyo, northern Tanzania ($6^{\circ} 26' \text{ S}$; $38^{\circ} 54' \text{ E}$; Fig. 1) in June 2013. Within inshore waters of northern Tanzania, seagrass beds are widely distributed, but species composition varies. *Halodule wrightii*, *Halophila ovalis* and *Halodule uninervis* are the dominant plant species in the upper intertidal zone, while, in the mid-littoral zone *Thalassia hemprichii* and a mixture of *Cymodocea rotundata* and *C. ser-rulata* are dominant. *Thalassodendron ciliatum* and *Syringodium isoetifolium* occupy deeper pools and subtidal areas (Semesi *et al.*, 1998). To account for potential use of multiple habitats by teleosts that could result in fishes using habitats outside of sampling areas, or prey resources moving among habitats (Blaber, 1980; Fischer & Bianchi, 1984; Staunton-Smith *et al.*, 1999; Ley & Halliday, 2007; Mwandya *et al.*, 2010; Abrantes *et al.*, 2015), the most abundant sea-grasses and macroalgae in habitats overlapping with and adjacent to fish sampling (see below) were collected. Owing to sampling limitations, phytoplankton and microphytobenthos were not sampled and thus not considered for this preliminary study, despite their potential importance in nearshore food webs. Because of the absence of other preservation methods (*e.g.* freezing), seagrass and algae were preserved in 70% ethanol and stored for 3 weeks prior to preparation for stable-isotope analysis.

The most common fish species found in Tanzania seagrass habitats belong to the families Apogonidae, Blenniidae, Centriscidae, Gerreidae, Gobiidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Scaridae, Scorpaenidae, Siganidae, Syngnathidae and Teraponidae (Muhando, 1995). Fishes were collected by local fishermen during routine fishing practices in Bagamoyo with two hand-pulled beach seines *c.* 100 m long spanning the height of the water column. The seines were pulled across the seagrass bed adjacent to Bagamoyo on consecutive days (23–24 June 2013) by local fishermen, who aided with specimen collection. The seine had weights attached to the footrope and buoys attached to the headline, which kept the net open vertically (Tietze *et al.*, 2011) and ensured that a variety of fish species (benthic, demersal and pelagic) were caught. All fishes were caught to be sold as food and thus sacrificed by fishermen upon landing the catch. Individuals were identified, measured (total length, L_T) and a small muscle sample was collected from individuals of the most common species caught before they were brought to market for sale, with the approval of fishermen (Table SI, Supporting Information). In the absence of other preservation methods (*e.g.* freezing), muscle samples were preserved in 70% ethanol and stored for 3 weeks prior to preparation for stable-isotope analysis.

STABLE-ISOTOPE ANALYSES

Muscle samples were only processed for teleost species in which at least seven individuals were caught, in order to reduce biases from uncommon species. Among commonly caught fishes, a randomly selected sub-set of samples were analysed for species of which >10 individuals were

TABLE I. Habitat and feeding ecology of teleosts in northern Tanzania sampled for stable-isotope analysis

Teleost	Common name	Habitat use	Diet
<i>Carangoides armatus</i>	Longfin trevally	Pelagic	Small fishes, cephalopods, crustaceans and copepods ^{1,2}
<i>Leiognathus equulus</i>	Common ponyfish	Demersal	Predominantly small crustaceans, and polychaetes and small fishes ³⁻⁶
<i>Lethrinus mahsena</i>	Mahsena emperor	Demersal	Echinoderms, crustaceans, fishes, molluscs, tunicates, sponges, polychaetes ^{7,8}
<i>Lutjanus fulviflamma</i>	Blackspot snapper	Demersal	Predominantly crustaceans, and small fishes and other invertebrates ⁹⁻¹¹
<i>Pelates quadrilineatus</i>	Fourlined terapon	Demersal	Predominantly copepods and other invertebrates, and small fishes ^{10,12}
<i>Saurida undosquamis</i>	Brushtooth lizardfish	Demersal	Predominantly fishes, and crustaceans and cephalopods ¹³⁻¹⁶
<i>Scomberoides tol</i>	Needlescaled queenfish	Pelagic	Fishes ¹
<i>Secutor insidiator</i>	Pugnose ponyfish	Demersal	Zooplankton (copepods, mysids, larval fishes) and polychaetes and crustaceans ^{5,17,18}
<i>Siganus sutor</i>	Shoemaker spinefoot	Demersal	Algae, seagrass, sponges ^{10,19,20}
<i>Sillago sihama</i>	Silver sillago	Pelagic juveniles and demersal adults	Copepods and diatoms (juveniles), polychaetes and crustaceans (adults) ^{6,21,22,23}
<i>Trichiurus lepturus</i>	Largehead hairtail	Demersal	Euphausiids, planktonic crustaceans, small fishes (juveniles) and predominantly fishes, and squids and crustaceans (adults) ²⁴⁻²⁹
<i>Upeneus sulphureus</i>	Sulphur goatfish	Demersal	Crustaceans, molluscs, worms, invertebrates ³⁰

1, Fischer & Bianchi (1984); 2, Sommer *et al.* (1996); 3, Tiews *et al.* (1972); 4, Woodland *et al.* (2001); 5, Mavuti *et al.* (2004); 6, Hajisamae *et al.* (2006); 7, Carpenter & Allen (1989); 8, Ali' *et al.* (2016); 9, Kamukuru & Mgaya (2004); 10, Lugendo *et al.* (2006); 11, Nanami & Shimose (2013); 12, Warburton & Blaber (1992); 13, Matsumiya *et al.* (1980); 14, Rao (1981); 15, Ibrahim *et al.* (2003); 16, Thangavelu *et al.* (2012); 17, Seah *et al.* (2009); 18, Sebastian *et al.* (2011); 19, Almeida *et al.* (1999); 20, Chong-Seng *et al.* (2014); 21, Weerts *et al.* (1997); 22, Hajisamae *et al.* (2004); 23, Motlagh *et al.* (2012); 24, Martins *et al.* (2005); 25, Chiou *et al.* (2006); 26, Bittar & di Benedetto (2009); 27, Yan *et al.* (2011); 28, Bittar *et al.* (2012); 29, Rohit *et al.* (2015); 30, Surya *et al.* (2013).

