

## Importance of terrestrial subsidies for estuarine food webs in contrasting East African catchments

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**Abstract.** Little is known on the degree to which terrestrial organic matter delivered to tropical estuaries contributes to estuarine consumers. Here, stable isotope analysis is used to constrain this contribution for contrasting east African estuaries whose catchments differ in relative C3/C4 vegetation cover. As these two types of vegetation differ strongly in  $\delta^{13}\text{C}$ , we anticipated that terrestrial subsidies would be reflected in a gradient in estuarine consumer  $\delta^{13}\text{C}$  values, following the relative importance of C3 (characterised by low  $\delta^{13}\text{C}$ ) vs. C4 (characterised by high  $\delta^{13}\text{C}$ ) cover. Five estuaries were sampled for aquatic biogeochemical parameters, primary producers and consumers of different trophic ecologies: the Zambezi (catchment with a C3/C4 cover of 61/39%) in Mozambique, the Tana in Kenya (36/64%) and the Betsiboka (42/58%), Rianila (85/15%) and Canal des Pangalanes (C3-dominated) in Madagascar. Sampling was done before and after the 2010/2011 wet season. There were positive relationships between the proportion of C4 cover in the catchment and turbidity,  $\delta^{13}\text{C}_{\text{DIC}}$ ,  $\delta^{13}\text{C}_{\text{DOC}}$ ,  $\delta^{13}\text{C}_{\text{POC}}$  and  $\delta^{15}\text{N}_{\text{PN}}$ . There were also significant positive relationships between  $\delta^{13}\text{C}_{\text{POC}}$  and consumer  $\delta^{13}\text{C}$  and between  $\delta^{15}\text{N}_{\text{PN}}$  and consumer  $\delta^{15}\text{N}$  for all consumer trophic guilds, confirming the incorporation of organic material transported from the catchments by estuarine consumers, and implying that this material is transported up to high trophic level fish. Bayesian mixing models confirmed that C4 material was the most important source for the highly turbid, C4-dominated estuaries, contributing up to 61–91% (95% CI) to phytodetritivorous fish in the Betsiboka, whereas for the less turbid C3-dominated estuaries terrestrial subsidies were not as important and consumers relied on a combination of terrestrial and aquatic sources. This shows that the ecology of the overall catchment affects the estuaries at the most basic, energetic level, and activities that alter the turbidity and productivity of rivers and estuaries can affect food webs well beyond the area of impact.

**Key words:** Africa; Bayesian mixing models; catchment; estuaries; stable isotopes; terrestrial subsidies.

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### INTRODUCTION

The stability of biological communities depends in part on the availability of food and on

the stability of trophic interactions among the different species (Polis and Strong 1996, Polis et al. 1997). Information on sources of energy is therefore central for understanding the dynamics

and persistence of communities through time. In rivers and estuaries, two contrasting sources of material can support food webs: aquatic primary production (autochthonous sources) and production imported from the terrestrial environment (allochthonous sources). The relative importance of these sources depends partially on the availability of terrestrial and aquatic material (Polis et al. 1997, Bouillon et al. 2004). While the availability of autochthonous material is regulated by physical and biological factors such as light (e.g., Boston and Hill 1991) and nutrient availability (Flindt et al. 1999), turbidity, water depth (e.g., Krause-Jensen and Sand-Jensen 1998) and substrate type (Rizzo and Wetze 1985), the availability of terrestrial material depends on a different set of factors such as hydrodynamics and geomorphology and landscape characteristics of the catchment (Polis et al. 1997, Hoinghaus et al. 2011).

Rivers and estuaries are subjected to high human pressure, as their settings make them ideal for human settlement. This pressure has been intensified over the last century, especially in tropical areas where increasing population numbers place increasing pressure on these environments (Junk 2002). Impacts such as deforestation, urbanisation, agriculture and flow regulation can directly affect the energetic connectivity between land and rivers, and these impacts can be transported downstream to the estuaries. Although much research on the importance of terrestrial subsidies has been conducted on temperate lakes (e.g., Bartels et al. 2012), rivers (e.g., Kendall et al. 2001) and to a lesser extent on estuaries (e.g., Chanton and Lewis 2002, Sakamaki et al. 2010), information on the main sources of energy for tropical estuaries is still lacking. Processes in these areas are likely to be very different to those in temperate systems given the much higher seasonality, productivity and biological diversity of their waters, and the types of human impacts they are subjected.

Tropical African rivers generally have highly seasonal flow regimes and well defined wet seasons, leading to annual cycles in habitat and nutrient availability and productivity. During the wet seasons, flood waters can transport terrestrial organic matter into rivers and waterways, while during the dry season there is a smaller input of terrestrial material into the aquatic

environment. Therefore, human impacts on the catchment can affect not only the ecology of the river, but also that of the downstream estuary. For example, deforestation and land clearing can lead to high amounts of suspended matter to enter the waters, increasing turbidity and limiting estuarine primary production (May et al. 2003, Mead and Wiegner 2010). On the other hand, the construction of hydroelectrical reservoirs is known to lead to significant retention of sediments and nutrients (e.g., Syvitski et al. 2005). Despite this importance, although some studies focused on the importance of wetland habitats such as mangroves or saltmarshes for aquatic food webs (Dittmar et al. 2001, Abrantes and Sheaves 2008), to our knowledge no study has considered the effect of impacts in the upstream catchment on the sources of nutrition supporting estuarine food webs.

Because it is difficult to quantify terrestrial detritus in animal guts, and because gut contents only give information on ingested material and not on what is assimilated and incorporated into animal tissues, many studies use stable isotope analysis to determine the importance of terrestrial detritus vs. aquatic producers for aquatic food webs (e.g., del Giorgio and France 1996). Stable carbon isotope ratios ( $\delta^{13}\text{C}$ ) are particularly useful for this purpose because of the small fractionation from food source to consumer (0–1‰; DeNiro and Epstein 1978, McCutchan et al. 2003), and because different producers can have different  $\delta^{13}\text{C}$  (France 1996). However, even with the use of stable isotopes, there is still some controversy related to the importance of allochthony, with some studies suggesting that terrestrial detritus is important for estuarine food webs (e.g., Abrantes and Sheaves 2010, Wai et al. 2011), while most did not find evidence of incorporation of terrestrial detritus by aquatic consumers (e.g., Deegan and Garritt 1997, Chanton and Lewis 2002) and suggest that transported material is not available to be assimilated by aquatic consumers as it is mostly refractory (Wiegner et al. 2009).

There are some limitations to the interpretation of stable isotope data in estuarine systems. For example,  $\delta^{13}\text{C}$  of estuarine producers can be spatially and temporarily variable (e.g., Cloern et al. 2002), and  $\delta^{13}\text{C}$  of dissolved inorganic carbon (DIC) can influence  $\delta^{13}\text{C}$  of aquatic producers

(Lin et al. 1991, Bouillon et al. 2000). Moreover, it is methodologically difficult to collect pure phytoplankton, so  $\delta^{13}\text{C}$  of particulate organic matter (POM) is often used as a proxy to phytoplankton  $\delta^{13}\text{C}$  (e.g., del Giorgio and France 1996, Bouillon et al. 2000). However, POM is composed by both phytoplankton and detritus or different origins (both aquatic and terrestrial), and it can be difficult to separate the contributions of the two, although the latter can be constrained using for example chlorophyll *a*:POC ratios or POC:PN ratios (e.g., Kendall et al. 2001). On the other hand, zooplankton feeds both on the detritus and algae fractions of POM, but in a selective manner, depending on the relative abundance of these sources (Cole et al. 2006, Van den Meersche et al. 2009). A similar situation occurs in the benthic food chains, where benthic algae and organic matter of different origins are differentially assimilated by phytodetritivorous species (D'Avanzo and Valiela 1990). All these factors make it difficult to identify and quantify the incorporation of terrestrial subsidies into estuarine food webs using stable isotopes (Bouillon et al. 2008). Stable isotope measurements of dissolved organic and inorganic carbon (DIC, DOC), C:N ratios of POM (e.g., Deegan and Garritt 1997, Kaldy et al. 2005), and the comparison of stable isotope data between seasons and/or systems with different ecology and impacts can be useful to improve the interpretation of stable isotope data of consumers (e.g., Abrantes and Sheaves 2010, Sakamaki et al. 2010).

In this study, stable isotope analysis is used to constrain the importance of terrestrial subsidies for aquatic animal communities in east African estuaries. Estuaries of four rivers and one coastal canal were sampled for primary producers, aquatic invertebrates, fish and a range of water biogeochemical parameters to (1) identify differences in the main sources of carbon at the base of the food web between systems with different ecological characteristics and subjected to different impacts and (2) identify any seasonality in importance of allochthonous sources for food webs in these areas. The systems considered drain areas with different mixes of C3/C4 vegetation, providing an ideal situation to study the contribution of terrestrial sources for aquatic food webs, as these producers are well separated in  $\delta^{13}\text{C}$  ( $\sim -27\text{‰}$  vs.  $\sim -12\text{‰}$ ). They also differ in

land use patterns in their catchments, allowing stable isotope data to be linked to different impacts. Since  $\delta^{15}\text{N}$  can be indicative of the incorporation of sewage (e.g., Schlacher and Connolly 2007), urbanisation (e.g., McClelland and Valiela 1997) or agricultural development (e.g., Anderson and Cabana 2005),  $\delta^{15}\text{N}$  was also used as indicator of incorporation of transported material into the waterways. Besides, the use of more than one tracer can give more information on sources of nutrition than the use of one tracer alone.

## METHODS

### Study sites

Estuaries of four east African rivers were sampled for consumers, primary producers and a range of biogeochemical parameters: the Zambezi in Mozambique, the Tana in Kenya and the Betsiboka and Rianila in Madagascar (Fig. 1). At each estuary, sampling was done close to the river mouth. A fifth area which was considered is the Pangalanes Canal, an artificial channel that runs parallel to the east coast of Madagascar (Fig. 1).

