

## Original Article

# Diet and trophic interactions between catadromous eels and sympatric fish in Kenyan east flowing river systems

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## Abstract

Biotic interactions such as competition and predation are important ecological drivers of population structure. Interactions among higher trophic level fish can contribute to further population declines in species, such as eels, made vulnerable by overexploitation or environmental change. Furthermore, trophic interactions may further predispose eel populations to collapse, but this is poorly understood, particularly along the Western Indian Ocean (WIO) rivers. This study evaluated stomach contents of fish captured with glass and commercial fyke nets in the Athi and Ramisi Rivers, which discharge into the WIO. Stomach contents were examined using dissecting microscope to establish diet composition. Eels primarily consumed assorted fish (43%), and crustaceans (36%); such as penaeid shrimp (14%) and prawns (13%) and crab (9%), thus belonged to a higher trophic level (TL) of 3.47 than native (2.98) or introduced (2.8) sympatric fish species. Diet breadth of eels was significantly lower (0.20) than for sympatric fish species (0.27), attributed to higher diet specialization. The TL of carnivorous fish (3.19) and their diet compared well with those of eels, even though diet preference differed significantly among fish types. Consequently, eels ranked as vulnerable by the IUCN are further threatened by previously undescribed competition from carnivorous fish.

**Keywords:** biotic interactions, niche breadth, diet overlap, feeding guilds, trophic levels

## Introduction

Globally, freshwater fish with a life-history involving long-distance inter-ecosystem migration, are driven by a quest for quality breeding and feeding grounds (McIntyre *et al.*, 2016). In tropical systems, these strategies are particularly exemplified by diadromous eels, migrating between freshwater and saline oceanic habitats (Lin *et al.*, 2018). However, global declines in wild eel populations have been observed in both temperate and subtropical regions, and are largely blamed on anthropogenic stressors, such as climate induced changes in oceanic circulation, habitat degradation, overexploitation (Jellyman *et al.*, 2000; Revenga, 2003; Strayer and

Dudgeon, 2010), in addition to biotic stressors, notably associated with the introduction of alien and exotic fish species (Jacoby *et al.*, 2015). Nonetheless, other biotic interactions, for instance between eels and predatory introduced and indigenous fish, are also of particular concern, not only due to dietary overlap, but also predation on vulnerable stages and species. Biotic interactions such as intra- and inter-specific competition, predation, mutualism, facilitation, and commensalism, are among the powerful ecological drivers, influencing species occurrence, community structure and functioning in terrestrial and aquatic ecosystems (Ben-Natan *et al.*, 2004; Tadesse, 2018).

Despite the western Indian Ocean (WIO) being regarded as an eel biodiversity hotspot by hosting 25 % (4/16) of global panmictic eel biodiversity (Schabetsberger *et al.*, 2016), inter- and intra-specific biotic interactions and associated pressures remain poorly documented. Furthermore, recent upgrading of three (*Anguilla mossambica*, *A. bengalensis*, and *A. bicolor*) of the four WIO eel taxa to near threatened (Hanzen *et al.*, 2019), is largely attributed to prevailing anthropogenic stressors such as river modification, pollution (Jellyman, 2021), but also exotic introduction which needs evaluation.

Sympatric fish interacting through predation and competition have been shown to impact piscivorous freshwater fishes in the tropical (Hickley *et al.*, 2008; Okwiri *et al.*, 2019), as well as temperate habitats (Jonsson and Jonsson, 2004), but are even more critical to trans-habitat migratory species, such as Atlantic salmon (*Salmo salar*) (Jonsson and Jonsson, 2004). Both predation and competition results in loss of fitness among interacting species, acting through direct mortality and/or reduction in performance (Tadesse, 2018). James *et al.* (2003) attributed declines in native Australian riverine fish including predatory and migratory eels, to increased competition for food and space with the introduced predatory trout and carp species. In view of the documented introduction of similar species into African rivers, similar interactions are suspected with regards to WIO eels, but this has rarely been explored.

In most temperate and subtropical locales, eels are monospecific, and consequently intraspecific competition among eel species has only been demonstrated with the introduction of *Anguilla japonica* into European rivers which was partially blamed for declines in native *A. anguilla* (Hulme *et al.*, 2010). In the WIO, although differences in habitat use among eel species is reported, with *A. bengalensis* and *A. bicolor* occurring exclusively at upstream and downstream reaches, respectively, and *A. marmorata* and *A. mossambica* being less selective (Van Someren and Whitehead, 1959; Okeyo, 1998), whether such patterns are linked to biotic interactions, requires validation.

In Kenya, the larger east flowing rivers, such as the Athi and Tana, apart from experiencing greater anthropogenic stressors, such as damming, pollution and over-exploitation, have in the past seen multiple introductions of exotic fish such as trout, carps, local tilapiines and catfish (Okeyo, 1998; Seegers *et al.*, 2003; Wanja,

2013). Subsequently, this has led to possible competition with indigenous species which has not been well documented. In contrast, the smaller east flowing rivers such as Ramisi and others, not only experience lower hydrological modification and pollution, but also have fewer documented fish introductions. It is thus unclear whether the documented eel declines in the WIO region are associated with trophic interactions resulting from diet overlaps of species co-existence within these systems. Hence the current study was designed to further understand the potential causes for the decline in eel populations in the WIO region.

## Materials and methods

### Study Rivers

The study focused on two Kenyan east flowing rivers; Athi-Galana-Sabaki and Ramisi, both draining into the Indian Ocean (Fig. 1). Both river catchments receive bimodal seasonal rainfall, during the long (March–May) and short (October–December) rains. The average temperature in both catchments is about 26 °C, with an annual precipitation of 400 mm at the downstream coastal locations and 800 mm annually at upstream highland locations. In this paper, the name Athi will be used interchangeably to designate the Athi-Galana-Sabaki River.

#### *The Athi-Galana-Sabaki River*

The Athi-Galana-Sabaki River is the second largest eastward flowing river in Kenya. The river headwaters are on the southern slopes of the Aberdare range, the Ngong hills and the eastern flank of Mount Kilimanjaro, draining the Kapiti plains and parts of the Yatta plateau, with a catchment of over 70,000 km<sup>2</sup> (Okeyo, 1998). The major tributaries of the Athi River include the Nairobi, Kiboko, and Tsavo Rivers. The Tsavo River that is fed by the Mzima Springs, is the only permanent inflow in the middle reaches of the drainage. The river in the upstream reaches including the headwaters and associated tributaries, is commonly referred to as Athi River.

The midstream reaches of the river occur below Lugard's Falls (after the Tsavo River confluence), where the river name changes to the Galana River. In the downstream reaches, the river is commonly called the Sabaki, which flows into the Indian Ocean 11.3 km north of Malindi town. Two sampling locations were selected for sampling: one each in the upstream (Kiaoni) and downstream (Sabaki Bridge) reaches of the Athi-Galan-Sabaki River. The upstream location was located 200 kms from the estuary, while

the downstream location was 3.3 kms inland from the ocean. Previous studies such as those of Okeyo (1998), Kimakwa (2004) and Wanja (2013) have reported on fish diversity especially for sympatric species. These are fish populations that exist in the same geographic area, frequently encountering one another, and supposedly coexist with eels. In this context, sympatric fish were composed of both indigenous and introduced fish species. Seeger *et al.* (2003) have reported the presence of exotic fish species along the Athi River.