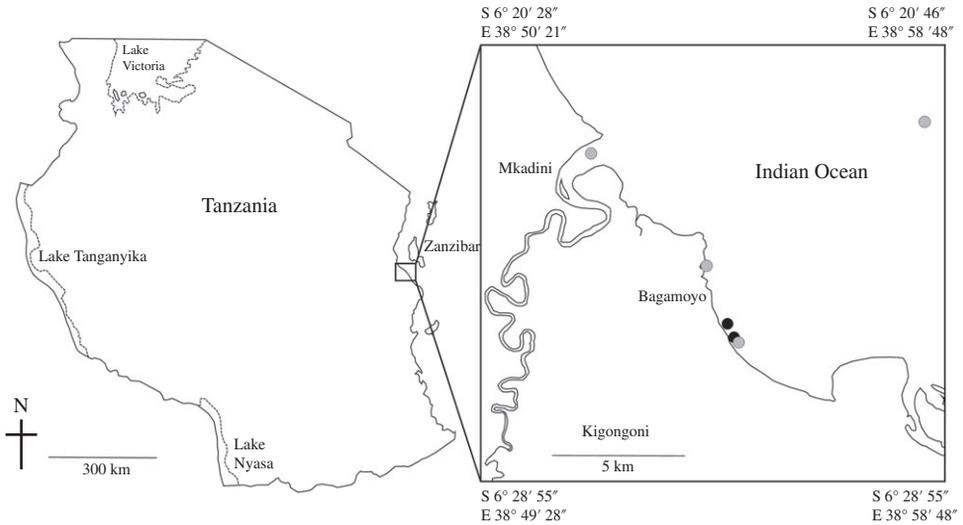


FIG. 1. Fishing locations at Bagamoyo, Tanzania, for study of habitat and feeding ecology of teleosts by stable-isotope analysis. ●, Location of beach-seine sampling; ○, locations of primary producer collections.

sampled [$n = 10$ samples each for *Carangoides armatus* (Rüppell 1830), *Leiognathus equulus* (Forsskål 1775), *Lethrinus mahsena* (Forsskål 1775), *Lutjanus fulviflamma* (Forsskål 1775), *Pelates quadrilineatus* (Bloch 1790), *Saurida undosquamis* (Richardson 1848), *Sillago sihama* (Forsskål 1775) and *Upeneus sulphureus* Cuvier 1829]. Muscle tissue was removed from 70% ethanol, triple rinsed in de-ionized water, dried to a constant weight, homogenized and weighed into tin capsules prior to analysis. Preservation in ethanol can affect $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in a range of organisms, including primary producers and fish, which can become enriched in ^{13}C due to the preservation method (Hobson *et al.*, 1997; Kaehler & Pakhomov, 2001; Kiszka *et al.*, 2014). All samples collected for the present study, however, were preserved and prepared using the same method and fishes and producers have been observed to exhibit similar increases in $\delta^{13}\text{C}$ following ethanol preservation (0.5–1.5‰; Kaehler & Pakhomov, 2001), suggesting the interpretation of the data is unlikely to be substantially affected by the preservation method used. Direct comparisons with stable-isotope data from other studies, however, should be conducted with caution.

Primary producers were triple rinsed in de-ionized water, epiphytes were removed from seagrasses and samples were dried for 48–72 h, then acidified within a glass desiccator with 25 ml of 100% HCl for 10 days to remove inorganic carbon (Carabel *et al.*, 2006). After acidification, samples were re-rinsed, dried and homogenized before being weighed for analysis. All samples were analysed at the Florida International University Stable Isotope Laboratory, with variation among analytical standards = 0.11 and 0.16‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, for muscle samples and 0.07 and 0.14‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, for algae and seagrass samples, indicating high levels of analytical precision. Mean C:N of muscle tissue was 3.21 ± 0.11 s.d., suggesting lipid extraction was not necessary (Post *et al.*, 2007).

QUANTITATIVE ANALYSIS

Multiple analysis of variance (MANOVA) was used to test for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of producers (seagrasses and algae) and fishes (species), with subsequent analysis of variance (ANOVA) to test for significant difference among producers and among fishes and *post hoc* Tukey's tests to identify paired differences among fishes. Teleost species were classified as isotopically similar if they exhibited no significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (based on MANOVA, ANOVAs and *post hoc* Tukey's test), suggesting that they fed within the

same food web at similar trophic levels. Published diet data (summarized in Table I) were then compared among isotopically similar species to identify potential trophic redundancy. If two species did not exhibit significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and published diet data suggested they fed on species within the same foraging categories (e.g. fishes, crustaceans and plankton), they were classified as potentially trophically redundant.