For each catchment, the proportion of C3 and C4 vegetation was estimated based on the data from Still and Powell (2010). Their crop-corrected estimates of relative C3 and C4 vegetation cover were used and integrated over the catchments using ArcGIS v10. Catchment areas were delineated from a vector representation of African water basins (FAO 2002), from which the percentage of C4 vegetation in each catchment was calculated (Still and Powell 2010). Due to the presence of large reservoirs and the associated retention of organic matter in these water bodies, the calculated C3/C4 cover for the Tana and the Zambezi was constrained to the catchment area below the Kiambere and Cahora Bassa reservoir, respectively. The Tana and the Betsiboka catchments had the highest C4 cover (Tana: 59% overall, and 64% for the area below the Kiambere reservoir; Betsiboka: 58%), the Zambezi basin had intermediate C4 cover (37% when considering the whole catchment, and 39% for the area below the Cahora Bassa reservoir), and the Rianila had the lowest C4 cover of 15%. As the fifth site is part of the Pangalanes Canal, a complex and artificial network of interconnected

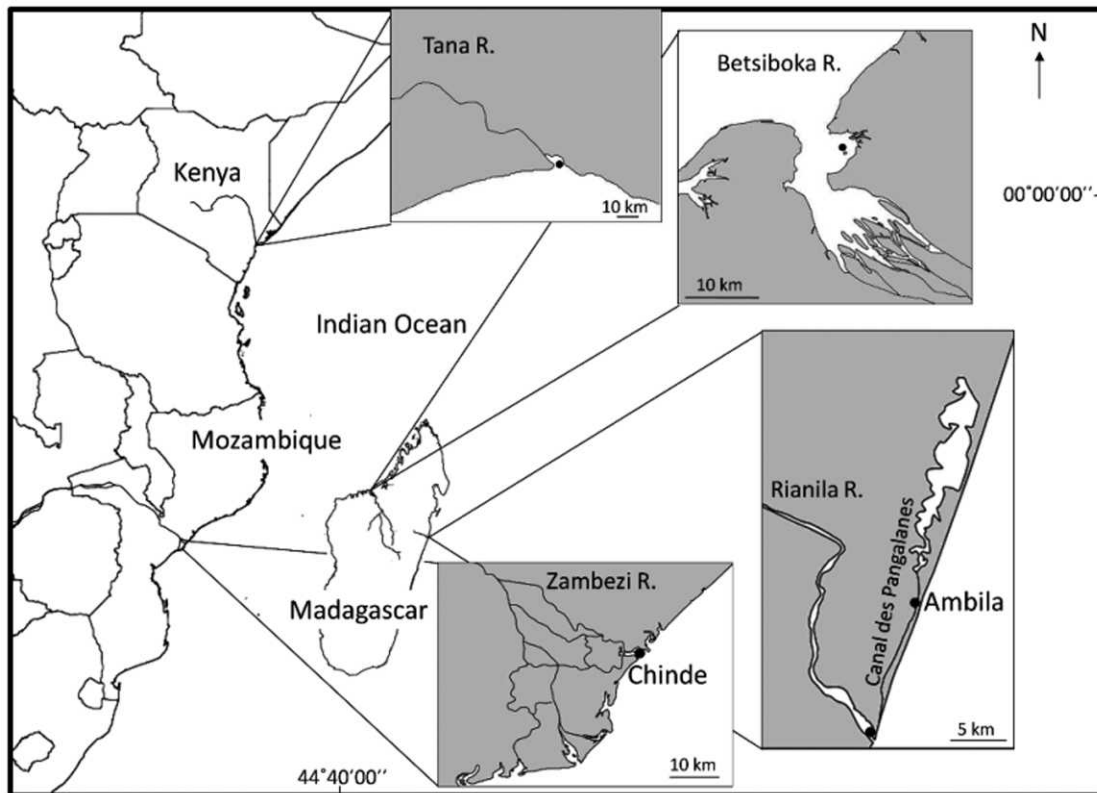


Fig. 1. Map showing the sampling sites considered in this study.

lagoons, no clear catchment area can be confidently assigned to this system. Based on personal observations and the proximity to the Rianila catchment, we can however assume that vegetation around that area is C3-dominated, with a similar proportion of C3/C4 cover as in the Rianila catchment (15/85%). In all catchments, both C3 and C4 vegetation cover is mostly natural, but the values given are corrected for estimated crop contributions as outlined in Still & Powell (2010).

The Zambezi is the longest river in eastern Africa. It runs for ~2570 km, drains an area of 1,570,000 km<sup>2</sup> (Davies 1986) and has an average discharge of 3341 m<sup>3</sup>·s<sup>-1</sup> (Vörösmarty et al. 1998). Due to the Kariba and Cahora Bassa dams, the natural flood cycles are lost, seasonal flows less pronounced and the hydrological and energetic connectivity between river and floodplain is greatly reduced. Nowadays, inundation of the delta depends mostly on rainfall within the lower Zambezi subcatchment (mean annual rainfall in

the area: 1060 mm) or on water releases from the dams (Beilfuss and Davies 1998). The climate is subtropical humid with a rainy season from November to April, and a dry season from May to October. In the delta, wetlands cover ~13,000 km<sup>2</sup> and include extensive floodplain grasslands surrounded by coastal forest-woodland mosaic, with mangroves closer to the coast. Most of the delta is undeveloped, with virtually no agriculture or industrial use (Turpie et al. 1999). The estuary was sampled near Chinde Village (18.574° S, 36.478° E; Fig. 1), in one of the main distributary channels of the Zambezi. The region has a population density of only 38 inhabitants km<sup>-2</sup>. Tides are semi-diurnal, and range between 1.0 m at neap tides and 3.7 m at spring tides.

The Betsiboka is the second longest river in Madagascar (~525 km). With a mean annual discharge of 280 m<sup>3</sup>·s<sup>-1</sup> (Vörösmarty et al. 1998), it runs with a very gradual slope through the northwest coast, draining an area of ~49,000 km<sup>2</sup>. The whole catchment is highly affected by



deforestation and land clearing for cattle grazing and agriculture. Consequently, there are massive problems of erosion (Randrianarijaona 1983) and very high sediment loads, amongst the highest in the world, are annually transported into the waterway (Raharimahefa and Kusky 2010). The water is therefore extremely turbid. For most of its part, the catchment is highly dominated by C4 grasses (>80% in parts). Madagascar's west coast has a hot and rainy season between November and March, and a cooler, dry season between April and October. The river discharges in Bombetoka Bay, where the City of Mahajanga (population ~155,000) is located. Here, mangroves occupy an area of ~460 km<sup>2</sup>. Sampling was done in the north part of the bay (15.750° S, 46.315° E; Fig. 1). Tides are semi-diurnal with spring tide ranges up to 3.8 m.

The Rianila, in eastern Madagascar, runs into the Indian Ocean near Andevoranto (population ~10,500) with a mean annual discharge of 408 m<sup>3</sup>·s<sup>-1</sup> (Aldegheri 1972). Given the topography of the area, the Rianila is much shorter (134 km), steeper and faster than the Betsiboka. Its 5875 km<sup>2</sup> catchment is dominated by primary and degraded rainforests (C3), with some eucalyptus, fruit trees, rice (C3) and sugarcane (C4) plantations. Waters are clear, allowing for aquatic production. Mats of benthic algae as well as filamentous green algae and some seagrass *Ruppia maritima* occur in the estuary. The area experiences some rainfall year-round, but with a peak season between December and March. The Rianila was sampled just inside the sandy bar on the mouth of the estuary (18.973° S, 49.098° E; Fig. 1). Tides are semidiurnal with an average tidal range <1 m.

The Canal des Pangalanes consists of artificially linked coastal lagoons and man-made canals that run parallel to the shore for ~600 km along the east coast of Madagascar and connect to the sea by rivers that cross the area. There is little water movement in the system. The canal is bordered by C3 reeds and grasses, and is separated from the sea by a relatively narrow strip of land (15–20 m wide in our study area). The waters are very clear and visible mats of algae (periphyton) were abundant, especially in the post-wet season. There is some infiltration of seawater through the dunes, so the water is slightly saline (~10). Sampling was done in

Ambila-Lemaitso (from hereon Ambila) (18.876° S, 49.140° E; Fig. 1), a sparsely populated area (0.011 inhabitants km<sup>-2</sup>) ~13 km north of the Rianila estuary.

The Tana River is ~1000 km long, with a catchment of ~120,000 km<sup>2</sup>. It originates in Mount Kenya and the Aberdares highlands, where most vegetation is C3, but runs mostly through tropical arid and semi-arid zones where the catchment has an increasing C4 cover, including a large part with 90–100% C4 cover (Still and Powell 2010). The ~1300 km<sup>2</sup> delta has extensive freshwater and estuarine wetlands, including floodplain forests and mangroves. The waters are very turbid, with a high sediment load (Bouillon et al. 2009, Tamoooh et al. 2012). Human activities in the lower catchment include nomadic pastoralism, some farming along the riverbank and wood collection for fuel and charcoal. There are some villages and towns along the river, but the region is mostly not urbanized. Rainfall in most of the catchment is low and occurs during two wet seasons, the “long rains” (March–May, generally more abundant) and the “short rains” (October–December). Mean monthly freshwater discharge is between ~80 m<sup>3</sup>·s<sup>-1</sup> in September and ~300 m<sup>3</sup>·s<sup>-1</sup> in May (Maingi and Marsh 2002). The Tana estuary was sampled near Kipini (2.531° S, 40.525° E; Fig. 1; population ~4000). Tides are semi-diurnal, with a tidal range of ~1.5–3.0 m at neap and spring tides respectively (Kitheka et al. 2005).

At all five study areas, the substrate is mostly sandy, with some muddy areas along the edges. Because of a lack of substrate suitable for attachment, macroalgae are very rare. While the waters in Rianila and Ambila are clear, due to the high turbidity levels in the Betsiboka, Zambezi and Tana estuaries, aquatic productivity is expected to be low (Bouillon et al. 2007, Ralison et al. 2008, Tamoooh et al. 2012) and almost no seagrass occurs in these estuaries. Seagrass was only observed in the Rianila where it was abundant in the pre-wet season, but rare in the post-wet season.