2020). The Ramisi catchment also transverse the 600 ha Buda evergreen tropical dry savannah forest, which is a remnant of the once more extensive East African coastal forest (Wekesa *et al.*, 2019). The catchment harbours a relatively low human population density of 105 persons. km<sup>-2</sup>, dominated by small-holder subsistence farmers (KCIDP, 2018). Similarly, two sampling locations were selected in the Ramisi River; in the upstream (Eshu) and downstream (Taliani) reaches. The upstream location was 35 km from

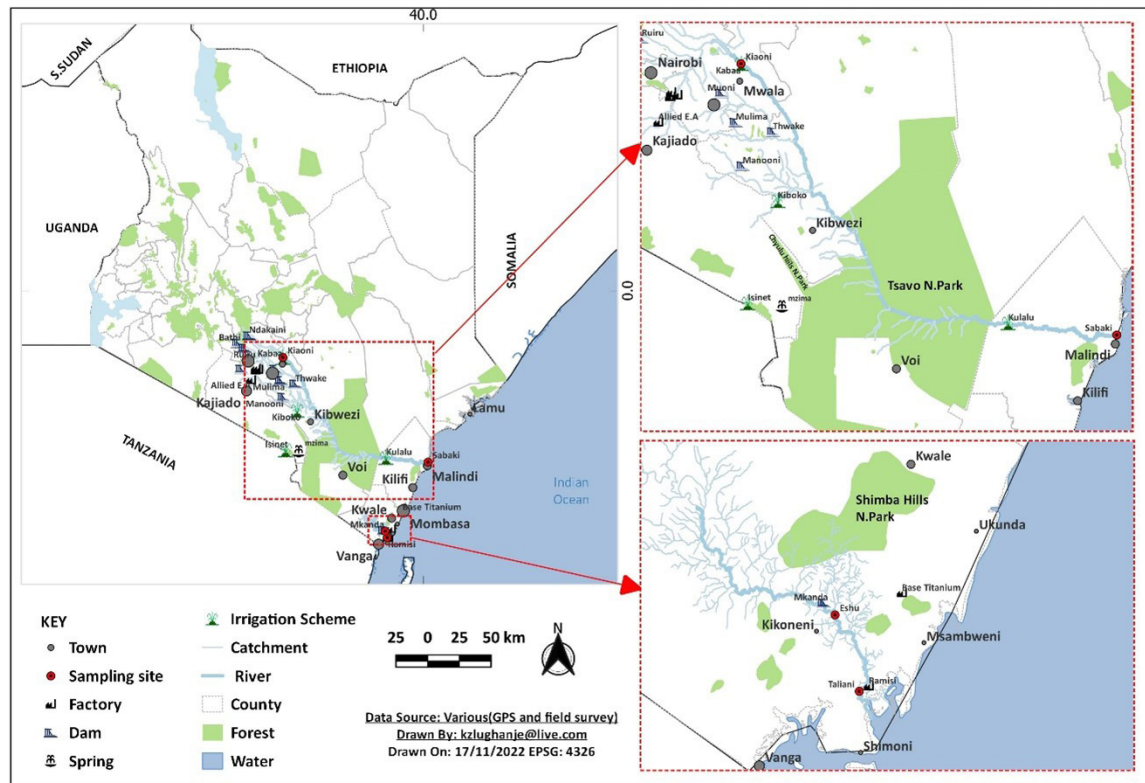


Figure 1. A map of Kenya highlighting the two east flowing rivers and a detailed sketch of the upstream and downstream sampling locations on the Athi-Galana-Sabaki (Kiaoni and Sabaki) and Ramisi (Eshu and Taliani) Rivers, Kenya.

### The Ramisi River

The Ramisi River is located within Kwale County on the southern coast of Kenya (Fig. 1). The river rises from the Shimba hills, and flows over 60 km to discharge into the Indian Ocean through the Kiwamba mangrove forest at Shimoni, with a catchment of 1800 km<sup>2</sup> (Kiteresi *et al.*, 2012). The Ramisi catchment receives average annual rainfall of about 1200 mm and has an average temperature of around 26 °C (KCIDP, 2018). The main vegetation in the area is drought resistant savannah woodlands and coastal dryland forests, noted for endemic flora and fauna (KWTA,

the estuary, whereas the downstream location was 4 km upstream of the ocean. Unlike at Athi River, information on fish species diversity and the presence of exotic species is scant.

### Fish sampling

Fish sampling was undertaken monthly at the upstream and downstream locations of both the Athi and Ramisi Rivers. At both locations along the rivers, fish were sampled from freshwater and estuarine habitat types such as riffles, vegetation and pools. Fish were captured using double and glass eel fyke

nets deployed fortnightly in the different habitats types overnight from April 2021 to March 2022. At each sampling location, six different sampling sites were randomly selected and the fyke nets deployed in each. Landed fish and eels were temporarily incapacitated using clove oil diluted with river water to ease handling. Landed fish were identified in the field using Wanja (2013) and Okeyo and Ojwang (2015), pictures taken, counted and a representative sample (~30 %) separated for dissection and subsequent gut content analysis. Reference specimens of each species encountered were preserved in 5 % formalin for species confirmation, and the remaining live fish released into the river, whenever appropriate. Reference specimens of fish collected are lodged at the Department of Biological Sciences laboratory at Egerton University. Fish species identification and information on distribution were obtained from Eccles (1992), Skelton (1993), and FishBase (Froese and Pauly, 2019).

Selected fish were first dissected in the field prior to gut content removal. Each gut removed was preserved in 5 % formalin for subsequent laboratory gut content evaluation.

### Fish gut content evaluation

Prior to removal of gut contents in the laboratory, the relative fullness for each stomach was assessed and fullness index scores allocated using the modified point method as in Hyslop (1980): empty stomach (0), quarter (5), half (10), three quarter (15) and completely full (20) stomachs. Stomach contents were then emptied into a petri dish, washed with distilled water and constituent food items separated and identified under a dissecting microscope to the lowest taxonomic level possible. Guides for invertebrate (Gerber and Gabriel, 2002) and vertebrates (Keppeler *et al.*, 2020) were used for taxonomic identification of dietary items.

### Food importance index

The contribution of each identified food item to the gut content was estimated and recorded. The data was subsequently used to compute the Hyslop (1980) food importance index (FI) scores using the following equation:

$$\%FI = \frac{\text{Total points for each food item}}{\text{Total number of points for all food types}} \quad (1)$$

Dietary composition and FI were compared between locations using analysis of similarity (ANOSIM).

Table 1. Diet importance in stomach of fish from the Athi and Ramisi Rivers, Kenya.

Food items	Occurrence (n)	Food index Scores (FI) (%)	Athi (%)	Ramisi (%)
Annelid worm	1	0.2	0.2	0.0
Polychaeta worms	2	0.3	0.4	0.0
Beetle	21	2.4	3.5	1.6
Bivalve	1	0.2	0.0	0.8
Caddisflies	37	5.6	6.8	0.0
Chironomidae	5	0.8	0.9	0.0
Damselfly	3	0.5	0.6	0.0
Mayflies	11	1.7	2.0	0.0
Pond snails	4	0.6	0.7	0.0
Stoneflies	1	0.2	0.2	0.0
Unidentified Insect	26	3.3	4.2	2.5
Animal detritus (AOM)	60	9.0	10.5	2.5
Plant organic matter (POM)	66	9.9	11.8	1.6
Unidentified detritus (DOM)	32	4.8	3.5	10.7
Vegetation	62	9.3	9.8	7.4
Plant seeds	1	0.2	0.0	0.8
Crab	43	6.5	6.1	8.0
Penaeid Shrimps	128	19.0	22.3	6.0
Prawns	36	5.4	0.2	28.7
Fish	122	18.4	16.0	30.0
Birds	2	0.3	0.4	0

AOM-animal organic matter detritus, POM-plant detritus origin, and DOM-unidentified dead organic matter detritus

### Diet breadth

Data on frequency of occurrence (F) and relative abundance (Pi) of each food item were used to compute the Levin (1968) standardized diet breadth index (B) for both eel and sympatric fish species as follows:

$$B (\text{breadth}) = 1/\sum(P_{ij})^2 \quad (2)$$

Where B is Levin's standardized niche breadth,  $p_i$  is the proportion/ relative abundance of each food item i in the gut content of fish species j.

The B values obtained were compared between rivers, reaches and fish types (eels and sympatric resident and introduced fish) using one way-ANOVA.

### Diet overlap

Dietary item frequency of occurrence data (F) were also used in computing the Pianka dietary overlap index (O) for each fish type using the following equation as in Pianka (1981):

$$O_{ij} = \sum(P_{ij}P_{ik})/\sqrt{\sum(P_{ij})^2\sum(P_{ik})^2} \quad (3)$$

Where  $O_{ij}$  is Pianka's niche overlap between fish species j and species k,  $P_{ij}$  is the proportion of the food type i in the gut of fish type j, while  $P_{ik}$  is the proportion of food type i in the gut of fish type k.

Pianka's index values commonly range from 0 (total diet separation) to 1 (total overlap). Data on diet overlaps were subsequently applied to pairwise One-way Analysis of Similarity (ANOSIM) correlation to detect diet overlaps among fish types, rivers and locations.

### Fish trophic levels (TL)

Each food item encountered in the gut was allocated a food trophic level (TL/T<sub>is</sub>). The food trophic levels for each dietary items were obtained from Kihia *et al.* (2015), and Keppeler *et al.* (2020) among others. Food trophic level values obtained ranged from 0-1.2 for vegetation, seeds and plant detritus; 1.2-1.5 was allocated for herbivorous fauna such as snails (1.3), coleopteran, dipteran, trichopteran and ephemeropterans (1.5). Animal detritus was allocated a level of 1.5, while unidentified detritus (DOM) (1.2) and plant detritus (POM) (1.4). Filter feeding annelids and bivalves were allocated an intermediate value of (1.5); documented carnivorous invertebrates such as prawns and penaeid shrimps (2.1), crab (2.2), while carnivorous vertebrates such as birds and finfish (3.0).