MANOVA results were also used along with the position of teleost $\delta^{13}\text{C}$ values in relation to $\delta^{13}\text{C}$ values of algae and seagrasses to categorize species into foraging groups: primary algal food-web foragers with similar $\delta^{13}\text{C}$ values, but lower $\delta^{15}\text{N}$ values than other algal food-web foragers; secondary algal food-web foragers with higher trophic level than primary algal pathway foragers based on significantly higher $\delta^{15}\text{N}$ values; primary seagrass food-web foragers with similar $\delta^{13}\text{C}$ values, but lower $\delta^{15}\text{N}$ values than other seagrass food-web foragers; secondary seagrass food-web foragers with higher trophic level than primary seagrass pathway foragers based on significantly higher $\delta^{15}\text{N}$ values; intermediary foragers, i.e. species that overlapped in $\delta^{13}\text{C}$ with both seagrass and algal food-web foragers. Because different trophic pathways can lead to similar isotopic values of consumers (reviewed by Martinez del Rio *et al.*, 2009) and to complement stable-isotope values, published diet data (Table I) were employed to assess trophic similarities, i.e. species were assigned to foraging groups based on stable-isotope analysis, with published diet data used to assess similarities within and across foraging groups.

Minimum convex polygons (MCP) and standard ellipses were constructed and the areas of each were calculated to estimate isotopic niche widths of each teleost species (Layman *et al.*, 2007; Jackson *et al.*, 2011). To limit bias, small sample-size correction for standard ellipses (SEA_c), which represent the core isotopic niche for a species, were used to calculate core isotopic niche overlap among teleosts, both within defined foraging groups and across defined foraging groups (Jackson *et al.*, 2011).

To evaluate the effect of fish size on trophic interactions, linear relationships between fish L_T and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each foraging group were investigated. Data normality were assessed with Shapiro–Wilk tests and data were log transformed when non-normal for linear regressions. Statistical analyses were performed in R (www.r-project.org) with the *siar* package (Parnell *et al.*, 2008; Parnell *et al.*, 2010) and JMP 10 statistical software (www.jmp.com).

RESULTS

Tissue samples were collected from six different seagrass species (*Cymodocea rotundata*, *Halodule uninervis*, *Halodule wrightii*, *Halophila ovalis*, *Syringodium isoetifolium*, *Thalassodendron ciliatum*), four species of green macroalgae (*Avrainvillea obscura*, *Caulerpa sertularioides*, *Chaetomorpha vieillardii*, *Ulva lactuca*), one species of brown macro-algae (*Sargassum oligocystum*) and one species of red macro-algae (*Gracilaria canaliculata*). Seagrasses were significantly more enriched in ^{13}C (−14.4 to −8.0‰) than algae (−19.3 to −14.4‰; $F_{1,14} = 38.71$, $P < 0.01$; Fig. 2). Seagrasses had a wider range of $\delta^{15}\text{N}$ values (7.5‰) than algae (4.2‰), but means were not significantly different for $\delta^{15}\text{N}$ between algae and seagrasses ($F_{1,14} = 0.60$, $P > 0.05$; Fig. 2).

Teleost muscle samples were collected from 233 individuals (Table SI, Supporting Information). Among these fishes, at least seven individuals were sampled from 12 species: *L. fulviflamma*, *S. undosquamis*, *L. equulus*, *P. quadrilineatus*, *Trichiurus lepturus* L. 1758, *C. armatus*, *L. mahsena*, *Scomberoides tol* (Cuvier 1832), *Secutor insidiator* (Bloch 1787), *Siganus sutor* (Valenciennes 1835), *S. sihama* and *U. sulphureus* (Table II). Other fish species caught during the study were uncommon, with only one to two total individuals caught among 71% of species not sampled for stable-isotope analysis (Table SI, Supporting Information).