### Sampling design

To identify the importance of terrestrial subsidies for estuarine animal communities, the Zambezi, Betsiboka, Rianila and Ambila were sampled before and after the 2010/2011 wet

season (from hereon pre-wet and post-wet season respectively). Sampling included fish, invertebrates, primary producers and a range of aquatic biogeochemical parameters. For the pre-wet season, the Betsiboka, Rianila and Ambila were sampled in November 2010 and the Zambezi in December 2010. For the post-wet season, the Zambezi was sampled in April 2011, and the remaining systems in May 2011. Unlike in Madagascar and Mozambique, where freshwater flow is highly seasonal, with one wet season per year, Kenya has two rainy seasons. This means that it would be difficult to detect any seasonal differences in consumer stable isotope composition that result from differences in incorporation of terrestrial material between seasons, as the time period between seasons is not long enough for animal muscle tissue to reflect new diet sources. So, the Tana River was only sampled once, in November 2010, during the “short rains”.

For the Zambezi, Betsiboka, Rianila and Ambila, at each sampling time, consumers were living for >4 months under dry or wet season conditions before capture. After a change in diet, a certain time period is necessary for the isotopic composition of consumers to reflect a new diet, depending both on growth and on metabolism (Hesslein et al. 1993, Guelinckx et al. 2007). For muscle of small (< ~ 400 g), growing fish, carbon half-lives can vary between ~1 and 2.5 months, and nitrogen between ~1 and 3.5 months (Guelinckx et al. 2007, Buchheister and Latour 2010, Weidel et al. 2011). Since most fish captured in the present study were small growing juveniles, given the time lag between the end of the 2009/2010 wet season and the pre-wet sampling (~7 months), and between the beginning of the 2010/2011 wet season and the post-wet sampling period (~6 months), any seasonal change in ultimate sources of nutrition should be reflected on consumer stable isotope composition. For small aquatic invertebrates, half-lives are much shorter, and large shifts in stable isotope composition can be detected within weeks of a change in diet (McIntyre and Flecker 2006, Dubois et al. 2007). If material transported from the catchment with the flood waters is important for estuarine food webs, then we would expect seasonal differences in importance of terrestrial organic matter for animal nutrition, which should agree

with the type of surrounding vegetation (C3 vs. C4) and/or land use at each site.

Material of terrestrial origin transported into estuaries can be directly consumed by herbivores and detritivores or mineralized into dissolved inorganic carbon (DIC). The latter typically results in a  $^{13}\text{C}$ -depletion of the DIC pool, which will be reflected in the  $\delta^{13}\text{C}$  of aquatic producers.  $\delta^{13}\text{C}_{\text{DIC}}$  in river systems is thus influenced by a combination of factors, including the dominant weathering regimes (silicate vs. carbonate weathering), gas exchange across the water-air interface, and metabolism (balance of primary production and respiration).  $\delta^{13}\text{C}_{\text{DIC}}$  in estuarine systems can thus vary not only along the salinity gradient, but also seasonally since the  $\delta^{13}\text{C}_{\text{DIC}}$  in the freshwater end-member can show considerable variability due to changes in e.g., the relative importance of carbonate vs. silicate weathering or aquatic metabolism (primary production vs. respiration). Hence,  $\delta^{13}\text{C}_{\text{DIC}}$  was also measured at each site and season, and results related to consumer  $\delta^{13}\text{C}$ . Concentrations and stable isotope composition of particulate organic carbon (POC and  $\delta^{13}\text{C}_{\text{POC}}$ ), particulate nitrogen (PN and  $\delta^{15}\text{N}_{\text{PN}}$ ), dissolved organic carbon (DOC and  $\delta^{13}\text{C}_{\text{DOC}}$ ) and total suspended matter (TSM) were also determined and compared to consumer  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to help separate the contribution of terrestrial from aquatic sources.

#### Sample collection and analysis

*Biogeochemical parameters.*—Water samples for biogeochemical analyses were collected from ~0.2 m below the surface, where water depth was >1.5 m. With the exception of Ambila, where tidal amplitude is limited, samples were collected at receding tides, closer to the low than to the high tide. All samples were processed within 2 h of collection. Samples for POC, PN and  $\delta^{13}\text{C}_{\text{POC}}$  were obtained from filtering a known volume of water into pre-combusted 25 mm GF/F filters (0.7  $\mu\text{m}$  nominal pore size) under vacuum. Filters were then dried overnight at 60°C. In the lab, filters were decarbonated for 4 h with HCl fumes, redried and packed into Ag capsules. POC, PN and  $\delta^{13}\text{C}_{\text{POC}}$  were determined in an element analyser-isotope ratio mass spectrometer (EA-IRMS) using the thermal conductivity detector (TCD) signal of the EA to quantify POC and PN. Acetanilide and sucrose (IAEA-C6)

were used to calibrate  $\delta^{13}\text{C}_{\text{POC}}$  and to quantify POC and PN.

DOC and  $\delta^{13}\text{C}_{\text{DOC}}$  samples were obtained by filtering water through 47 mm GF/F filters, and further filtering the filtrate through 0.2  $\mu\text{m}$  Acrodisc syringe filters into 40 ml glass vials. The filtrate was preserved by addition of 50  $\mu\text{l}$  of  $\text{H}_3\text{PO}_4$  and analyzed as described in Bouillon et al. (2009). Samples for  $\delta^{13}\text{C}_{\text{DIC}}$  were taken in duplicate in 12 ml exetainer vials, poisoned with 20  $\mu\text{l}$  of  $\text{HgCl}_2$  and analysed as described in Gillikin and Bouillon (2007). TSM was determined by filtering a measured volume of water onto pre-weighed, pre-combusted (4 h at 500°C) 47 mm GF/F filters under vacuum. Filters were then dried at 60°C overnight and reweighed to calculate TSM.  $\delta^{15}\text{N}_{\text{PN}}$  was measured from a cut-out of these 47 mm GF/F filters, packed in Ag cups.

*Biological material.*—1. *Primary producers.*—Aquatic and terrestrial primary producers were collected from each site. Terrestrial plants (including mangroves and saltmarsh plants) were collected from the vicinity of each estuary and more upstream in the catchment. Green leaves of 3–10 individuals were combined in each replicate. Macrophytes were hand-picked where present, and several individuals combined in each replicate. When possible, microphytobenthos (MPB) was sampled based on its vertical migration properties using a modification of the Couch (1989) method: the surface layer of sediments was removed with a spatula, spread in ~1 cm deep layers onto flat trays as soon as possible after collection, and covered with three layers of 63  $\mu\text{m}$  nylon screen. The sediment and mesh were kept damp with local water and left in continuous light for ~24 h. The day after, due to vertical migration, algae accumulated at the surface of the upper mesh and between the layers. Algae were then washed and scraped from the upper mesh and dried overnight at 60°C. Epiphytes were removed from mangrove roots (at the Zambezi, Betsiboka and Tana) or reeds (at Ambila) by scraping with a scalpel and carefully removing attached detritus. Epiliths were removed from submerged pebbles the same way. Material from >10 separate mangrove roots/reeds/pebbles was combined in each replicate. Phytoplankton was not sampled because it is methodologically difficult to collect and

because it can be spatially and temporarily variable in  $\delta^{13}\text{C}$  (Bouillon et al. 2000), especially in areas of tidal influence. Thus, a sample collected at any point in time is unlikely to be representative of the phytoplankton available in the area over time.

2. *Zooplankton.*—Zooplankton was collected with a 250  $\mu\text{m}$  plankton net towed ~1 m below the surface for ~50 m. Material collected from three different areas was combined in one replicate. All samples were collected at ebb tide. Collected material was then filtered through a 500  $\mu\text{m}$  mesh to remove debris and placed in a 200 ml jar where sediment was allowed to settle and zooplankton guts allowed to clear for ~4 h. The top water, containing mostly zooplankton but also some unidentified detrital material, was then carefully collected on a 250  $\mu\text{m}$  sieve, and dried at 60°C for 48 h. For  $\delta^{13}\text{C}$  analysis, samples were acidified in Ag capsules by adding 20–50  $\mu\text{L}$  of 5% HCl drop-by-drop onto the weighed samples to remove carbonates (Jaschinski et al. 2008, Kolasinski et al. 2008).  $\delta^{15}\text{N}$  was measured on untreated samples. Due to the very high suspended sediment load, it was not possible to collect zooplankton from the Betsiboka.

Tissue lipid content is known to affect bulk  $\delta^{13}\text{C}$ , as lipids are depleted in  $^{13}\text{C}$  relative to proteins and carbohydrates (DeNiro and Epstein 1977, McConnaughey and McRoy 1979). We corrected zooplankton  $\delta^{13}\text{C}$  data for lipid content using the mass balance equation:  $\delta^{13}\text{C}_{\text{ZP-C}} = \delta^{13}\text{C}_{\text{ZP-M}} + (6.3 \times ((\text{C:N} - 4.2) \cdot \text{C:N}^{-1}))$  (Fry 2002, Smyntek et al. 2007), where  $\delta^{13}\text{C}_{\text{ZP-M}}$  is the measured  $\delta^{13}\text{C}$  of zooplankton,  $\delta^{13}\text{C}_{\text{ZP-C}}$  is the lipid-corrected  $\delta^{13}\text{C}$ , 6.3 is the average difference in  $\delta^{13}\text{C}$  between protein and lipids in zooplankton, and 4.2 is the C:N value of lipid extracted zooplankton (Smyntek et al. 2007). Measured zooplankton C:N ratios varied between 5.3 and 9.6 (weight/weight ratios), which led to changes in  $\delta^{13}\text{C}$  of +1.3 to +3.6‰ (mean  $\pm$  standard error (SD): +2.7  $\pm$  0.7‰).