Data on the relative contribution of each food item (FI) calculated and respective food item trophic level (T<sub>is</sub>) were subsequently used to compute fish trophic levels (TL) as in Choi *et al.* (2008) and Kihia *et al.* (2015) using the following equation:

$$TL_f = 1.0 + (\sum_i^s FI_{is} \times T_{is}) \quad (4)$$

Where TL<sub>f</sub> is trophic level of fish species f, FI<sub>is</sub> is relative importance of diet item i to s, T<sub>is</sub> is trophic level of diet item i to s.

The trophic levels obtained were then used to categorize the sympatric fish species into three feeding guilds: Carnivorous (>2.8); omnivorous (2.5-2.8); and herbivorous (<2.5). Subsequently, the trophic levels of eels, native and introduced fish were compared among rivers reaches using the Mann-Whitney test.

## Results

### Diet composition and preference among eels and sympatric fish

Stomachs contents of 350 (283, 67) sympatric fish and 75 (31, 44) eels from the Athi and Ramisi Rivers, respectively were examined. Thirty-eight fish specimens (5, 33) including eels and sympatric fish, respectively had empty stomachs and were excluded from subsequent diet evaluations. At the Athi River, 30 (13, 17 eels) and 254 (83, 171) sympatric fish were evaluated at the upstream and downstream locations. At Ramisi, 40 (36, 4 for upstream and downstream, respectively) eels and 63 (38, 25 for upstream and downstream, respectively) sympatric fish were evaluated.

A total of 21 food types were identified among which penaeid shrimps (19 %) and fish (18%) were most common (Table 1). Vegetation, caddisflies, crabs, detritus, prawns, beetles, unidentified insect and mayflies, were consumed by between 2 and 10 % of fish, while birds, annelid worms, bivalves, seeds, flies and stoneflies were the least consumed (Table 1).

The diet contribution between the rivers differed significantly (One-way analysis of similarity (ANOSIM), Global R=0.46, p<0.05), as well as by location (R=0.403, p<0.05) (Appendix 1). Fish in the Athi River consumed 19 food items, dominated mainly by penaeid shrimps (22 %), fish (16 %) and vegetation (10 %). Caddisflies (7 %) and crabs (6 %) were of intermediate importance (Table 1). Fish in the Ramisi River consumed 12 food items dominated by fish (30 %), prawns

**Table 2.** Dietary resource and their importance in the upstream and downstream reaches of Athi River among eels and sympatric native and exotic fish.

Focal river	Athi-Galana-Sabaki Food index (FI)							
	Upstream/Kiaoni (%)				Downstream/Sabaki (%)			
Reaches								
Food items	Eels	Native	Exotic	All	Eels	Native	Exotic	All
Annelid worms			0.63	0.5	-	-	-	-
Polychaetae				-	2.5	-	0.61	0.6
Beetles		-	10.75	9.0	-	0.72	0.61	0.6
Pond snails	7.14	3.57	0.63	2.0	-	-	0.61	0.3
Caddisflies		10.71	21.52	19.0	-	-	-	-
Damselflies		-	-	-	-	0.72	1.22	0.9
Mayflies		14.29	4.4	5.5	-	-	0.61	0.3
Stoneflies				-	-	-	0.61	0.3
Chironomidae			3.16	3.2	-	-	-	-
Unidentified Insects			7.5	6.0	2.5	2.88	3.66	3.2
AOM		21.43	13.30	13.5	7.5	10.1	7.93	8.75
POM		28.57	18.35	18.5		8.0	9.76	7.87
DOM		10.71	2.53	3.5	2.5	5.76	1.83	3.4
Vegetation	7.14	10.71	14.0	13.0	7.5	5.76	9.76	8.0
Crabs		-	-	-	20	10.80	6.10	9.6
Penaeid Shrimps		-	-	-	35	37.0	34.0	35
Prawns		-	0.63	1.0	-	-	-	-
Fish	78.57	-	2.53	8.0	22.5	18.71	22.0	21.0
Bird	7.14	-	-	0.5	-	-	0.61	0.3

AOM-animal organic matter detritus, POM-plant detritus origin, and DOM-unidentified dead organic matter detritus

(29 %) and unidentified detritus (11 %), while crabs (8 %), vegetation (7.4 %) and penaeid shrimps (6 %) were of intermediately importance (Table 1). Fish in the Athi consumed a higher variety of invertebrate (12) than at the Ramisi River (5) (Table 1).

Fish at the upstream location (Kiaoni) in the Athi River consumed 14 dietary items dominated by detritus (36 %), mainly composed of plant organic matter (18.5 %), and followed by caddisflies (19 %) and vegetation (13 %), while beetle (7.5 %) fish (8 %) and mayflies (5 %) were of intermediate importance. In contrast, fish at the downstream location of the Athi River also consumed 14 items but were dominated by penaeid shrimps (35 %) and fish (21 %), while crabs (10 %) and vegetation (8 %) were of intermediate importance (Table 2). Although fish at both locations in the Athi consumed a similar number of items (14), beetles, caddisflies, chironomids and prawn were only encountered upstream while penaeid, crab, damselfly and stoneflies were encountered at the downstream location. Exotic fish at both reaches consumed the highest number of food items (13); at the upstream location (Kiaoni) dominated by caddisflies (22 %), and (15) at the downstream location (Sabaki) dominated by penaeid shrimps (33 %) and fish (22 %).

At the upstream location of the Ramisi River, fish consumed 10 items dominated by prawns (37 %) and fish (35 %) while crabs (7 %), dead organic matter (DOM) and vegetation (6 %) were of intermediate importance. In contrast, at the downstream location, fish consumed 7 items dominated by DOM and penaeid shrimps (27 %), and fish and crabs (12 %). Prawns, bivalves and seeds were only consumed at the upstream location in the Ramisi, while penaeid shrimps were only encountered at the downstream location (Table 3). Similarly, exotic fish consumed the highest number of food items at both upstream (8) dominated by prawns (27 %) followed by fish (23 %) and downstream (6) largely composed of penaeid shrimps (33 %) and plant detritus (POM) (22 %) (Table 3).

Fish (29 %) and prawns (28 %) were the most important for dissimilarity between both locations in the Ramisi contributing to 57 % of the dissimilarity. On the other hand, penaeid shrimps contributed to the dissimilarity at both locations in the Athi (upstream and downstream) as well as between downstream locations of the Athi and Ramisi (Appendix 2). Prawns (18.62 %) and fish (17.48 %) contributed to the dissimilarities between the upstream locations of the Athi and Ramisi Rivers respectively (Appendix 2).

**Table 3.** Dietary resource and their importance in the upstream and downstream reaches of Ramisi River among eels and sympatric native/residents and exotic/introduced fish.

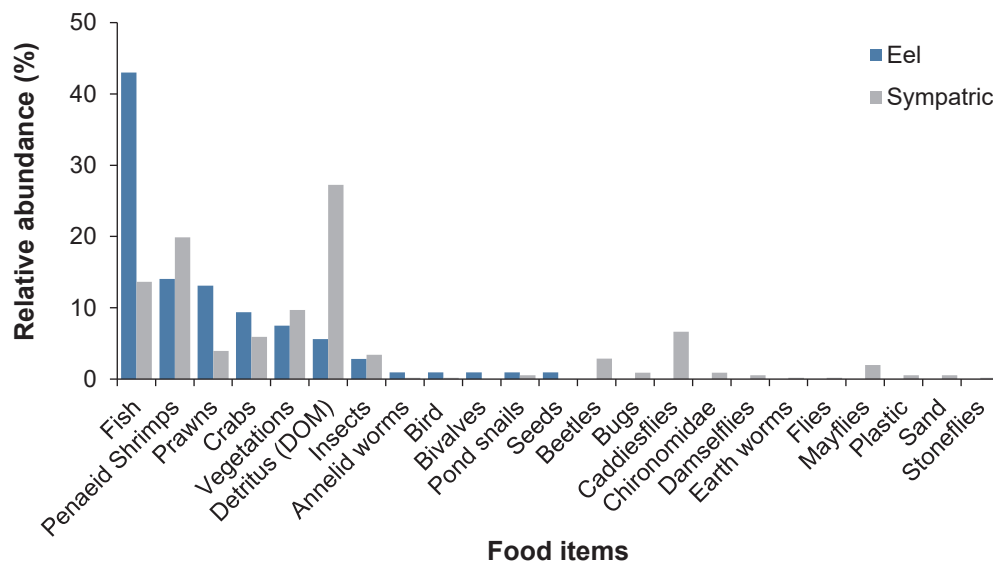
Focal river	Ramisi Food index (FI)								
	Upstream/Eshu (%)				Downstream/Taliani (%)				
	Reaches	Eels	Native	Exotic	All	Eels	Native	Exotic	All
Beetles	-	-	4.55	1.0	-	-	11.11	4.0	
Bivalves	2.13	-	-	1.1	-	-	-	-	
Unidentified insects	4.26	-	4.45	3.1	-	-	-	-	
AOM	-	7.41	4.55	3.13	-	-	-	-	
POM	-	-	-	-	-	-	22.22	7.69	
DOM	-	3.70	22.73	6.3	33.33	45.46	-	27.0	
Vegetation	6.40	7.41	4.55	6.3	17.00	9.10	11.11	12.0	
Plant seeds	2.13	-	-	1.1	-	-	-	-	
Crabs	4.25	11.0	9.1	7.3	-	18.18	11.11	12.0	
Penaeid Shrimps	-	-	-	-	17.00	27.27	33.33	27.0	
Prawns	30.0	55.56	27.3	36.5	-	-	-	-	
Fish	51.1	14.82	23.0	35	33.33	-	11.11	12.0	