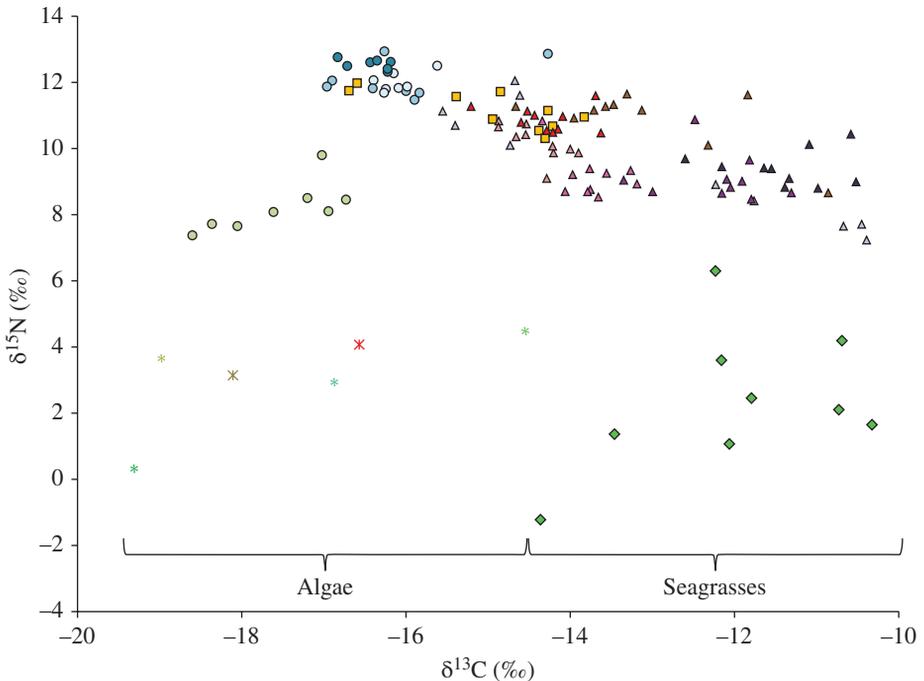


FIG. 2. Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in ‰) of teleosts and primary producers collected from northern Tanzania. Fishes: \circ , *Siganus sutor*; \bullet , *Trichiurus lepturus*; \oplus , *Scomberoides tol*; \circ , *Secutor insidiator*; \square , *Carangoides armatus*; \triangle , *Leiognathus equulus*; \blacktriangle , *Upeneus sulphureus*; \blacktriangle , *Sillago sihama*; \triangle , *Saurida undosquamis*; \blacktriangle , *Lutjanus fulvivlamma*; \blacktriangle , *Lethrinus mahsena*; \blacktriangle , *Pelates quadrilineatus*. Primary producers: $*$, *Avrainvillea obscura*; $*$, *Chaetomorpha vieillardii*; $*$, *Ulva lactuca*; $*$, *Caulerpa sertularioides*; \times , *Sargassum oligocystum*; \times , *Gracilaria canaliculata*; \blacklozenge , seagrasses.

Teleosts exhibited a wide range of $\delta^{13}\text{C}$ (-18.6 to -10.4 ‰) and $\delta^{15}\text{N}$ values (7.2 to 12.9 ‰; Fig. 2), with significant differences across many species (Table SII, Supporting Information). *Trichiurus lepturus*, *S. tol*, *S. insidiator* and *S. sutor* had $\delta^{13}\text{C}$ values within the range of algae $\delta^{13}\text{C}$ values (-18.6 to -14.3 ‰), with *S. sutor* exhibiting significantly lower $\delta^{15}\text{N}$ values (7.4 to 9.8 ‰) than the other three species (11.5 to 12.9 ‰) (Fig. 2). *Siganus sutor* is a herbivore (Table I) and was not isotopically similar or functionally redundant with other algal food-web foragers sampled (Table SII, Supporting Information). All remaining species evaluated had $\delta^{13}\text{C}$ values within the range of seagrass $\delta^{13}\text{C}$ values (-15.6 to -10.4 ‰; Fig. 2) and significantly different $\delta^{13}\text{C}$ values from algal food-web foragers (Table SII, Supporting Information), except for *C. armatus*, which overlapped in $\delta^{13}\text{C}$ with both algal and seagrass food-web foragers [Fig. 2 and Table SII (Supporting Information)]. *Sillago sihama* and *U. sulphureus* exhibited significantly higher $\delta^{15}\text{N}$ values than other seagrass food-web foragers, except for *L. equulus*, which overlapped in $\delta^{15}\text{N}$ values with all seagrass food-web foragers [Fig. 2 and Table SII (Supporting Information)].

Most species exhibited isotopic similarity (*i.e.* no significant difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) with two or three other species (67% of sampled species). *Carangoides armatus* and *L. equulus*, however, exhibited isotopic similarity with four and five other

TABLE II. Sample size (n), mean stable-isotope values $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, foraging group, based on $\delta^{13}\text{C}$ values and stable-isotope similarities and total length (L_T) of teleosts sampled in northern Tanzania

Teleost	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Foraging group	L_T (cm)	
		Mean \pm S.D.	Mean \pm S.D.		Mean \pm S.D.	Range
<i>Siganus sutor</i>	8	-17.56 \pm 0.70	8.21 \pm 0.75	Algal	12.0 \pm 2.8	8.5–16.2
<i>Trichiurus lepturus</i>	7	-16.42 \pm 0.25	12.55 \pm 0.16	Algal	51.7 \pm 5.6	40.5–57.0
<i>Scomberoides tol</i>	8	-16.06 \pm 0.84	12.05 \pm 0.55	Algal	23.6 \pm 3.4	18.5–29.8
<i>Secutor insidiator</i>	7	-16.10 \pm 0.25	12.00 \pm 0.30	Algal	10.1 \pm 0.5	9.3–10.6
<i>Carangoides armatus</i>	10	-14.95 \pm 1.00	11.15 \pm 0.57	Intermediate	12.9 \pm 1.6	10.9–16.6
<i>Saurida undosquamis</i>	10	-13.05 \pm 2.15	9.55 \pm 1.78	Seagrass	23.8 \pm 4.9	19.1–35.2
<i>Leiognathus equulus</i>	10	-14.41 \pm 0.34	10.20 \pm 0.52	Seagrass	12.1 \pm 0.9	10.9–13.2
<i>Upeneus sulphureus</i>	10	-14.28 \pm 0.46	10.89 \pm 0.38	Seagrass	14.5 \pm 1.5	12.7–16.5
<i>Sillago sihama</i>	10	-13.08 \pm 1.11	10.93 \pm 0.90	Seagrass	17.7 \pm 2.8	12.0–21.7
<i>Lutjanus fulviflamma</i>	10	-11.38 \pm 0.65	9.43 \pm 0.54	Seagrass	10.4 \pm 1.3	9.0–12.7
<i>Lethrinus mahsena</i>	10	-12.19 \pm 0.60	9.11 \pm 0.71	Seagrass	10.9 \pm 2.3	7.5–14.7
<i>Pelates quadrilineatus</i>	10	-13.73 \pm 0.35	9.17 \pm 0.66	Seagrass	10.1 \pm 0.9	8.6–11.2

species, respectively, and *L. fulviflamma* only exhibited isotopic similarity with *L. mahsena* (Table III). Published diet data paired with stable-isotope values suggested that only 23% of species comparisons were isotopically similar (*i.e.* exhibited no significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and only 15% were potentially trophically redundant based on published stomach contents data. If two species did not exhibit significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and published diet data (Table I) suggested they fed on species within the same foraging categories, they were classified as potentially trophically redundant (Table III).