3. *Macroinvertebrates and fish.*—At each site, a wide range of macroinvertebrate and fish species was collected to represent the estuarine community as completely as possible. Animal handling was carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC), under the guidelines from the Animal Ethics Committee of the KULeuven and

according to the laws and regulations of the countries involved. Fish were captured with the help of local fishermen using 18 mm cast nets, dip nets, seine nets and monofilament gill nets of different mesh sizes set from the estuary margins and from motorised boats or dugout canoes. In the Betsiboka, fish were also bought from the local market. Within one day from capture, fish were identified, measured (total length), and white muscle tissue was excised from the trunk below the dorsal fin. Because we were interested in the average stable isotope composition of each species, whenever possible five individuals of each species were combined in each replicate to reduce the effect of intraspecific variability. When different size classes were present, these were considered separately to account for ontogenetic variations in diet. If however stable isotope results were similar between sizes, these were grouped on the following analyses. Invertebrates were collected with seine nets, dip nets and a surber sampler, or hand picked (gastropods, crabs, oysters, barnacles). Samples were removed from the abdominal muscle of prawns and shrimps, the claws of crabs, the muscular foot of gastropods and the adductor muscle of bivalves. Peracarid crustaceans were collected by sieving the surface sediments with a 500  $\mu\text{m}$  sieve. These consumers were processed whole after being held in environmental water for  $\sim 24$  h to allow for their digestive systems to clear. As for zooplankton, peracarid and barnacle samples were acidified with HCl to remove possible carbonates before  $\delta^{13}\text{C}$  analysis.

All samples were dried for 48 h at  $60^\circ\text{C}$  within a day of collection. In the laboratory, samples were homogenized into a fine powder with a mortar and pestle, and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured with an EA-IRMS. Results are expressed as per mil (‰) deviations from the standards, as defined by the equation:  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 10^3$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  for carbon and  ${}^{15}\text{N}/{}^{14}\text{N}$  for nitrogen. Acetanilide and Leucine, run every 12 samples, were used as secondary standards for  $\delta^{13}\text{C}$  (two-point, with blank correction) and  $\delta^{15}\text{N}$  calibration. Results had a precision of  $\pm 0.1$ – $0.3$ ‰ for  $\delta^{13}\text{C}$  and  $\pm 0.1$ – $0.2$ ‰ for  $\delta^{15}\text{N}$  (SD), calculated from standards. C and N contents were assessed from the TCD signal of the EA, using acetanilide (71.09% C, 10.36% N) as a standard.

For fish with C:N ratios  $>3.5$ ,  $\delta^{13}\text{C}$  were mathematically corrected for lipid content based on C:N ratios using the equation:  $\delta^{13}\text{C}' = \delta^{13}\text{C}_{\text{measured}} - 3.32 + 0.99 \times \text{C:N}$  (Post et al. 2007). No correction is necessary for fish with C:N ratio  $<3.5$  (Post et al. 2007). Only 48 of the  $>1500$  fish samples had C:N  $>3.5$  (mean  $\pm$  SD:  $3.8 \pm 0.2$ ; maximum: 4.3). This led to an average difference between measured and corrected  $\delta^{13}\text{C}$  of only  $+0.4$ ‰ for these samples. Invertebrate  $\delta^{13}\text{C}$  were not corrected for lipid content because the shifts in  $\delta^{13}\text{C}$  associated with lipid removal can be very variable and taxon-specific (Logan et al. 2008, Mateo et al. 2008).

### Data analysis

Relationships between the proportion of C4 vegetation cover in the catchments (expressed in %) and  $\delta^{13}\text{C}$  values, as well as interrelationships between  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  of different pools were analyzed with linear regression. Furthermore, the effects of  $\delta^{13}\text{C}_{\text{POC}}$ ,  $\delta^{13}\text{C}_{\text{DIC}}$  and  $\delta^{13}\text{C}_{\text{DOC}}$  on consumer  $\delta^{13}\text{C}$  were also explored with analysis of covariance (ANCOVA). This was based on the mean  $\delta^{13}\text{C}$  of each trophic guild (for each site and season), with trophic guild as the fixed factor and  $\delta^{13}\text{C}_{\text{POC}}/\delta^{13}\text{C}_{\text{DIC}}/\delta^{13}\text{C}_{\text{DOC}}$  as the covariate. ANCOVA was also used to determine the effect of  $\delta^{15}\text{N}_{\text{PN}}$  and trophic guild on consumer  $\delta^{15}\text{N}$ . All analyses were done in Statistica v.7.

Bayesian mixing models were used to quantify the contribution of the main classes of producers to consumers, using SIAR (Stable Isotope Analysis in R; Parnell et al. 2008, Parnell et al. 2010). These models produce a range of feasible solutions given the available sources, while taking into account uncertainty and variation both in consumer and trophic enrichment factors (TEF). They also provide error terms that give information on the variability that can not be explained based on diet alone (residual error) (Parnell et al. 2010). Models were run for each site and season separately, and the groups were the different trophic guilds. Consumer data was previously checked for normality using the Shapiro-Wilk test and by the visual analysis of normal probability plots, in Statistica. When normality was not present, it was either due to the presence of one outlier species, which was subsequently removed from the dataset, or because data was bimodal, in which case models



Table 1. Salinity, total suspended matter (TSM), particulate organic carbon concentration (POC), %POC (expressed as a % of TSM) and POC/PN ratios at each site and season.

Site	Season	Salinity	TSM (mg·L <sup>-1</sup> )	POC (mg C·L <sup>-1</sup> )	%POC	POC/PN
Zambezi	Pre-wet	NM	21.5	1.7	7.7	6.6
	Post-wet		23.3	NM	NM	6.0
Rianila	Pre-wet	NM	1.7	0.7	40.5	10.6
	Post-wet		4.3	NM	NM	NM
Ambila	Pre-wet	NM	NM	0.9	22.2†	11.8
	Post-wet	9	3.8	NM	NM	9.8
Betsiboka	Pre-wet	NM	179.5	2.0	1.1	6.8
	Post-wet	30	150.7	NM	NM	NM
Tana	Short rains	NM	80.7	1.7	2.1	8.6

Note: NM, not measured.

† Value calculated based on the TSM of the post-wet season, assuming it was similar between seasons for this site, as no TSM data was collected in the post-wet season.

were run for the two groups separately. Because species of different trophic levels were considered, TEFs were set to zero and, instead, the stable isotope composition of consumers was corrected for trophic fractionation prior to analysis. For invertebrates, only penaeid prawns and palaemonid shrimps were used, as these were sampled from all sites and seasons. These were considered to be of trophic level (TL) 2.5. For fish, the trophic guilds used were phytodetritivores (considered to be of TL 2), planktivores (TL 3), carnivores (TL 3.5), and piscivores (TL 4). Trophic fractionation values used were 0.5 for  $\delta^{13}\text{C}$  and 3.0 for  $\delta^{15}\text{N}$  (McCutchan et al. 2003, Vanderklift and Ponsard 2003). A large TEF SD of 1.0‰ was used for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to account for the uncertainty in these fractionation values (e.g., McCutchan et al. 2003, Vanderklift and Ponsard 2003). Concentration dependencies were set to zero.

For the Zambezi and Betsiboka, models were run based only on  $\delta^{13}\text{C}$  as the possible sources had similar  $\delta^{15}\text{N}$ . Only plankton and C3 and C4 producers were considered as possible sources in these models. For the Tana, Rianila and Ambila, models were run based on both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Since C4 producers from the more upstream Tana catchment were not collected, the average values of C4 producers from Kenya (Koch et al. 1991) and Tanzania (Muzuka 1999) were used:  $-12.7 \pm 1.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $+8.1 \pm 2.6\text{‰}$  for  $\delta^{15}\text{N}$ . In the Rianila and Ambila, a range of aquatic producers was available, so these were also included in the models. For each site, for terrestrial sources,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of C3 and C4 sources considered were based on the average

values from both seasons. Because pure phytoplankton could not be collected, its values were estimated based on a double approach, while using both  $\delta^{13}\text{C}_{\text{ZP-M}}$  and  $\delta^{13}\text{C}_{\text{DIC}}$ . Thus, the used average and SD values for the phytoplankton source were calculated based on  $\delta^{13}\text{C}_{\text{ZP-M}}$  and on  $\delta^{13}\text{C}_{\text{DIC}} - 20\text{‰}$ , given the fractionation of  $\sim -20\text{‰}$  during the uptake for photosynthesis (Peterson and Fry 1987, Chanton and Lewis 1999). Since zooplankton could not be collected at the Betsiboka, the average  $\delta^{13}\text{C}_{\text{ZP-M}}$  value from the other sites ( $-21.7\text{‰}$ ) was used. For  $\delta^{15}\text{N}$ , source values for phytoplankton were based on the average and SD between  $\delta^{15}\text{N}_{\text{ZP}}$  and  $\delta^{15}\text{N}_{\text{PN}}$ . This led to a wide range of possible phytoplankton  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for each site/season. This high uncertainty should lead to conservative results regarding the importance of terrestrial sources to consumers.

## RESULTS

### Biogeochemical parameters

The different estuaries had very different environmental conditions. The C4-dominated Betsiboka was highly turbid, with the highest TSM concentration (151–180 mg·L<sup>-1</sup>; Table 1). The Tana also had high TSM of 80.7 mg·L<sup>-1</sup>, while the C3-dominated Rianila and Ambila had generally clear waters (TSM <5 mg·L<sup>-1</sup>). There was strong positive relationships between the estimated percentage C4 cover in the catchment and TSM concentration ( $R^2 = 0.68$ ,  $F_{1,6} = 12.539$ ,  $P = 0.0122$ ) and between estimated C4 cover and POC concentrations (only measured in the pre-wet season) ( $R^2 = 0.84$ ,  $F_{1,3} = 15.233$ ,  $P = 0.0299$ ). Accordingly, there was a negative relationship

Table 2. Carbon stable isotope composition of dissolved inorganic and organic carbon (DIC and DOC), particulate organic carbon (POC) and  $\delta^{15}\text{N}$  of particulate nitrogen (PN) at each site and season.