AOM-animal organic matter detritus, POM-plant detritus origin, and DOM-unidentified dead organic matter detritus

The anguillids encountered consumed 13 out of the 21 food items identified dominated by fish (43 %), and crustaceans (37 %) composed of penaeid shrimps (14 %) and prawns (13 %), while crabs (10 %) were of intermediate value. Pond snails, birds, bivalves, polychaete worms, and seeds were the least consumed (Fig. 2). Among the eels, *A. bengalensis* was purely carnivorous, feeding on fish (55 %), prawn (23 %), crab (5 %), and even birds (2 %). *A. mossambica* was mainly carnivores on fish (32 %), penaeid shrimp (21 %), and crabs (16 %), but also consumed detritus (11 %), particularly in the Athi River. Both *A. bicolor* and *A. marmorata* were omnivorous consuming fish, prawns, penaeid shrimps, insects, vegetation and detritus.

The sympatric fish consumed 19 dietary items dominated by penaeid shrimps (20 %), fish (14 %). Vegetation (10 %) was of intermediate importance while caddisflies (7 %) and crab (6 %) were less often consumed (Fig. 2). Both eels and sympatric fish shared crabs, fish, penaeid shrimps, prawns and vegetation.

Diet preferences of the fish types evaluated differed significantly (ANOSIM;  $p < 0.05$ ) among the sampling locations. Sympatric fish at the upstream location of the Athi River primarily consumed plant detritus (POM) and caddisflies (20 %) followed by vegetation (14 %). At the downstream location, penaeid shrimps (35 %) and fish (21 %) were the most important, with (animal



**Figure 2.** Diet preferences between sympatric species and eels in the two east flowing rivers, Kenya.

detritus) AOM and (plant detritus) POM (9 %) followed by crab and vegetation (8.0 %) being intermediately consumed. On the other hand, eels at the upstream location primarily consumed fish (79 %) but also birds (7.2 %). In contrast, penaeid shrimps (35 %), followed by fish (23 %) and crabs (20 %) were more consumed at the downstream location, comparable to those of sympatric fish (Fig. 3). Unlike at the upstream location, fish at the downstream location of the Athi consumed birds (0.33 %), especially exotic fish species. At the upstream location of the Ramisi River, sympatric fish mainly consumed prawns (43 %), fish (18 %), plant detritus (12 %) and crabs (10 %), while at the downstream location, sympatric species largely consumed detritus (35 %), penaeid shrimps (30 %), detritus (DOM) (25 %) and crabs (15 %). Fish and beetles (5 %) were least consumed (Fig. 3). Eels at the upstream location of the Ramisi consumed fish (51 %) and prawns (30 %) while at the downstream location detritus (DOM), fish, penaeid shrimps and vegetation were comparably consumed (Fig. 3).

At the upstream locations of both rivers, eels mainly consumed fish, while at downstream locations penaeid shrimps, fish and crabs were commonly encountered. Prawns were only consumed at the upstream location of Ramisi while penaeid shrimps were consumed at downstream locations.

Introduced sympatric predatory carnivorous fish especially *Bagrus docmak* primarily consumed 15 items dominated by penaeid shrimps (37 %), fish (24 %) and vegetation (10 %), while animal detritus (AOM) (8 %) and crabs (7 %) were intermediately consumed. Resident predatory carnivorous fish which were composed of *Glossogobius giuris*, *Eleotris fusca*, *Oligolepis acutipennis* and *Pisodonophis cancrivorus* consumed nine (9) food items dominated by penaeid shrimps (35 %), fish (19 %) and crabs (14 %), while prawn (11 %) and animal detritus (AOM) (10 %) were intermediately consumed (Appendix 3). Among the resident predatory carnivorous fish, *Oligolepis acutipennis* (70 %), followed by *Glossogobius giuris* (47 %) and *Pisodonophis cancrivorus* (39 %),

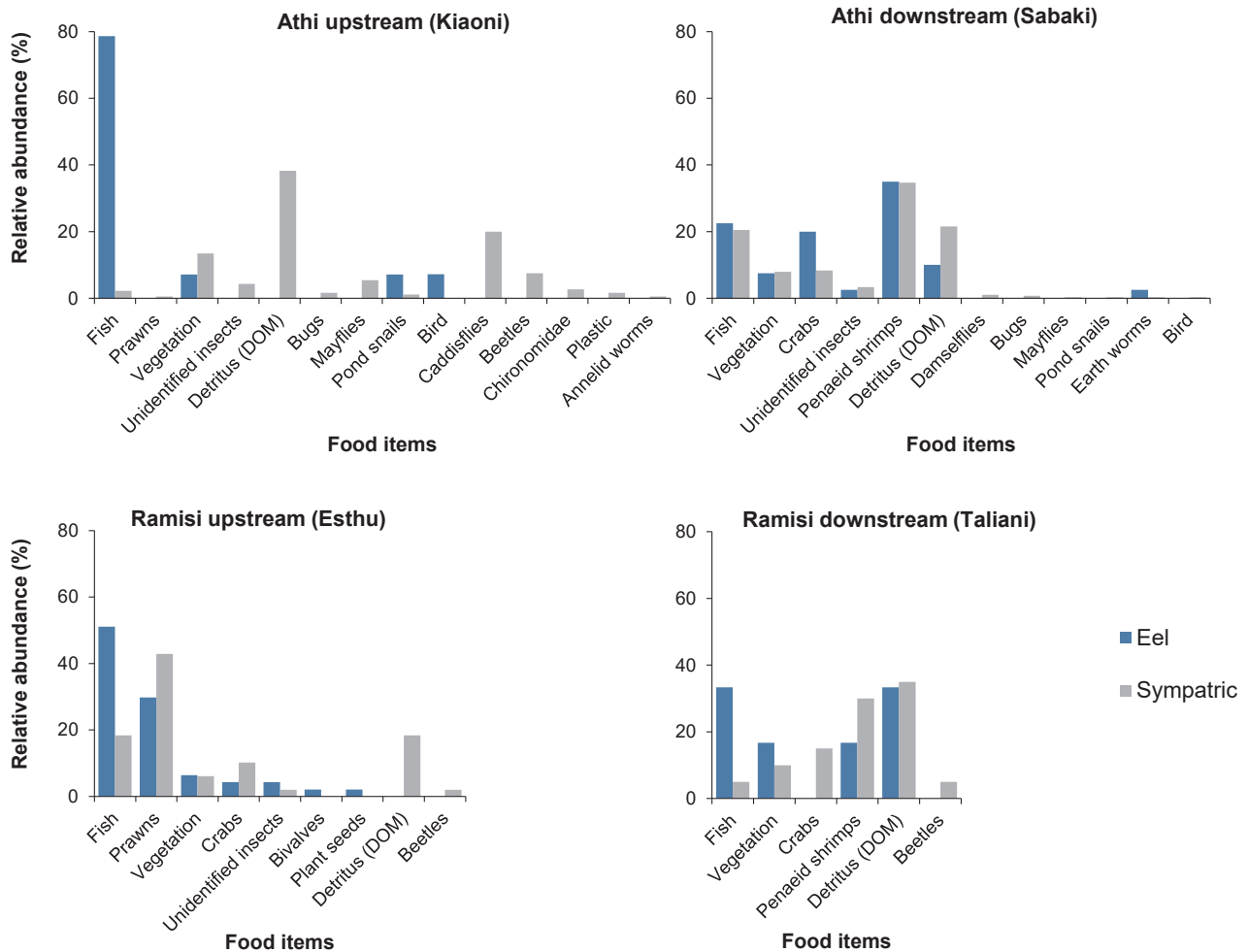


Figure 3. Diet preferences between sympatric fish and eels fish from the Athi and Ramisi Rivers.