Most species exhibited relatively narrow isotopic niche widths (mean MCP \pm S.D. = $2.04 \pm 1.75\%$, mean SEA_c = $1.37 \pm 1.28\%$), with *S. undosquamis* and *S. sihama* exhibiting considerably larger isotopic niche widths than the other 10 species (Fig. 3 and Table IV). Fishes foraging in the algal food web did not exhibit significant differences in MCP size or SEA_c size with fishes foraging in the seagrass food web ($F_{1,11} = 2.04$, $P > 0.05$ and $F_{1,11} = 1.15$, $P > 0.05$, respectively).

There were no relationships between L_T and $\delta^{13}\text{C}$ values, suggesting stability in the trophic channels they occupy over the size range sampled [Fig. 4(a) and Table V]. Carnivorous fishes that fed in the algal food web, however, exhibited a statistically significant enrichment in $\delta^{15}\text{N}$ with L_T [$y = 0.01x + 11.84$, $P < 0.05$; Fig. 4(b) and Table V], which was unlikely to be ecologically significant (slope of best fit line = 0.01% cm⁻¹).

DISCUSSION

Ecosystem-level changes attributed to natural and anthropogenic drivers continue to alter community structure and ecosystem function worldwide and their effects are predicted to lead to permanent changes in some regions (Jackson *et al.*, 2001; Worm *et al.*, 2006). In addition to sea-level rise, habitat degradation and unsustainable resource use are among the most concerning immediate threats to coastal regions, especially in

TABLE III. Isotopic similarities of teleosts sampled and potential trophic redundancy based on stable-isotope data from this study and published diet data (shown in Table I)

Foraging group	Teleosts	Algal			Intermediate	Seagrass						
		<i>Siganus sutor</i>	Tl	St	Si	Ca	Su	Le	Us	Ss	Lf	Lm
Algal	<i>Trichiurus lepturus</i> (Tl)											
	<i>Scomberoides tol</i> (St)		*									
	<i>Secutor insidiator</i> (Si)		*	*								
Intermediate	<i>Carangoides armatus</i> (Ca)			*	*							
Seagrass	<i>Saurida undosquamis</i> (Su)											
	<i>Leiognathus equulus</i> (Le)					ns	ns					
	<i>Upeneus sulphureus</i> (Us)					*	ns					
	<i>Sillago sihama</i> (Ss)							*	ns			
	<i>Lutjanus fulviflamma</i> (Lf)											
	<i>Lethrinus mahsena</i> (Lm)							*			*	
	<i>Pelates quadrilineatus</i>							ns	*			

ns, Species that were not significantly different ($P > 0.05$) in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and thus isotopically similar.

*Isotopic similarity and potentially trophic redundancy.

developing areas like East Africa, where the livelihood of coastal residents is dependent on artisanal fishing and other harvesting practices (de Boer *et al.*, 2001; Aller *et al.*, 2014; Cullen-Unsworth *et al.*, 2014). Within coastal ecosystems, natural and anthropogenic perturbations that lead to local shifts in species abundances and behaviours can cause geographically extensive shifts in food-web structure, because of connectivity and proximity of aquatic microhabitats, leading to considerable ecological and economic consequences (reviewed by Heithaus *et al.*, 2008; Kaplan *et al.*, 2010; Estes *et al.*, 2011). As such, maintaining food-web structure is a critical component for conservation and resource management and gaining an understanding of food-web organization provides insight into the effects overfishing and habitat degradation may have on ecosystem health and resilience to chronic perturbations like climate change.

The present results suggest that in the seagrass meadows of northern Tanzania, where artisanal fishing is of major socio-economic importance (de Graaf & Garibaldi, 2014), the most abundant teleost fishes appear to vary in their reliance on seagrass and algal trophic pathways, emphasizing the importance of both basal carbon sources in shaping fish-community composition. Other seagrass ecosystems support similar diversity among producers and consumers, promoting high levels of productivity and high degrees of trophic overlap (Nagelkerken *et al.*, 2006; Nyunja *et al.*, 2009;