Site	Season	$\delta^{13}\text{C}_{\text{DIC}}$ (‰)	$\delta^{13}\text{C}_{\text{DOC}}$ (‰)	$\delta^{13}\text{C}_{\text{POC}}$ (‰)	$\delta^{15}\text{N}_{\text{PN}}$ (‰)
Zambezi	Pre-wet	-4.5	-23.1	-24.9	2.7
	Post-wet	-5.1	-21.9	-24.7	3.4
Rianila	Pre-wet	-9.9	-27.2	-26.8	2.8
	Post-wet	-7.9	-25.0	-27.5	0.9
Ambila	Pre-wet	-10.5	...	-25.2	5.0
	Post-wet	-9.7	-26.4	-25.6	5.3
Betsiboka	Pre-wet	-1.8	-22.5	-21.3	10.2
	Post-wet	-2.0	-20.0	-22.3	10.0
Tana	Short rains	-8.5	-20.9	-22.7	8.2

between estimated C4 cover and %POC (expressed as a % of TSM) ( $R^2 = 0.79$ ,  $F_{1,3} = 11.537$ ,  $P = 0.0426$ ). POC/PN ratios were the highest in Rianila and Ambila (10.6 and 11.8 respectively), followed by Tana (8.6), and the Betsiboka and Zambezi had the lowest ratios (6.0 to 6.8) (Table 1). There was no significant relationship between estimated C4 cover and POC/PN ratios ( $P = 0.0932$ ).

There were also significant positive relationships between the estimated proportion of C4 vegetation cover and  $\delta^{13}\text{C}_{\text{DIC}}$  ( $R^2 = 0.51$ ,  $F_{1,7} = 7.405$ ,  $P = 0.0297$ ),  $\delta^{13}\text{C}_{\text{DOC}}$  ( $R^2 = 0.70$ ,  $F_{1,6} = 13.958$ ,  $P = 0.0097$ ),  $\delta^{13}\text{C}_{\text{POC}}$  ( $R^2 = 0.82$ ,  $F_{1,7} = 31.683$ ,  $P = 0.0008$ ) and  $\delta^{15}\text{N}_{\text{PN}}$  ( $R^2 = 0.64$ ,  $F_{1,6} = 10.574$ ,  $P = 0.0174$ ), as well as between  $\delta^{13}\text{C}_{\text{DIC}}$  and  $\delta^{13}\text{C}_{\text{DOC}}$  ( $\delta^{13}\text{C}_{\text{DOC}} = \delta^{13}\text{C}_{\text{DIC}} \times 0.63 - 19.1$ ;  $R^2 = 0.51$ ,  $F_{1,6} = 6.350$ ,  $P = 0.0453$ ), and between  $\delta^{13}\text{C}_{\text{DIC}}$  and  $\delta^{13}\text{C}_{\text{POC}}$  ( $\delta^{13}\text{C}_{\text{POC}} = \delta^{13}\text{C}_{\text{DIC}} \times 1.1 + 20.5$ ;  $R^2 = 0.46$ ,  $F_{1,7} = 5.984$ ,  $P = 0.0444$ ), but no relationship between  $\delta^{13}\text{C}_{\text{DOC}}$  and  $\delta^{13}\text{C}_{\text{POC}}$  was present ( $P = 0.0651$ ). Mean  $\delta^{13}\text{C}_{\text{DIC}}$ ,  $\delta^{13}\text{C}_{\text{DOC}}$ ,  $\delta^{13}\text{C}_{\text{POC}}$  and  $\delta^{15}\text{N}_{\text{PN}}$  can be found in Table 2.

#### Primary producers

As expected, C3 terrestrial producers had the lowest  $\delta^{13}\text{C}$  and C4 producers the highest  $\delta^{13}\text{C}$  at all sites (Table 3). Although there were both C3 and C4 producers in all catchments, the available aquatic producers varied between estuaries: algae were abundant at the clearer sites of Rianila and Ambila, and seagrass was also present at the Rianila, while at the Betsiboka, Tana and Zambezi, aquatic producers were scarce. The Betsiboka and Rianila were the only sites where aquatic primary producers that occurred at both seasons showed seasonal differences in  $\delta^{13}\text{C}$  and/or  $\delta^{15}\text{N}$  (Table 3).

#### Zooplankton

Measured zooplankton  $\delta^{13}\text{C}$  ranged between  $-23.7$  and  $-19.3$ ‰, and corrected values ranged from  $-21.6$  to  $-17.2$ ‰ (Table 4). It was not possible to collect zooplankton from the Betsiboka due to the very high sediment load and low zooplankton abundances. In the Zambezi, zooplankton  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were similar between seasons, but in the Rianila  $\delta^{15}\text{N}_{\text{ZP-C}}$  was higher and  $\delta^{13}\text{C}_{\text{ZP-C}}$  lower after the wet season, while in Ambila  $\delta^{13}\text{C}_{\text{ZP-C}}$  was higher after the wet season (Table 4).

The C3-dominated Rianila and Ambila had the lowest  $\delta^{13}\text{C}_{\text{ZP}}$  (Table 4), but there was no significant relationship between estimated C4 cover and  $\delta^{13}\text{C}_{\text{ZP}}$  ( $P = 0.1947$  for  $\delta^{13}\text{C}_{\text{ZP-M}}$ ;  $P = 0.1790$  for  $\delta^{13}\text{C}_{\text{ZP-C}}$ ). There were also no significant relationships between  $\delta^{13}\text{C}_{\text{DIC}}$  and  $\delta^{13}\text{C}_{\text{ZP-C}}$  ( $P = 0.1364$ ) or between  $\delta^{13}\text{C}_{\text{DOC}}$  and  $\delta^{13}\text{C}_{\text{ZP-C}}$  ( $P = 0.2266$ ). These relationships were also absent when using the measured, non lipid corrected values ( $P > 0.05$  in both cases). Since the uptake of DIC by phytoplankton leads to a fractionation of  $\sim -20$ ‰ (Peterson and Fry 1987, Chanton and Lewis 1999),  $\delta^{13}\text{C}_{\text{DIC}}$  can give information on phytoplankton  $\delta^{13}\text{C}$ , which in turn can affect  $\delta^{13}\text{C}_{\text{ZP}}$ . However, both  $\delta^{13}\text{C}_{\text{ZP-M}}$  and  $\delta^{13}\text{C}_{\text{ZP-C}}$  were much higher than phytoplankton  $\delta^{13}\text{C}$  estimated based on these fractionation values and there was no relationship between  $\delta^{13}\text{C}_{\text{POC}}$  and  $\delta^{13}\text{C}_{\text{ZP-C}}$  ( $P = 0.1613$ ) or  $\delta^{13}\text{C}_{\text{ZP-M}}$  ( $P = 0.1507$ ), nor between  $\delta^{15}\text{N}_{\text{PN}}$  and  $\delta^{15}\text{N}_{\text{ZP}}$  ( $P = 0.2316$ ).

#### Relationships between biogeochemical parameters and consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

A total of 3183 fish (pre-wet: 1130; post-wet: 2053) and 3120 invertebrate individuals (pre-wet: 1608; post-wet: 1512) were sampled (Appendix

Table 3.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (mean  $\pm$  SD; in ‰) of the main producer categories found at each estuary and in the surrounding catchment in the pre and post wet season.  $n$  is the number of species considered, followed in brackets by the range in number of replicates per species and number of individuals pooled in each replicate. When more than two species are included, mean and SD are calculated based on the average of the different species. When only one species is included, mean and SD are between the replicates for that species.

Estuary	Producers	$\delta^{13}\text{C}_{\text{Pre}}$	$\delta^{15}\text{N}_{\text{Pre}}$	$n_{\text{Pre}}$	$\delta^{13}\text{C}_{\text{Post}}$	$\delta^{15}\text{N}_{\text{Post}}$	$n_{\text{Post}}$
Zambezi	C3 producers	-29.1 $\pm$ 1.8	3.2 $\pm$ 3.2	9(1-3;1-5)	-29.4 $\pm$ 3.0	4.0 $\pm$ 0.3	2(2-3;2)
	C4 grasses	-12.7 $\pm$ 0.5	4.0 $\pm$ 1.6	8(2-3;1-5)	-12.8 $\pm$ 0.5	5.9 $\pm$ 1.5	9(2-3;1-5)
	Epiphytes	-25.3 $\pm$ 1.0	3.1 $\pm$ 1.0	1(3)	-26.0 $\pm$ 0.4	4.2 $\pm$ 0.5	1(3)
Rianila	C3 producers	-28.5 $\pm$ 0.3	3.3 $\pm$ 2.7	7(3;2-3)	-29.7 $\pm$ 0.9	4.2 $\pm$ 3.7	4(3;5)
	C4 grasses	-12.4 $\pm$ 0.2	3.5 $\pm$ 2.3	3(3;3)	-12.0 $\pm$ 0.3	2.3 $\pm$ 6.0	2(2-3;5)
	MPB†	-14.8 $\pm$ 0.4	1.8 $\pm$ 0.5	1(3)	-9.0 $\pm$ 0.3	-0.3 $\pm$ 0.1	1(3)
	Filamentous algae sp.1†	-20.5	3.0	1(1)	-21.4 $\pm$ 0.7	3.2 $\pm$ 0.3	1(3)
	Filamentous algae sp.2†	NA	NA	NA	-15.8 $\pm$ 0.1	3.5 $\pm$ 0.0	1
	Epiliths†	NC	NC	NC	-23.1 $\pm$ 0.5	4.4 $\pm$ 0.3	1(2)
	<i>Ruppia maritima</i>	-10.5 $\pm$ 0.3	5.6 $\pm$ 0.2	1(3;1)	NC	NC	NC
Submerged macrophytes	NA	NA	NA	-20.0 $\pm$ 1.8	3.1 $\pm$ 1.2	1(3;3)	
Ambila	C3 producers	-27.1 $\pm$ 0.8	-1.7 $\pm$ 2.8	2(2-3;5)	-29.8 $\pm$ 0.9	0.2 $\pm$ 2.9	4(2-3;5)
	C4 producers	NC	NC	NC	-12.4 $\pm$ 0.4	-0.4 $\pm$ 0.7	1(2;5)
	Periphyton†	-14.6 $\pm$ 0.1	0.2 $\pm$ 0.2	1(3)	-13.0 $\pm$ 0.1	0.4 $\pm$ 0.2	1(3)
	Epiphytes on reeds†	-25.3 $\pm$ 1.0	3.1 $\pm$ 0.5	3	-23.5 $\pm$ 0.9	3.7 $\pm$ 0.5	1(2;2)
	Macroalgae	-15.3 $\pm$ 1.6	3.1 $\pm$ 2.3	3(3;3)	NA	NA	NA
Betsiboka	C3 producers	-29.1 $\pm$ 0.3	5.0 $\pm$ 0.8	2(3-4;3)	-29.0 $\pm$ 0.5	5.0 $\pm$ 1.8	4(2-3;2-5)
	C4 grasses	-13.4 $\pm$ 0.6	1.5 $\pm$ 3.8	3(2-3;5-10)	-12.7 $\pm$ 0.1	9.1 $\pm$ 0.2	1(3;5)
	MPB†	-12.7	3.6	1(3)	-17.2 $\pm$ 0.6	13.6 $\pm$ 2.0	1(3;5)
	Epiphytes†	-18.3 $\pm$ 0.6	6.9 $\pm$ 0.3	1(3)	-24.8 $\pm$ 0.1	8.2 $\pm$ 0.1	1(3;5)
	Green filamentous algae†	-13.5	13.1	1(1)	-19.0 $\pm$ 0.6	6.5 $\pm$ 0.2	1(3)
	Epiliths†	-18.8	8.9	1(3)	NA	NA	NA
Tana	C3 producers	-28.6 $\pm$ 0.4	4.1 $\pm$ 3.9	3(1-2;3-5)	...	...	...
	MPB†	-16.6	4.3	1(3)	...	...	...
	Epiphytes†	-14.6 $\pm$ 0.8	13.7 $\pm$ 0.4	1(3)	...	...	...