**Table 4.** Summary statistics of One-way ANOSIM pairwise correlation between fish type and food item preferences (P values in bold with an asterisk are significant at  $p < 0.05$ ).

Fish types	Eel	Carnivorous	Herbivorous	Omnivorous	Native	Introduced
Eel	1					
Carnivorous	<b>0.083*</b>	1				
Herbivorous	0.0001	0.008	1			
Omnivorous	0.007	<b>0.19*</b>	<b>0.082*</b>	1		
Native	0.008	0.11	0.044	0.034	1	
Introduced	<b>0.011*</b>	0.11	0.092	0.098	0.77	1

consumed penaeid shrimps, while *Eleotris fusca* (56 %) consumed prawns. 50 % of *Otolithes ruber* followed by *O. acutipennis* (30 %) and *G. giuris* (29 %) consumed fish.

Introduced omnivorous fish (*Clarias gariepinus*) consumed 15 items but mostly preferred caddisflies (17 %), animal detritus (AOM) and vegetation (15 %) while fish (9 %), were of intermediate value. In contrast, resident omnivorous fish consumed seven (7) items dominated by penaeid shrimps (33 %) and fish (27 %) (Appendix 3). On the other hand, introduced sympatric herbivorous fish such as *O. niloticus* consumed 10 items, with preference for plant detritus (43 %) and caddisflies (15 %) while unidentified detritus (DOM) (11 %) and beetles (8%) were of moderate importance (Appendix 3).

Subsequently, Analysis of variance revealed a significant difference between the diets of fish types (eels and sympatric fish) (Global  $R=0.09$ ,  $p < 0.05$ ). Although, similarity in diet preference between sympatric carnivorous guild and eels was observed ( $p=0.08$ ) (Table 4), especially for resident predatory carnivorous (ANOSIM;  $p=0.1$ ) (Appendix 4). This was attributed to their consumption on fish and penaeid shrimps.

### Sympatric fish species trophic interactions, diet overlaps and feeding guilds in the Athi and Ramisi Rivers

Sympatric fish in the Ramisi River belonged to significantly ( $t=6$ ,  $df=682$ ,  $p < 0.05$ ) higher trophic levels ( $3.11 \pm 0.1$ ) than those of the Athi River ( $2.94 \pm 0.03$ ). The fish species examined for gut content in the Ramisi were composed of five species, dominated by *Eleotris fusca* and *Clarias gariepinus* while in the Athi there were 13 species dominated by *Bagrus docmak* and *Clarias gariepinus*. Among the fish examined, there were a total of 10 sympatric native fish species dominated by *Pisodonophis cancrivorus*, followed by *Otolithes ruber*, *Glossogobius giuris* and *Eleotris fusca*. On the other hand, introduced fish were dominated by *Bagrus docmak*, *Clarias gariepinus* and *O. niloticus*, encountered from

the two rivers (Table 5). The highest TL was recorded on *Oligolepis acutipennis* ( $3.66 \pm 0.18$ ).

In the Athi River, among the 10 native fish species, 5 species (*Glossogobius giuris*, *Oligolepis acutipennis*, *Otolithes ruber*, *Terapon jarbua*, and *Pisodonophis cancrivorus*) had the highest TL of above 3.0, while *Mugil cephalus* and *Macolor niger* had TLs of less than 2.4. Among the three introduced species in Athi River, two (*Bagrus docmak*, and *Clarias gariepinus*) had the highest TL, while *O. niloticus* had the lowest ( $>2.4$ ). In the Ramisi River, two out of three of the native species, *Eleotris fusca* and *Pisodonophis cancrivorus* had the highest TL with *Ambassis gymnocephalua*, having the lowest (Table 5).

Mean diet breadth of sympatric fish examined was ( $1.49 \pm 0.08$ ) for both the Athi and Ramisi Rivers, but there were significant differences among rivers ( $t=3.4$ ,  $df=85$ ,  $p=0.01$ ) and residency ( $t=6$ ,  $df=292$ ,  $p < 0.05$ ). The diet breadth of sympatric fish from Athi River was higher ( $1.65 \pm 0.05$ ) than Ramisi ( $1.32 \pm 0.1$ ) (Table 5). Among all sympatric fish species examined, the widest diet breadth was recorded in introduced omnivorous *Clarias gariepinus* in both rivers (Table 5). Among the native fish from the Athi River, the widest diet breadth was recorded for the carnivorous *Arius africanus* and herbivorous *Labeobarbus oxyrhynchus* and *O. spilurus spilurus*, with the lowest recorded on herbivorous *Labeo cylindricus* and *Mugil cephalus*. Among the introduced sympatric species in the Athi, the widest diet breadth found in the omnivorous *Clarias gariepinus* and the carnivorous *Bagrus docmak* (Table 5).

At the Ramisi, among the native fish examined, predatory carnivorous *Eleotris fusca* ( $2.80 \pm 0.14$ ) and *Pisodonophis cancrivorus* ( $2.25 \pm 0.47$ ) had the widest diet breadth while carnivorous *A. gymnocephalua* ( $1.00 \pm 0.67$ ) had the narrowest. Among the introduced species in the Ramisi, omnivorous *Clarias gariepinus* ( $4.37 \pm 0.20$ ) had a wider breadth than *O. niloticus* ( $2.20 \pm 0.25$ ), which was higher compared to all the species.

**Table 5.** Trophic levels (TL) and diet breadth of sympatric fish species from the Athi and Ramisi Rivers. The values in bold with an asterisk represent higher species TL and diet breadth (B).

Rivers	Species	Ecological status	Feeding guilds	N	Trophic level (TL)	Diet breadth (B)
Athi	<i>Arius africanus</i>	Native	Carnivores	5	<b>2.95±0.22*</b>	3.34±0.3
	<i>Glossogobius giuris</i>	Native	Carnivores	23	<b>3.30±0.10*</b>	2.47±0.14
	<i>Oligolepis acutipennis</i>	Native	Carnivores	8	<b>3.66±0.18*</b>	1.697±0.22
	<i>Otolithes ruber</i>	Native	Carnivores	3	<b>3.46±0.27*</b>	1.92 ±0.39
	<i>Pisodonophis cancrivorus</i>	Native	Carnivores	24	3.13±0.10	2.53±0.14
	<i>Terapon jarbua</i>	Native	Omnivores	4	3.06±0.24	2.56±0.34
	<i>Labeo cylindricus</i>	Native	Herbivores	1	2.4±0.47	1.00±0.67
	<i>Labeobarbus oxyrhynchus</i>	Native	Herbivores	7	2.49±0.18	4.90±0.25
	<i>Mugil cephalus</i>	Native	Herbivores	3	2.27±0.27	1.00±0.39
	<i>Oreochromis spilurus niger</i>	Native	Herbivores	11	2.49±0.14	3.08±0.20
	<i>Oreochromis spilurus spilurus</i>	Native	Herbivores	13	2.44±0.13	2.98±0.19
	<i>Bagrus docmak</i>	Introduced	Carnivores	77	<b>3.12±0.06*</b>	3.65±0.08
	<i>Clarias gariepinus</i>	Introduced	Omnivores	39	2.60±0.08	<b>6.65±0.11*</b>
	<i>Oreochromis niloticus</i>	Introduced	Herbivores	35	2.44±0.08	2.48±0.12
Ramisi	<i>Ambassis gymnocephala</i>	Native	Carnivores	5	2.3±0.15	1.00±0.67
	<i>Eleotris fusca</i>	Native	Carnivores	22	3.24±0.1	2.80±0.14
	<i>Pisodonophis cancrivorus</i>	Native	Carnivores	7	3.1±0.2	2.25±0.47
	<i>Clarias gariepinus</i>	Introduced	Omnivores	11	<b>3.36±0.15*</b>	<b>4.37± 0.20*</b>
	<i>O. niloticus</i>	Introduced	Herbivores	7	2.29±0.9	2.20±0.25

#### Diet and niche breadth (B) and trophic levels between eel species, feeding guilds and residency

Eels belonged to significantly ( $F=113$ ,  $p<0.05$ ) higher trophic levels (TL) ( $3.47±0.69$ ), especially for *A. bengalensis* ( $3.61±0.07$ ) at all sites, followed by *A. bicolor* ( $3.20±0.15$ ), compared to ( $2.90±0.03$ ) for either native ( $2.98±0.6$ ) or introduced ( $2.8±0.04$ ) sympatric fish. The trophic level of *A. bicolor* ( $3.67± 0.34$ ) increased in the Ramisi compared to the Athi ( $3.09±0.16$ ). *Anguilla marmorata* had the lowest TL ( $2.45±0.49$ ) at all sites (Table 6). The sympatric native fish ( $3.00±0.02$ ) had a higher trophic level compared to introduced fish ( $2.88±0.02$ ) but did not differ significantly (Mann-Whitney  $U=24987$ ,  $p>0.05$ ). The TL recorded for the Athi River was higher for native ( $3.0±0.02$ ) than introduced fish ( $2.86±0.02$ ) though significantly ( $F=146$ ,  $p<0.05$ ) lower compared to Ramisi River for either introduced fish ( $3.01±0.06$ ) or native ( $2.99±0.05$ ). Sympatric carnivorous fishes recorded a higher trophic level ( $3.19±0.04$ ) in the Athi, but in the Ramisi the TL was comparable with omnivorous species, especially for introduced fish (Table 6).