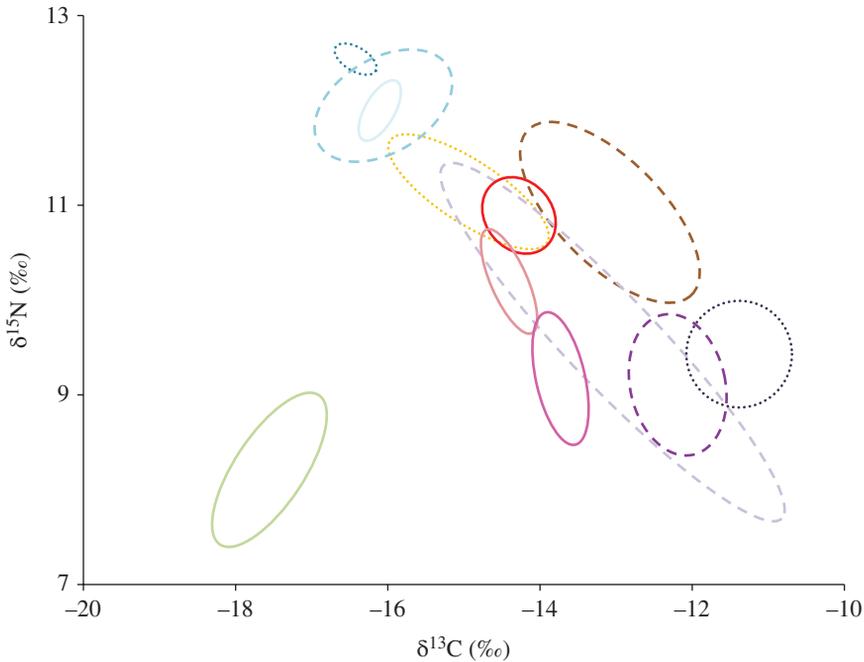


FIG. 3. Standard ellipse areas ($\%{}^2$) of sampled teleosts within the algal guild (....., *Trichiurus lepturus*; ---, *Scomberoides tol*; ---, *Secutor insidiator*; ---, *Siganus sutor*), seagrass guild (---, *Saurida undosquamis*; ---, *Leiognathus equulus*; ---, *Upeneus sulphureus*; ---, *Sillago sihama*; , *Lutjanus fulvivflamma*; ---, *Lethrinus mahsena*; ---, *Pelates quadrilineatus*) and with intermediate diets (....., *Carangoides armatus*).

Mendoza-Carranza *et al.*, 2010). Trophic diversity and redundancy within ecosystems are often associated with stability and resilience to perturbations, because of their role in promoting the retention of functional roles within food webs (Walker, 1992; Peterson *et al.*, 1998; Thompson *et al.*, 2012). Among the most abundant teleosts within the study site, isotopic overlap occurred among 92% of study species (*i.e.* core isotopic niche space overlapped with at least one other species based on SEA_c s), but there was considerable variability among individuals and foraging groups. Algal pathway foragers exhibited high isotopic similarity (*i.e.* no significant differences in $\delta^{13}C$ and $\delta^{15}N$) and high potential trophic redundancy within their foraging group (75% of algal food-web foragers exhibited potential trophic redundancy; Table III), suggesting resilience may be higher than expected from reviewed literature (Ross, 1986). In contrast, seagrass pathway foragers also exhibited considerable isotopic overlap, but low potential redundancy within their foraging group based on stable-isotope values and published diet data (9% redundancy; Table III). As such, the most abundant fishes in northern Tanzanian seagrass beds probably vary in their abilities to mitigate the effects of species declines, based on individual and foraging group differences in trophic redundancy, if stable isotopes and published diet data provide reliable estimates of foraging behaviour (Rastetter *et al.*, 1999; Layman *et al.*, 2012; Thompson *et al.*, 2012).

Based on published diet data (Table I), fishes were expected to segregate isotopically into four groups, predominantly based on prey size and type, which may lead to higher

TABLE IV. Minimum convex polygon (MCP) area (in % σ^2), standard ellipse area (SEA_c, in % σ^2), overlap of SEA_c within foraging group (algal, seagrass or mixed), overlap of SEA_c across foraging group, and unique isotopic niche space (area of SEA_c that did not overlap with any other species) of teleosts in northern Tanzania sampled for stable-isotope analysis

Teleosts by foraging group	MCP area	SEA _c	Overlap within foraging group (%)	Overlap across foraging group (%)	Unique isotopic space (%)
Algal					
<i>Siganus sutor</i>	1.62	1.35	0	0	100
<i>Trichiurus lepturus</i>	0.15	0.13	23	0	77
<i>Scomberoides tol</i>	2.17	1.54	17	3	80
<i>Secutor insidiator</i>	0.26	0.22	100	0	0
Intermediate					
<i>Carangoides armatus</i>	1.98	1.27	–	65	35
Seagrass					
<i>Saurida undosquamis</i>	6.13	4.75	40	15	50
<i>Leiognathus equulus</i>	0.71	0.44	65	7	32
<i>Upeneus sulphureus</i>	1.09	0.60	81	72	6
<i>Sillago sihama</i>	4.64	2.67	5	0	95
<i>Lutjanus fulviflamma</i>	1.99	1.24	23	0	77
<i>Lethrinus mahsena</i>	2.54	1.49	87	0	13
<i>Pelates quadrilineatus</i>	1.24	0.73	22	0	78

potential redundancy: group 1, *S. sutor* was the only herbivore sampled and thus similarities with other species were not expected and none were found; group 2, *L. equulus*, *P. quadrilineatus* and *S. sihama* feed on small crustaceans and plankton (e.g. amphipods, isopods and larvae); group 3, *L. mahsena*, *L. fulviflamma*, *S. insidiator* and *U. sulphureus* feed on larger crustaceans, benthic molluscs and small fishes; group 4, *C. armatus*, *S. undosquamis*, *S. tol* and *T. lepturus* predominantly feed upon fishes and larger invertebrates. Thus, overlap within and across these four groups (e.g. feeding on

TABLE V. Test statistics for linear regression investigating the relationship between total length and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of teleosts in northern Tanzania sampled for stable-isotope analysis. Algae¹ and algae² species had $\delta^{13}\text{C}$ indicative of feeding within macro-algal food webs, but fed at different trophic levels due to differences in $\delta^{15}\text{N}$ values (algae¹ species had lower $\delta^{15}\text{N}$ values than algae² species) and similarly for seagrass¹ and seagrass²

Foraging group	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	r^2	F	d.f.	P	r^2	F	d.f.	P
Algae ¹	0.34	3.08	1,7	>0.05	0.41	4.22	1,7	>0.05
Algae ²	0.07	1.45	1,21	>0.05*	0.25	6.65	1,21	<0.05
Intermediate	0.12	0.92	1,9	>0.05	0.11	8.54	1,9	>0.05
Seagrass ¹	0.05	1.93	1,39	>0.05	0.09	3.68	1,39	>0.05
Seagrass ²	0.07	1.32	1,19	>0.05	0.01	0.24	1,19	>0.05

*Indicates data that were log₁₀ transformed due to non-normality.