Note: NA, not available; NC, not collected.  
 †Samples from different areas combined into one sample.

A). At each site, different consumer trophic guilds had different  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Table 5). There was a significant relationship between  $\delta^{13}\text{C}_{\text{DIC}}$  and consumer  $\delta^{13}\text{C}$  for planktivorous fish ( $R^2 = 0.63$ ,  $F_{1,7} = 11.936$ ,  $P = 0.0106$ ) but not for any of the other trophic guilds ( $P > 0.05$  in all cases) (Fig. 2A). On average, planktivorous fish had  $\delta^{13}\text{C}$  values  $12.9 \pm 2.2\text{‰}$  ( $\pm$ SD;  $n = 9$ ) lower than  $\delta^{13}\text{C}_{\text{DIC}}$ . No relationship between  $\delta^{13}\text{C}_{\text{ZP-C}}$  and consumer  $\delta^{13}\text{C}$  or between  $\delta^{13}\text{C}_{\text{DOC}}$  and

consumer  $\delta^{13}\text{C}$  (Fig. 2B) was found for any of the trophic guilds ( $P > 0.05$ ).

There were positive linear relationships between  $\delta^{13}\text{C}_{\text{POC}}$  and consumer  $\delta^{13}\text{C}$  (Fig. 2C) and between  $\delta^{15}\text{N}_{\text{PN}}$  and consumer  $\delta^{15}\text{N}$  for all trophic guilds (Fig. 3). In both cases, these relationships were similar for all trophic guilds, so ANCOVAs were used to test for differences in the relationship between guilds, after the assumptions of normality, homogeneity of varian-

Table 4. Measured ( $\delta^{13}\text{C}_{\text{ZP-M}}$ ) and lipid corrected ( $\delta^{13}\text{C}_{\text{ZP-C}}$ ) zooplankton carbon stable isotope composition,  $\delta^{15}\text{N}$  and C/N ratios. When  $n = 2$ , range is presented, and when  $n = 3$ , mean  $\pm$  SD is indicated.

Site	Season	$n$	$\delta^{13}\text{C}_{\text{ZP-M}}$ (‰)	$\delta^{13}\text{C}_{\text{ZP-C}}$ (‰)	$\delta^{15}\text{N}_{\text{ZP}}$ (‰)	ZP C/N ratio
Zambezi	Pre-wet	2	-19.5 to -19.1	-17.3 to -17.1	4.3 to 4.9	6.2 to 6.4
	Post-wet	2	-21.6 to -19.8	-19.7 to -16.6	3.4 to 3.6	8.8 to 8.9
Rianila	Pre-wet	1	-23.0	-19.8	2.6	8.7
	Post-wet	2	-24.1 to -23.3	-22.2 to -21.0	5.9 to 6.3	6.4 to 6.7
Ambila	Pre-wet	3	-22.3 $\pm$ 1.4	-20.5 $\pm$ 1.1	3.5 $\pm$ 0.3	6.1 $\pm$ 1.1
	Post-wet	3	-21.7 $\pm$ 0.0	-18.2 $\pm$ 0.0	2.7 $\pm$ 0.3	9.6 $\pm$ 0.0
Betsiboka	Pre-wet	...	...	...	...	...
	Post-wet	...	...	...	...	...
Tana	Short rains	3	-21.5 $\pm$ 0.3	-18.6 $\pm$ 0.3	11.1 $\pm$ 0.5	7.8 $\pm$ 0.1

Table 5. Mean consumer ( $\pm$  SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for invertebrates and fish of different trophic guilds (phytodetritivores, omnivores, planktivores, carnivores and piscivores) at each site and season.

Guild	Season	Zambezi	Rianila	Ambila	Betsiboka	Tana
$\delta^{13}\text{C}$						
Invert.	Pre	$-20.6 \pm 2.4$ (17)	$-21.3 \pm 2.8$ (12)	$-21.5 \pm 3.8$ (14)	$-14.5 \pm 2.5$ (28)	$-17.0 \pm 3.0$ (27)
	Post	$-22.0 \pm 1.9$ (15)	$-21.6 \pm 2.0$ (10)	$-21.1 \pm 4.1$ (19)	$-16.9 \pm 2.8$ (21)	NA
Phytod.	Pre	$-23.5 \pm 3.0$ (4)	$-22.1 \pm 4.2$ (6)	$-18.4 \pm 2.9$ (2)	$-13.3 \pm 2.5$ (4)	$-19.2 \pm 5.1$ (6)
	Post	$-23.2 \pm 3.0$ (10)	$-21.0 \pm 4.5$ (6)	$-18.7 \pm 2.6$ (4)	$-17.1 \pm 3.9$ (6)	NA
Omniv.	Pre	$-22.1 \pm 0.9$ (4)	NA	$-16.8 \pm 2.3$ (2)	NA	$-17.9$ (1)
	Post	$-20.0 \pm 2.1$ (3)	$-21.7 \pm 2.2$ (2)	$-20.5 \pm 4.6$ (4)	$-16.7$ (1)	NA
Planktiv.	Pre	$-18.9 \pm 2.7$ (4)	$-19.5 \pm 2.1$ (2)	$-22.1 \pm 3.2$ (2)	$-16.8 \pm 0.7$ (9)	$-19.0 \pm 2.3$ (8)
	Post	$-20.5 \pm 2.8$ (11)	$-19.4 \pm 1.0$ (3)	$-22.6 \pm 3.7$ (4)	$-17.2 \pm 1.5$ (15)	NA
Carniv.	Pre	$-21.5 \pm 2.2$ (16)	$-19.3 \pm 2.4$ (13)	$-17.7 \pm 2.5$ (5)	$-15.5 \pm 1.5$ (20)	$-17.8 \pm 1.3$ (11)
	Post	$-20.0 \pm 2.3$ (35)	$-19.6 \pm 2.4$ (18)	$-18.5 \pm 1.6$ (5)	$-16.5 \pm 2.0$ (42)	NA
Pisciv.	Pre	$-18.3 \pm 2.5$ (5)	$-21.6 \pm 2.4$ (6)	$-21.7 \pm 1.3$ (2)	$-15.8 \pm 0.8$ (11)	$-20.4 \pm 2.5$ (3)
	Post	$-18.9 \pm 1.9$ (7)	$-18.8 \pm 2.1$ (11)	$-20.5 \pm 1.4$ (3)	$-16.6 \pm 1.2$ (22)	NA
Unknown	Pre	NA	$-20.4 \pm 4.5$ (6)	NA	$-13.9 \pm 5.0$ (3)	$-20.6$ (1)
	Post	$-23.7 \pm 0.8$ (4)	NA	$-19.1 \pm 7.6$ (4)	$-16.0 \pm 5.6$ (6)	NA
$\delta^{15}\text{N}$						
Invert.	Pre	$7.8 \pm 1.4$	$7.0 \pm 1.2$	$5.9 \pm 1.6$	$10.5 \pm 1.9$	$10.5 \pm 2.2$
	Post	$6.9 \pm 2.0$	$6.7 \pm 1.4$	$6.1 \pm 1.2$	$8.7 \pm 1.3$	NA
Phytod.	Pre	$6.2 \pm 1.3$	$6.3 \pm 1.3$	$5.4 \pm 1.1$	$11.4 \pm 2.4$	$11.6 \pm 2.3$
	Post	$6.4 \pm 1.8$	$6.2 \pm 1.4$	$6.3 \pm 0.6$	$7.4 \pm 1.0$	NA
Omniv.	Pre	$9.0 \pm 0.4$	NA	$8.3 \pm 0.1$	NA	12.6
	Post	$9.8 \pm 1.1$	$8.4 \pm 0.5$	$8.3 \pm 1.0$	10.8	NA
Planktiv.	Pre	$10.5 \pm 1.8$	$10.2 \pm 2.2$	$8.6 \pm 0.2$	$11.3 \pm 1.1$	$12.3 \pm 1.6$
	Post	$10.1 \pm 1.0$	$8.8 \pm 0.6$	$8.6 \pm 0.7$	$10.8 \pm 1.2$	NA
Carniv.	Pre	$9.6 \pm 1.1$	$10.1 \pm 1.6$	$8.5 \pm 1.0$	$11.8 \pm 0.8$	$12.7 \pm 0.9$
	Post	$9.4 \pm 1.3$	$9.6 \pm 1.5$	$8.3 \pm 0.6$	$10.6 \pm 1.7$	NA
Pisciv.	Pre	$12.2 \pm 1.5$	$10.4 \pm 0.8$	$8.7 \pm 0.8$	$12.5 \pm 1.0$	$11.4 \pm 1.4$
	Post	$10.7 \pm 1.4$	$10.4 \pm 0.9$	$8.4 \pm 0.6$	$11.8 \pm 0.9$	NA
Unknown	Pre	NA	$8.2 \pm 0.9$	NA	$9.0 \pm 2.3$	12.9
	Post	$7.8 \pm 1.6$	NA	$7.4 \pm 1.1$	$9.6 \pm 2.3$	NA