The lower TL recorded for sympatric fishes, subsequently corresponded to a wider diet breadth compared to eels. The narrow diet breadth for eels was accounted for by their active diet selection. The sympatric herbivorous species had the least TL ( $2.40±0.05$ ), at all sites especially in the Ramisi. Native sympatric

species in the Athi had a higher TL ( $3.0±0.02$ ) while introduced species ( $3.01±0.05$ ) recorded the highest in the Ramisi (Table 6); although significantly lower ( $F=4.0$ ,  $p=0.03$ ) than eels at all sites. Sympatric species diet breadth (B) ( $0.27±0.05$ ) was always significantly higher ( $t=3.15$ ,  $df=132$ ,  $p<0.05$ ) compared to eels ( $0.20±0.1$ ) in both rivers. Native sympatric fish had lower diet breadth ( $0.43±0.04$ ) than introduced fish ( $0.57±0.06$ ), attributed to dietary specialization. Similarly, at both locations native species ( $0.23±0.15$ ,  $0.20±0.30$  for Athi and Ramisi respectively) had lower diet breadth than corresponding introduced fishes ( $0.32±0.13$ ,  $0.26±0.43$  for Athi and Ramisi, respectively).

Omnivorous fish recorded a higher diet breadth ( $0.43±0.3$ ) followed by carnivorous species ( $0.30±0.4$ ) which corresponded to an intermediate diet breadth at all sites. The least diet breadth was encountered among herbivores ( $0.27±0.3$ ) at all sites largely due to their specialized feeding habit on dead organic matter (DOM). Among the rivers, omnivorous fish at both Athi ( $0.53±0.1$ ) and Ramisi ( $0.33±0.2$ ) corresponded to the widest breadth; significantly higher ( $p<0.05$ ) compared to eels, except for introduced fishes in the Ramisi River (Table 6). Introduced sympatric species always recorded the widest diet breadth in the Athi ( $0.40±0.2$ ) and Ramisi ( $0.39±0.4$ ) compared to resident sympatric species and eels, which did not differ

**Table 6.** Levin's diet breadth indices and trophic levels among sympatric species feeding guilds and eels from the Athi and Ramisi Rivers. The values in bold with an asterisk represent higher TL and diet breadth (B) for eel species and sympatric feeding guilds.

Rivers	Fish categories	Fish type	N	Trophic level (TL)	Diet breadth (B)
Athi	Eels	<i>A. bengalensis</i>	15	<b>3.79±0.13*</b>	0.10±0.18
		<i>A. bicolor</i>	9	3.09±0.16	0.16±0.23
		<i>A. mossambica</i>	7	3.34±0.19	<b>0.27±0.26*</b>
	Sympatric	Carnivores	243	<b>3.19±0.04*</b>	0.22±0.06
		Omnivores	115	2.65± 0.07	<b>0.53±0.10*</b>
		Herbivores	106	2.44±0.06	0.22±0.08
		Introduced	322	2.86±0.02	0.32±0.13
Native		167	3.0±0.02	0.23±0.15	
Eel	31	3.42±0.04	0.31±0.5		
Ramisi	Eels	<i>A. bengalensis</i>	34	<b>3.53± 0.08*</b>	0.17±0.12
		<i>A. bicolor</i>	2	<b>3.67± 0.34*</b>	0.11±0.49
		<i>A. marmorata</i>	1	2.45±0.47	<b>0.19±0.69*</b>
		<i>A. mossambica</i>	3	2.8±0.27	0.12±0.40
	Sympatric	Carnivores	29	<b>3.21± 0.10*</b>	0.23±0.14
		Omnivores	23	<b>3.28±0.14*</b>	<b>0.33± 0.20*</b>
		Herbivores	14	2.26±0.14	0.11±0.21
Introduced		31	3.01±0.06	0.26±0.43	
Native		38	2.99±0.05	0.20±0.30	
Eel	40	3.36±0.04	0.31±0.3		

significantly (F=0.1, p=0.91). Among the eels, highest breadth was encountered in *A. mossambica* (0.27±0.3) from the Athi and *A. marmorata* (0.19±0.69) from the Ramisi, demonstrating unselective feeding habits.

**Diet overlap between eels and sympatric fish**

Among the sympatric fish evaluated in the Athi, the greatest overlap was observed between omnivores and herbivores (0.50±0.1), but also in predatory carnivores (0.24±0.1). In the Ramisi, the greatest overlap was between carnivores and omnivores (0.35±0.2) (Table 7).

Among the eel species evaluated in the Athi, the greatest overlap was between *A. bengalensis* and *A. mossambica* (0.65±0.1), especially in fish diet items. The least overlap was encountered between *A. bicolor* and *A. mossambica* (0.29±0.1). Highest diet overlap was observed

between *A. bengalensis* and *A. bicolor* (0.92±0.6) in the Ramisi, while the lowest was observed between *A. marmorata* and *A. mossambica* (0.08±0.1) (Table 8).

The greatest dietary overlap for resource portioning were observed between sympatric carnivorous species and *A. bicolor* (0.81±0.01) in the Athi, followed by *A. bengalensis* (0.48±0.1), and lower in *A. mossambica* (0.18±0.1), respectively (Table 9). The sympatric carnivorous fishes responsible for the overlaps included *G. giuris*, *Arius africanus* and *Oligolepis acutipennis*, particularly in the along the estuarine areas. *Anguilla mossambica* had a higher overlap (0.29±0.2) with sympatric omnivorous species (Table 9) contributed by *Clarias gariepinus*. *Anguilla bicolor* (0.07±0.1) recorded the least diet overlap with sympatric herbivorous species. On the other hand, in the Ramisi River, diets of *A. bicolor*

**Table 7.** Dietary overlap among sympatric feeding guilds from Athi and Ramisi Rivers. The values in bold with an asterisk represent higher diet overlaps between feeding guilds.

Rivers	Feeding guilds	Carnivores	Omnivores	Herbivores
Athi	Carnivores	-	-	-
	Omnivores	<b>0.24±0.1*</b>	-	-
	Herbivore	0.17±0.6	<b>0.50±0.1*</b>	-
Ramisi	Carnivores	-	-	-
	Omnivores	<b>0.35±0.2*</b>	-	-
	Herbivores	0.08±0.1	0.26±0.2	-

**Table 8.** Pianka symmetrical niche overlaps among eel taxa from Athi and Ramisi Rivers. The values in bold with an asterisk represent higher overlaps between eel species.

Rivers	Eel species	<i>A. bengalensis</i>	<i>A. bicolor</i>	<i>A. marmorata</i>	<i>A. mossambica</i>
Athi	<i>A. bengalensis</i>	-			
	<i>A. bicolor</i>	0.43±0.4	-		
	<i>A. marmorata</i>	-	-	-	
	<i>A. mossambica</i>	<b>0.65±0.1*</b>	0.29±0.1	-	-
Ramisi	<i>A. bengalensis</i>	-			
	<i>A. bicolor</i>	<b>0.92±0.6*</b>	-		
	<i>A. marmorata</i>	0.20±0.01	0.20±0.01	-	
	<i>A. mossambica</i>	0.41±0.2	0.45±0.16	0.08±0.1	-

(0.74±0.11) overlapped with those of omnivorous fish such as *C. gariepinus*, while *A. bengalensis* (0.52±0.1) overlapped with those of carnivorous fish (Table 9) such as *Ambassis gymnocephala* and *Eleotris fusca*. The diet of *A. mossambica* occasionally overlapped with those of herbivorous (0.89±0.3) and omnivorous species (0.46±0.4). Consequently, the Athi River recorded the highest overlap (0.33±0.18) as compared to the Ramisi River (0.31±0.15), demonstrating greater relative amounts of inter and intraspecific competition on consumer-resource interaction between eels and sympatric fishes. No significant differences were however ( $p>0.05$ ) observed on both niche and dietary overlap among the fish taxa and rivers evaluated.