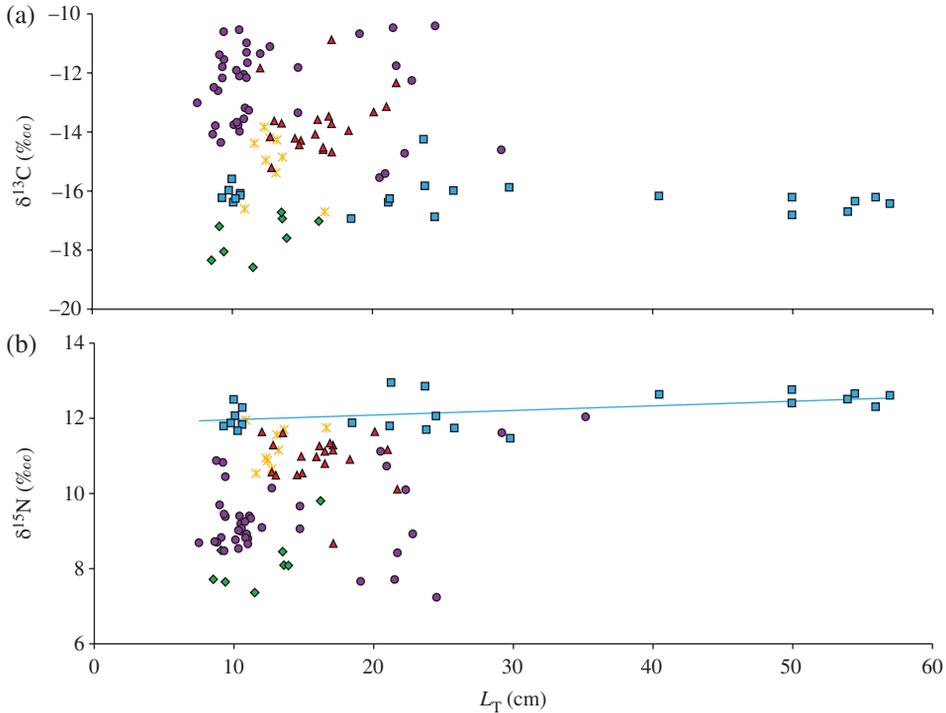


FIG. 4. Relationship of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values with total length (L_T) of teleosts collected from northern Tanzania. \blacklozenge , primary algal foragers; \blacksquare , secondary algal food web consumers; \bullet , primary seagrass food web consumers; \blacktriangle , secondary seagrass food web consumers; \times , intermediate foragers.

crustaceans among fishes in groups 2 and 3 and feeding on fishes in groups 3 and 4) was expected, with higher redundancy and overlap within than across groups. Isotopic similarity, however, only occurred in 23% of interspecific comparisons and potential trophic redundancy was only 15%. Low overlap may be the product of the number of species sampled; however, other species caught during sampling but not analysed were much less common (Table SI, Supporting Information) and probably represent only a small proportion of the energy pathways within food webs in northern Tanzanian seagrass beds. Limited overlap may have also been attributed to interspecific variability in dietary preferences within foraging groups, leading to small realized niche widths due to prey specificity (Chase & Leibold, 2003; Hayward & Kerley, 2008), or more specialized foraging behaviours than described in other studies (reviewed by Devictor *et al.*, 2010). Indeed, species that exhibit generalized trophic interactions under some contexts can exhibit specialized behaviours and trophic interactions when resources are limited, competition is high or disturbance and risk are persistent (Warburton *et al.*, 1998; Matich *et al.*, 2011; Izen *et al.*, 2016). Most species analysed during the study exhibited narrow core niche widths, suggesting less generalized trophic interactions. Alternatively, species-specific differences in ^{13}C and ^{15}N discrimination factors or similar stable-isotope values resulting from different dietary pathways may have led to over or under-estimations of isotopic overlap and similarities among species in the present study (reviewed by Martinez del Rio *et al.*, 2009). Also, stomach

contents and stable isotopes provide complementary but different information [stable isotope analysis provides insight into trophic interactions, with limited taxonomic resolution, but integrated over longer temporal scales than stomach contents (Layman *et al.*, 2012)], which should be considered carefully when comparing present results with other studies. The planktonic food web was not considered during this study and some species (*e.g.* *S. tol*) may be more likely to derive their basal carbon from this source (see citations in Table I). Yet, redundancy is determined by the prey items consumed rather than basal carbon source for predators (Walker, 1992; Naeem, 1998; Rastetter *et al.*, 1999), supporting present conclusions. Future studies should incorporate both methods *in situ* for describing food-web structure in this region.