Notes: Numbers in parentheses after the  $\delta^{13}\text{C}$  values are the number of trophic groups (species/size class) considered. NA, not available. Pre and Post indicate pre-wet season and post-wet season respectively.

es (Cochran C,  $P = 0.3608$  for  $\delta^{13}\text{C}$  and  $P = 0.3818$  for  $\delta^{15}\text{N}$ ) and parallelism between lines ( $P = 0.092$  for  $\delta^{13}\text{C}$  and  $P = 0.4825$  for  $\delta^{15}\text{N}$ ) were met. Only invertebrates and phytodetritivorous, planktivorous, carnivorous and piscivorous fish were considered, as omnivorous species were not present at all sites. For  $\delta^{13}\text{C}$ , this resulted in a significant model ( $R^2 = 0.36$ ,  $F_{5,39} = 4.4179$ ,  $P = 0.0028$ ), with a significant effect of  $\delta^{13}\text{C}_{\text{POC}}$  on consumer  $\delta^{13}\text{C}$  ( $P < 0.0001$ ), but no effect of trophic guild ( $P = 0.7087$ ), meaning that the relationships between  $\delta^{13}\text{C}_{\text{POC}}$  and consumer  $\delta^{13}\text{C}$  were similar for all trophic guilds. The overall equation describing this relationship is:  $\delta^{13}\text{C}_{\text{consumer}} = 0.68 \times \delta^{13}\text{C}_{\text{POC}} - 2.62$  (Fig. 2C). For  $\delta^{15}\text{N}$ , the ANCOVA also resulted in a significant model ( $R^2 = 0.62$ ,  $F_{5,39} = 12.974$ ,  $P < 0.0001$ ) with an effect of both  $\delta^{15}\text{N}_{\text{PN}}$  and trophic guild on consumer  $\delta^{15}\text{N}$  ( $P < 0.0001$  in both cases). Since the regression lines for the five trophic guilds were parallel, trophic guild can only have an effect on the intercept of the relationship, i.e., on

the height of the regression lines, which is related to trophic position. The overall regression equation was:  $\delta^{15}\text{N}_{\text{consumer}} = 0.34 \times \delta^{15}\text{N}_{\text{PN}} + \text{TG}_{\text{intercept}}$  where TG is trophic guild. The value of the intercepts agreed well with consumer trophic position: phytodetritivorous fish had the lowest intercept (5.8‰), followed by invertebrates (6.1‰), planktivorous and carnivorous fish had similar intercepts of 8.5‰ and 8.4‰ respectively, and piscivorous fish had the highest intercept of 9.1‰ (Fig. 3).

### Stable isotope mixing models

Bayesian mixing model results are graphically presented for phytodetritivorous and carnivorous fish for illustration (Fig. 4), and results for all trophic guilds are presented in Appendices B and C. The importance of C3, C4 and aquatic primary producers differed between trophic guilds, sites and seasons (Appendices B and C). For the C4-dominated Betsiboka and Tana, C4 producers were the main sources for all trophic



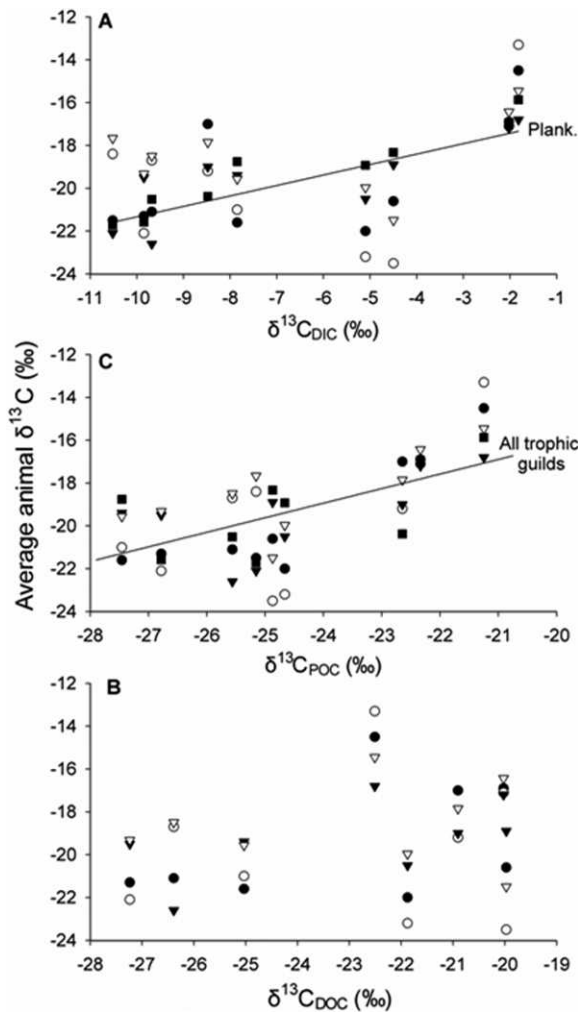


Fig. 2. Relationship between (A)  $\delta^{13}\text{C}_{\text{DIC}}$  and consumer  $\delta^{13}\text{C}$ , (B)  $\delta^{13}\text{C}_{\text{DOC}}$  and consumer  $\delta^{13}\text{C}$  and (C)  $\delta^{13}\text{C}_{\text{POC}}$  and consumer  $\delta^{13}\text{C}$ . In (A), line represents the regression equation between  $\delta^{13}\text{C}_{\text{DIC}}$  and planktivorous fish, the only significant relationship found ( $\delta^{13}\text{C}_{\text{consumer}} = 0.46 \times \delta^{13}\text{C}_{\text{DIC}} - 16.50$ ;  $R^2 = 0.36$ ,  $F_{5,39} = 4.4179$ ,  $p = 0.0028$ ). In (C), line represents the best fit for data from all trophic guilds ( $\delta^{13}\text{C}_{\text{cons}} = 0.68 \times \delta^{13}\text{C}_{\text{POC}} - 2.62$ ;  $R^2 = 0.53$ ,  $F_{4,31} = 8.769$ ,  $p < 0.0001$ ), as no differences between guilds were detected by ANCOVA.

guilds (Fig. 4; Appendix B). C4 sources contributed up to 61–84% (95% credibility interval (CI)) to phytodetritivorous fish at the Betsiboka, and up to 56–78% for phytodetritivores at the Tana (Fig. 4; Appendix B). For the Betsiboka, planktonic producers could also be important, but

these had wide 95% CI, that often included 0%. C3 producers were generally of low importance with 95% CI that included 0%, but had some importance for planktivorous (16–35%) and piscivorous fish (14–33%) at the pre-wet season (Appendix B). At the Tana, planktonic sources were also important for all trophic guilds, contributing up to 12–41% for phytodetritivorous fish, while C3 producers had some contribution for all trophic guilds with the exception of phytodetritivores (Appendix B).

For the C3-dominated estuaries, consumers relied on a combination of sources, both terrestrial and aquatic (Fig. 4; Appendix C). In the Zambezi, where aquatic sources were more limited than at the C4-dominated estuaries, both C3 and C4 producers were important for all trophic guilds. C3 sources had the greatest contribution of 45–69% for phytodetritivorous fish in pre-wet season, and C4 sources had the greatest importance of 53–73% for a group of piscivores at the post-wet season (Fig. 4; Appendix C). Plankton was also important for all trophic guilds, although the 95% CI were generally wide and often include 0%, meaning it is not possible to be certain about the contributions of this source.

For the Rianila and Ambila, where a range of aquatic producers was available, terrestrial sources had some importance, but this was much lower than in the Zambezi or the two C4-dominated estuaries (Fig. 4; Appendix C). At Rianila, no single source dominated and consumers seemed to rely to some extent on both C3 and on a combination of aquatic sources (Fig. 4; Appendix C). C3 producers were important for consumers of all trophic guilds at both seasons, contributing up to 11–50% for phytodetritivorous fish in the pre-wet season, for example (Appendix C). This importance decreased from the pre- to the post-wet season for phytodetritivorous fish, but increased for carnivorous fish, while for the remaining guilds there was no seasonality in this importance (Fig. 4; Appendix C). At Ambila, in addition to C3, C4 sources also had some importance for carnivorous and piscivorous fish, and this importance increased from the pre- to the post-wet season, when an importance of 10–50% for carnivorous fish was present, for example (Fig. 4; Appendix C).