## Discussion

### Diet composition and preference among eels and sympatric fish

The majority of the fish species encountered throughout the two rivers largely selected foods high in protein, such as penaeid shrimps and fish (Table 1). This demonstrates a prevalence of high trophic level fishes in the rivers, especially in the Ramisi. In particular, for the Athi River, the upstream locations showed more varied diet compositions, indicating unselective feeding patterns among upstream river fishes (Gerking, 2014). These fishes primarily consumed a wide range of prey items, especially for sympatric fish species.

The upstream location in the Athi River harbored unique food item strictly associated with freshwater taxa, and of lower trophic level such as vegetation, detritus and macroinvertebrates as previously described by Kihia *et al.* (2015) and Keppeler *et al.* (2020), associated with urban polluted rivers (Kobingi *et al.*, 2009). Additionally, the majority of the fishes encountered belonged to lower trophic levels, including tilapiines and *Clarias sp.*, which are primarily herbivores and omnivorous respectively. These results are in line with those of Tófoli *et al.* (2013) who noted *Clarias sp.* predominantly consumed chironomidae and trichopteran (Table 5), recognized as being extremely resistant to extreme pollution conditions (Walsh *et al.*, 2005).

On the other hand, the downstream estuarine locations revealed a lower diet composition attributed to higher diet specialization, with food items available only in brackish waters, such as shrimp and crabs, predominating (Itakura *et al.*, 2015). These findings are consistent with those of Maitra *et al.* (2018), who reported higher specialization among estuary fishes, accredited to greater food availability in brackish environments than freshwater (Kaifu *et al.*, 2013). The downstream location of the Athi River was mainly dominated by high protein rich diets as compared to the upstream location, which was linked to the presence of higher

**Table 9.** Overlap between sympatric species and eels from the Athi and Ramisi Rivers. The values in bold with an asterisk represent higher diet overlaps between eel species and sympatric feeding guilds.

Rivers	Guilds	<i>A. bengalensis</i>	<i>A. bicolor</i>	<i>A. marmorata</i>	<i>A. mossambica</i>
Athi	Carnivores	<b>0.48±0.1*</b>	<b>0.81±0.01*</b>	-	0.18±0.1
	Omnivores	0.10±0.13	0.33±0.06	-	0.29±0.2*
	Herbivores	0.04±0.3	0.07±0.07	-	0.17±0.2
Ramisi	Carnivores	<b>0.52±0.1*</b>	0.22±0.01	0.08±0.01	0.29±0.1
	Omnivores	0.45±0.1	<b>0.74±0.11*</b>	0.13±0.01	0.46±0.4
	Herbivores	0.01±0.4	0.005±0.1	0.03±0.01	<b>0.89±0.3*</b>

trophic level fish (Pasquaud *et al.*, 2010) with inclusion of marine fish species (Kimakwa, 2004).

Eels demonstrated a preference for higher protein rich diets over sympatric fish among the fish taxa evaluated at the Athi River upstream location, attributed to their higher trophic level (Jellyman and Sykes, 2003; Schulze *et al.*, 2004). However, at the downstream location, both eels and sympatric fish had comparable diets, indicating a larger interspecific interaction along the food web (Manko, 2016). Similarly, in the Ramisi River, eel fish species preferred high-protein diets such as fish and crustaceans (Itakura *et al.*, 2015). Previously, Sinha and Jones (1967) reported similar results, however sympatric fish were reported for the first time in this study, revealing incidences of inter- and intra-specific interactions among species (Zacharia, 2017). According to Simpfendorfer *et al.* (2011) and Manly *et al.* (2002), such information is critical in efforts to preserve endangered species and manage exploited populations, especially for eels, which have been reported to continuously decline (Hanzen *et al.*, 2019; Jellyman, 2021).

The current study further found out that eels belonged to higher trophic levels as a result of exclusively consuming fish and crustaceans, in addition to bivalves (Itakura *et al.*, 2015). Furthermore, sympatric carnivorous fishes had a substantial feeding relationship with eels, indicating probable diet similarities and overlaps (Guzzo *et al.*, 2015). Omnivorous fish also consumed a diet similar to those of eels. Similar findings have been observed in salmon and trout feeding on eel-preferred diets (Sinha and Jones, 1967; Moorhouse-Gann *et al.*, 2020).

Furthermore, some of the eel species encountered, demonstrated unselective feeding behavior, feeding even on detritus and vegetation. As such, displaying an ontogenic feeding patterns (Sagar *et al.*, 2005), hence sometimes described as important opportunistic predators and scavengers preying on a wide variety of food items (Jellyman, 1989; Jellyman, 2021; Itakura *et al.*, 2020). This partly suggests that eels serve as indicator species for freshwater biodiversity conservation linked to their feeding habits (Itakura *et al.*, 2020). The results of this study also revealed that, in addition to preying on sympatric fishes, eels preyed on birds, particularly at the upstream location in the Athi River (Fig. 3). Other studies have reported eels to be an important diet in a number of predators including birds, affecting eel populations

(Leukona, 2002). Furthermore, predatory exotic fish also included birds in their diets, Sabaki, classified as an Important Bird Areas (IBA) (Okuku *et al.*, 2022). Other studies, such as those of Ovegård *et al.* (2017) reported cormorant birds (*Phalacrocorax spp.*) preying on Percidae and Cyprinidae fish populations. Predation, along with other biotic interactions is thus demonstrated as a key component of ecological food webs (Hart and Pitcher, 2012), regulating community populations (Abrahams *et al.*, 2007).

### Sympatric fish species feeding guilds, trophic levels (TL) and diet breadth

The highest trophic level of sympatric fish species recorded for the Ramisi River (Table 5) is related to the prevalence of high trophic guilds encountered among sampling locations (Froese and Pauly, 2019), mainly contributed by resident sympatric fishes. The higher trophic-level fish included omnivorous *C. gariepinus*, while predatory carnivorous *E. fusca*, *P. cancrivorus*, and *A. gymnocephalus* were among the higher trophic level fish (Froese and Pauly, 2019). Unlike at Athi River, omnivorous *C. gariepinus* had the highest trophic level in Ramisi River, owing to its active diet selection, proliferated by a wider diet breadth. As such, the Ramisi River is associated with intrinsic ecosystem values earning a higher conservation credibility (Duffy, 2002; Barbier *et al.*, 2009).

The lower trophic level recorded for Athi River was primarily due to the presence of lower trophic level fish species, despite the fact that the estuarine location contributed more to the trophic level due to high trophic level diets (Maitra *et al.*, 2018; Keppeler *et al.*, 2020). The findings of this study are consistent with those of Romanuk *et al.* (2006), who demonstrated that the structures of a food web are known to shift between river systems from mountains to lowland areas.

### Diet and niche breadth (B) trophic interactions

Due to their specialized feeding habit on high trophic level diets (Drouineau *et al.*, 2018) eels belonged to significantly higher trophic levels than sympatric fish. This subsequently corresponds to a narrower diet breadth (Belpaire *et al.*, 2011). As a result, *A. bengalensis* had the highest trophic level, placed higher on the food web pyramid, while *A. marmorata* had the lowest TL and a wider breadth (Table 6), and linked to unselective feeding habits. The unselective feeding habits of *A. marmorata*, supposedly give credence to its least concern classification by IUCN. Sympatric fishes, on the other hand, had a broader diet breadth, indicating

the presence of numerous nutritional dietary options and unselective feeding habits. Predominantly, this feeding behavior was most noticeable in exotic fishes. Although, sympatric fish had the lowest trophic level, carnivorous fish had the highest trophic level, indicating quantified trophic overlaps with eels (Hecnar and M'Closkey, 1997; González-Bergonzoni *et al.*, 2020) compounded with lower diet breadth, indicating diet specialization. Omnivorous fish, on the other hand, recorded a wider diet breadth due to the consumption of a wide range of dietary items from the environment (Sánchez-Hernández *et al.*, 2011; Gerking, 2014). As a result, because they compete on identical diets, both feeding guilds may be harmful to eels, displaying overlapped niche breadth. Similar findings have been reported in European catfish (*Silurus glanis*) which potentially compete with freshwater eels due to niche breadth and overlaps (Bevacqua *et al.*, 2011).