While it is unclear if redundancy is accurately represented by overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and diet data from other studies, results suggest potential trophic redundancy among the most commonly caught fishes in this region is lower (15%) than many of the coastal marine ecosystems reviewed by Ross (1986; *c.* 40%). Such low overlap suggests trophic structure and resilience may be susceptible to disturbance events (Peterson *et al.*, 1998; Thompson *et al.*, 2012), particularly because these species are among the most frequently caught in the artisanal fisheries of the area. Other mechanisms, however, may be important in promoting resilience, especially in response to local fishing pressures (*e.g.* immigration, character displacement; Chase & Leibold, 2003; Worm & Duffy, 2003; Bell *et al.*, 2014). Studies in similar East African ecosystems suggest diverse fish assemblages are supported in coastal marine ecosystems (*e.g.* Kenya: Nyunja *et al.*, 2009; Abrantes *et al.*, 2014; Madagascar: Abrantes *et al.*, 2014; Mozambique: de Boer *et al.*, 2001; Gell & Whittington, 2002; Gullström *et al.*, 2002; Abrantes *et al.*, 2014; Tanzania: Dorenbosch *et al.*, 2005) and biodiversity is often correlated with ecological stability (Borrvall *et al.*, 2000; Downing *et al.*, 2012). As such, high levels of biodiversity and trophic connectivity may aid in the maintenance of food-web structure. Yet, it is unclear how resilient East African ecosystems are, the effects fishing has on trophic structure and the processes by which community structure is maintained. Thus, there is a need for continued research in this region that relies so heavily on subsistence and artisanal fisheries, with particular attention given to the ecological roles species play (Gullström *et al.*, 2002; van der Elst *et al.*, 2005).

Data from the present study also suggest that present estimates of isotopic niche widths and trophic redundancy may be conservative. While unsampled species from the study probably comprise a small proportion of the trophic structure within the ecosystem based on relative abundances [$n \geq 21$; Table SI (Supporting Information)], uncommon species can represent important components of food webs (Pendleton *et al.*, 2014; Calizza *et al.*, 2015) and isotopic data from these species may have increased estimates of trophic overlap and redundancy. Samples were also only collected from two seines and time of day, or day of year may affect interpretation of the data if there is temporal or spatial variability within the Bagamoyo seagrass beds (Schoenly & Cohen, 1991; Fisher *et al.*, 2001; Nelson *et al.*, 2015). More extensive sampling of other basal carbon sources (*e.g.* phytoplankton and microphytobenthos) and prey sampling would also provide additional insight into trophic structure and community resilience through redundancy, but data from the present study provide an important step forward in assessing food webs within the region.

IMPLICATIONS

Across East Africa, seagrass beds are among the most productive coastal habitats and provide important ecological services (Dorenbosch *et al.*, 2005; Mwandya *et al.*, 2010). Within productive ecosystems, functional redundancy can promote resilience to environmental perturbations; in the event of species declines or local extinctions, functionally redundant species are able to fill vacant niche space and assume additional ecological roles (Lawton & Brown, 1993; Naeem & Li, 1997; Peterson *et al.*, 1998). A high degree of niche partitioning and limited niche overlap within ecological communities, however, does not confirm a lack of resilience. Intense interspecific competition can lead to character displacement among species with similar fundamental niches and the potential for niche expansion among competitively inferior species may serve as a buffer against environmental change (Chase & Leibold, 2003; Pfennig & Pfennig, 2009; Bolnick *et al.*, 2010; Matich *et al.*, 2017). Yet, niche expansion can be challenging to predict in natural settings, especially under novel or unmonitored environmental conditions and how anthropogenic and ecological processes interact to affect such mechanisms is still unclear in many regions. Thus, maintaining species diversity and redundancy within ecosystems has continued to be a priority among conservation and management organizations, despite the challenges of combatting economic needs (van der Elst *et al.*, 2005; McClanahan *et al.*, 2006).

Relatively low isotopic similarity, low potential trophic redundancy (based on stable isotopes and diet data) and narrow isotopic niche widths suggest improving management strategies is an important step forward in maintaining artisanal and subsistence fishing in Tanzania and improving resource use in the future (Gullström *et al.*, 2002; van der Elst *et al.*, 2005; McClanahan *et al.*, 2006; de Graaf & Garibaldi, 2014). The present data are not sufficient to discern if the narrow niche widths among most teleosts in the seagrass beds of Bagamoyo are attributed to competition, life histories, food availability, human impacts or inadequate sampling and do not enable us to quantify prey diversity among fishes or its potential implications for local fishermen and economic stability is important. Within Bagamoyo seagrass beds, fishing is indiscriminate and narrow niche widths and limited trophic overlap may put species at greater risk of local ecological extinctions than generalist species with widely overlapping trophic niches (Boström *et al.*, 2006; Aller *et al.*, 2014). Changes in habitat quality, resource availability (*i.e.* food and space) and community composition attributed to natural or anthropogenic perturbations (*e.g.* destructive fishing practices and coastline development) can have detrimental effects on biodiversity and ecosystem stability (de Boer *et al.*, 2001; Petchey *et al.*, 2008). As such, continued monitoring of East Africa's coastal ecosystems and investigating relationships between species abundance, species targeted by fishermen and trophic ecologies will increase understanding of community dynamics and human impacts on coastal ecosystems and aid in developing more sustainable management plans, which may include more strict regulations on harvesting and gear selectivity.

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI. Species caught in beach seines with sample sizes and total length (L_T) ranges in the study of habitat and feeding ecology of teleosts in northern Tanzania sampled for stable-isotope analysis.

Table SII. *P*-values from species-specific comparisons of teleost $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the study of habitat and feeding ecology of teleosts in northern Tanzania using univariate ANOVAs and *post hoc* Tukey's test based on significant differences in stable-isotope values found between species using MANOVA.

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