#### Niche and diet overlap

In the Athi river, carnivorous and omnivorous fish diets overlapped with those of eels, particularly *A. bicolar* and *A. bengalensis*, which were more prominent on carnivorous guilds. On the other hand, omnivorous guilds partially overlapped with *A. mossambica* diets, indicating a possibility of unselective feeding behavior and ontogenic shifts in diet. Furthermore, the observed food resource partitioning between carnivorous *A. bicolar* and *A. bengalensis* render them vulnerable to competition pressure (Bevacqua *et al.*, 2011). In addition, the diet overlaps observed between the eel species such *A. bengalensis* and *A. mossambica* (Table 8), demonstrates their coexistence throughout their range, as a result of their needs to meet energy and nutritional requirements (Sih *et al.*, 1998). Subsequently, this may result in interspecific competition as described by Arai, (2016). These findings agree with those of Laffaille *et al.* (2004), who reported minimal intraspecific competition for food among different eel growth stages.

Conversely, at Ramisi River, omnivorous species diets largely overlapped with those of *A. bicolar*, whereas carnivorous fish diets overlapped with those of *A. bengalensis* (Table 9), demonstrating that omnivorous fishes share their diets habitually with eels. However, *A. mossambica* diets primarily overlapped with those of herbivorous followed by omnivorous species, indicating that eels can also be regarded as generalists (Jellyman, 2021). *Anguilla bengalensis* exhibited the largest food resource partitioning with *A. bicolar* among the eel diets evaluated. Following that, Athi River displayed

larger relative amounts of inter and intraspecific competition for consumer-resource interaction between eels and sympatric fish species than the Ramisi River, ascribed to higher diet overlaps.

#### Conclusions

Competition and predation are important ecological drivers that allow species to coexist in biotic communities where resources are limited in quantity and/or quality. The findings of this study revealed that species interactions were influenced by competition, and it is apparent that the diets of *A. bengalensis* and *A. bicolar* not only overlapped but also shared food items with sympatric carnivorous and omnivorous guilds. Furthermore, due to the greater overlap, eel taxa found in the Athi are more susceptible to competition with prominent interacting sympatric fishes. As such, there is more inter- and intraspecific competition between eels and sympatric fish species, as well as similar ecological specialization. This implies that these species are possibly vulnerable to previously undescribed competition from carnivorous fish. Therefore, diet overlap information is important for inferring trophic interactions and to enable a better understanding of ecological aspects determining fish community structure.

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# Supplementary material

**Table S.1.** One-way ANOSIM pairwise correlation on diet composition among sampling locations on the Athi and Ramisi Rivers. Significant differences are indicated in bold.

Sampling locations	Eshu	Kiaoni	Sabaki	Taliani	Athi	Ramisi
Eshu	1					
Kiaoni	0.003	1				
Sabaki	0.0007	0.002	1			
Taliani	0.004	0.006	0.003	1		
Athi	0.001	0.026	<b>0.70</b>	0.001	1	
Ramisi	<b>0.92</b>	0.004	0.006	0.005	<b>0.006</b>	1

**Table S.2.** One-way SIMPER analysis of diet contribution and composition among the sampled locations in the Athi-Galana-Sabaki and Ramisi Rivers, Kenya. Significant contributions to dissimilarities are in bold.

Reaches	Upstream		Downstream		Upstream vs Downstream				Focal rivers	
Sampling locations	Kiaoni vs Eshu		Sabaki vs Taliani		Kiaoni vs Sabaki		Eshu vs Taliani		Athi Vs Ramisi	
Taxon	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %
Penaeid Shrimp	0.00	0.00	34.13	<b>38.58</b>	26.79	<b>33.78</b>	5.90	6.43	19.24	<b>24.44</b>
POM	10.34	12.57	7.77	<b>8.79</b>	10.18	<b>12.83</b>	2.55	2.72	8.58	<b>10.89</b>
AOM	7.95	9.66	6.11	<b>6.92</b>	5.24	<b>6.60</b>	4.64	4.95	6.34	<b>8.049</b>
DOM	7.25	8.82	9.07	<b>10.26</b>	5.24	<b>6.60</b>	10.22	10.89	7.66	<b>9.73</b>
Fish	14.40	<b>17.48</b>	12.62	<b>14.26</b>	9.60	<b>12.1</b>	27.46	<b>29.27</b>	10.14	<b>12.88</b>
Prawns	15.34	<b>18.62</b>	0.00	0.00	0.04	0.05	26.11	<b>27.83</b>	7.81	10.00
Crabs	2.61	3.17	9.84	11.12	6.65	8.3	4.52	4.82	4.42	5.61
Vegetations	7.27	8.83	4.18	4.72	3.12	3.94	4.29	4.60	5.00	6.32
Unidentified insects	2.59	3.15	3.28	3.71	2.75	3.47	4.96	5.29	2.86	3.65
Damselflies	0.00	0.00	0.41	0.48	0.35	0.47	0.00	0.00	0.23	0.30
Mayflies	1.35	1.64	0.23	0.28	1.01	1.27	0.00	0.00	0.88	1.13
Polychaete worms	0.00		0.18	0.21	0.12	0.16	0.00	0.00	0.10	0.13
Pond snails	0.53	0.65	0.13	0.15	0.33	0.42	0.00	0.00	0.28	0.36
Beetles	3.15	3.83	0.40	0.45	2.10	2.64	0.34	0.36	1.3	1.68
Stoneflies	0.00	0.00	0.07	0.08	0.06	0.08	0.00	0.00	0.04	0.06
Bird	0.84	1.01	0.04	0.05	0.52	0.65	0.00	0.00	0.35	0.46
Annelid worms	0.08	0.10	0.00	0	0.05	0.07	0.00	0.00	0.03	0.04
Bivalves	0.47	0.60	0.00	0.00	0.00	0.00	0.65	0.70	0.26	0.34
Caddisflies	6.60	8.01	0.00	0.00	4.51	6.60	0.00	0.00	2.67	3.40
Chironomidae	1.11	1.34	0.00	0.00	0.68	0.85	0.00	0.00	0.37	0.48
							0.00			
Plant seeds	0.45	0.54	0.00	0.00	0.00	0.00	2.17	2.37	0.14	0.18

Table S.3. Diet composition and preferences among eels and feeding guild residency in the Athi-Galana-Sabaki and Ramisi Rivers.

Food items	Eel	Introduced carnivorous	Introduced herbivorous	Introduced Omnivorous	Native carnivorous	Native herbivorous	Native omnivorous
Annelid worm	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Polychaeta worms	0.9	0.7	0.0	0.0	0.0	0.0	0.0
Beetle	0.0	0.7	8.3	9.8	0.0	0.0	6.7
Bivalve	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Caddisflies	0.0	0.0	15.3	17.3	0.0	5.9	0.0
Chironomidae	0.0	0.0	2.8	2.3	0.0	0.0	0.0
Damselfly	0.0	1.4	0.0	0.0	0.0	0.0	6.7
Mayflies	0.0	0.7	0.0	5.3	0.0	7.8	0.0
Pond snails	0.9	0.7	0.0	0.8	0.0	2.0	0.0
Stoneflies	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Unidentified Insect	2.8	4.1	5.6	6.8	0.0	3.9	6.7
AOM	2.8	8.1	4.2	15.0	10.1	13.7	6.7
POM	0.0	3.4	43.1	8.3	2.2	31.4	0.0
DOM	2.8	2.0	11.1	0.8	0.7	27.5	13.3
Vegetation	7.5	10.1	6.9	15.0	7.9	5.9	0.0
Plant seeds	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Crab	9.3	6.8	0.0	2.3	14.4	0.0	0.0
Penaeid Shrimps	14.0	36.5	1.4	3.0	34.5	2.0	33.3
Prawns	13.1	0.0	1.4	4.5	10.8	0.0	0.0
Fish	43.0	23.6	0.0	9.3	18.7	0.0	26.7
Birds	0.9	0.7	0.0	0.0	0.0	0.0	0.0

Table S.4. One-way ANOSIM pairwise correlation between eel and different sympatric feeding guilds belonging to different ecological status and food item preferences (P values in bold are significant at  $p < 0.05$ ).

Residency guilds	Eel	Introduced carnivorous	Introduced Omnivorous	Introduced herbivorous	Native carnivorous	Native omnivorous	Native herbivorous
Eel	1						
Introduced carnivorous	0.003	1					
Introduced Omnivorous	0.016	<b>0.193</b>	1				
Introduced herbivorous	0.001	0.011	0.072	1			
Native carnivorous	<b>0.095</b>	0.025	0.070	0.007	1		
Native omnivorous	0.001	0.220	0.018	0.001	0.0003	1	
Native herbivorous	0.003	0.030	<b>0.120</b>	<b>0.973</b>	0.01	0.003	1