For all trophic groups considered, there were

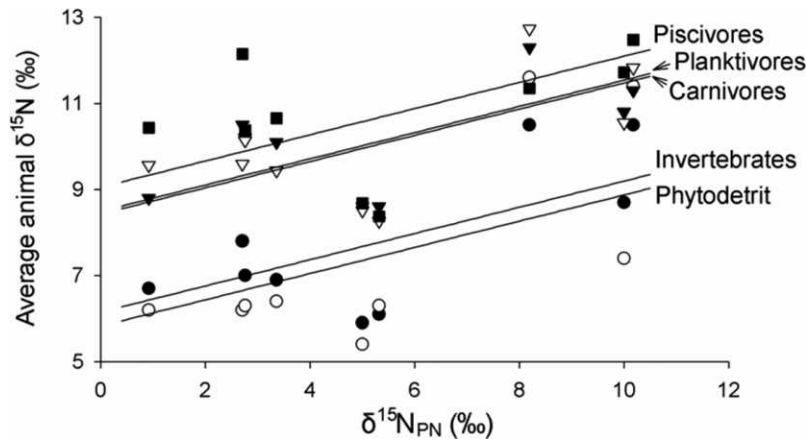


Fig. 3. Relationship between  $\delta^{15}\text{N}_{\text{PN}}$  and consumer  $\delta^{15}\text{N}$ . Black circles: invertebrates; white circles: phytodetritivorous fish; black triangles: planktivorous fish; white triangles: carnivorous fish; black squares: piscivorous fish. Lines indicate best fit for each trophic guild (TG) based on the average data per site/season, following results from ANCOVA:  $\delta^{15}\text{N}_{\text{cons}} = 0.304 \times \delta^{15}\text{N}_{\text{PN}} + \text{TG}_{\text{int}}$  ( $R^2 = 0.62$ ,  $F_{5,39} = 12.974$ ,  $p < 0.0001$ ), where  $\text{TG}_{\text{int}} = 5.8\text{‰}$  for phytodetritivorous fish,  $6.1\text{‰}$  for invertebrates and  $8.5\text{‰}$  for planktivorous,  $8.4\text{‰}$  for carnivorous and  $9.1$  for piscivorous fish.

strong positive relationships between the estimated proportion of C4 cover in the catchments and the importance of C4 producers to consumers as estimated using the Bayesian mixing models ( $P < 0.05$  in all cases; Fig. 5A), but there were no significant relationships with the estimated importance of C3 sources (Fig. 5B).

## DISCUSSION

### Variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Stable isotope results agreed well with the gradient in dominant vegetation (C3 vs. C4) and impacts (urbanisation, farmland) in the rivers' catchments, illustrating that rivers are energetically linked from the catchment to the estuary. For example,  $\delta^{13}\text{C}_{\text{POC}}$  was higher in the Betsiboka and Tana, indicating that the C4 grasslands from the catchment contribute significantly to the POC pool (Bouillon et al. 2007, Ralison et al. 2008, Bouillon et al. 2009), and even though there are large areas of C3 mangroves in the Tana estuary,  $\delta^{13}\text{C}_{\text{POC}}$  at this site was higher than that from the C3-dominated sites. Also, in these two highly turbid estuaries, %POC values were low (1.2–2.1%), indicating that most suspended material was refractory. Previous chlorophyll *a* data indeed indicate that the contribution of phytoplankton to POC in these estuaries is low

(Bouillon et al. 2007, Ralison et al. 2008), implying that  $\delta^{13}\text{C}_{\text{POC}}$  mostly reflects  $\delta^{13}\text{C}$  of terrestrial producers. In the less turbid sites of Rianila and Ambila, %POC was relatively high (22.2–40.5%), consistent with previous large-scale studies showing an inverse relationship between TSM and %POC (e.g., Meybeck 1982). High %POC values can reflect either a higher contribution of phytoplankton production, or a higher contribution of litter inputs (direct litter inputs or soil humus layer inputs). The higher POC/PN ratios in the Rianila and Ambila (9.8–11.8) support the latter case. In the Zambezi, a POC/PN ratio of 6.0–6.6 coupled with intermediate %POC (7.7%) could indicate that organic matter in this estuary is mostly of autochthonous origin.

$\delta^{15}\text{N}_{\text{PN}}$  values were also related to the environmental conditions in the catchments as  $\delta^{15}\text{N}_{\text{PN}}$  was higher at the two C4-dominated than at the three C3-dominated estuaries. High plant  $\delta^{15}\text{N}$  are generally associated with hot and dry environments such as in the semi-arid Tana and the grass-dominated Betsiboka catchments (Craine et al. 2009, Pardo and Nadelhoffer 2010). At the Betsiboka, high  $\delta^{15}\text{N}_{\text{PN}}$  could also result from the input of domestic sewage and animal manure (McClelland and Valiela 1997, Schlacher et al. 2005), material characterised by high  $\delta^{15}\text{N}$ ,

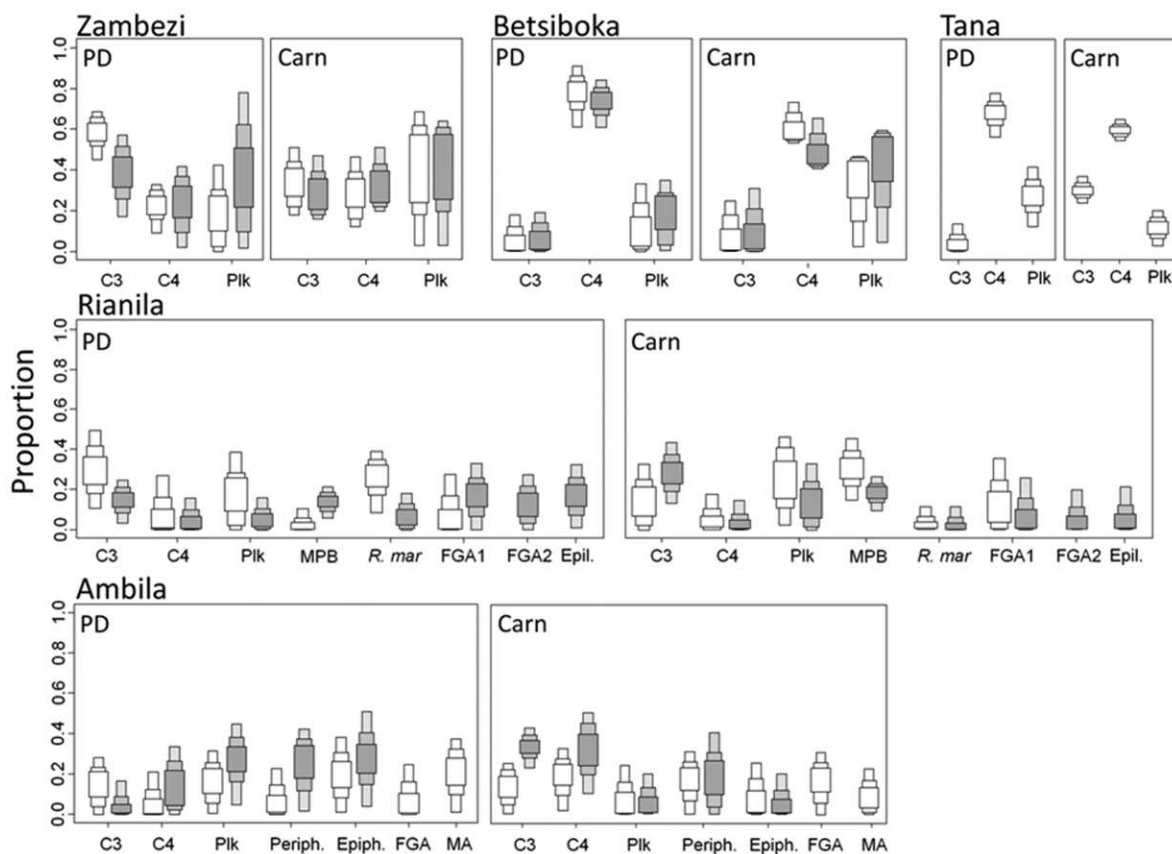


Fig. 4. Bayesian mixing model solutions for the proportions of C3, C4 and aquatic producers for phytotritivorous (PD) and carnivorous (Carn) fish from the different sites at the pre-wet (white boxes) and post-wet (grey boxes) seasons. Boxes indicate the 50%, 75% and 95% Bayesian credibility intervals. Epil = epiliths; Epiph = epiphytes; FGA = filamentous green algae; MA = macroalgae; MPB = microphytobenthos; Periph = periphyton; Plk = plankton, *R. mar.* = *Ruppia maritima*.

often >10% (Bateman and Kelly 2007). Mahajanga City, in the Betsiboka estuary, is one of the largest cities in Madagascar and cattle are abundant throughout the river's catchment.

There was however no relationship between  $\delta^{13}C_{ZP}$  and  $\delta^{13}C_{POC}$  or  $\delta^{13}C_{DIC}$  and  $\delta^{13}C_{ZP}$  was not related to the dominant vegetation in the catchments. This could be because zooplankton feeds selectively, preferring phytoplankton but assimilating both phytoplankton and detritus, depending on availability (Cole et al. 2006, Schlacher et al. 2009). Since the five estuaries differed greatly in turbidity and relative availability of phytoplankton and terrestrial detritus, the contribution of these two sources to zooplankton differed greatly between sites, and the absence of a relationship between  $\delta^{13}C_{ZP}$  and

$\delta^{13}C_{POC}$  or  $\delta^{13}C_{DIC}$  was not unexpected.

As with  $\delta^{13}C_{POC}$  and  $\delta^{15}N_{PN}$ , consumers from the Betsiboka and Tana had higher  $\delta^{13}C$  and  $\delta^{15}N$  than consumers from the remaining three sites. The fact that  $\delta^{13}C_{POC}$  and  $\delta^{15}N_{PN}$  agreed strongly with the dominant type of vegetation in the catchment ( $\delta^{13}C$  and  $\delta^{15}N$ ) and with impacts ( $\delta^{15}N$ ), together with the presence of strong relationships between  $\delta^{13}C_{POC}$  and consumer  $\delta^{13}C$  and between  $\delta^{15}N_{PN}$  and consumer  $\delta^{15}N$  for consumers over a range of trophic ecologies and across systems with different conditions, indicates that terrestrial detritus is incorporated into estuarine food webs. It also shows that this material is transported through several trophic links up to high trophic level fish, and does not only affect species feeding on basal sources like

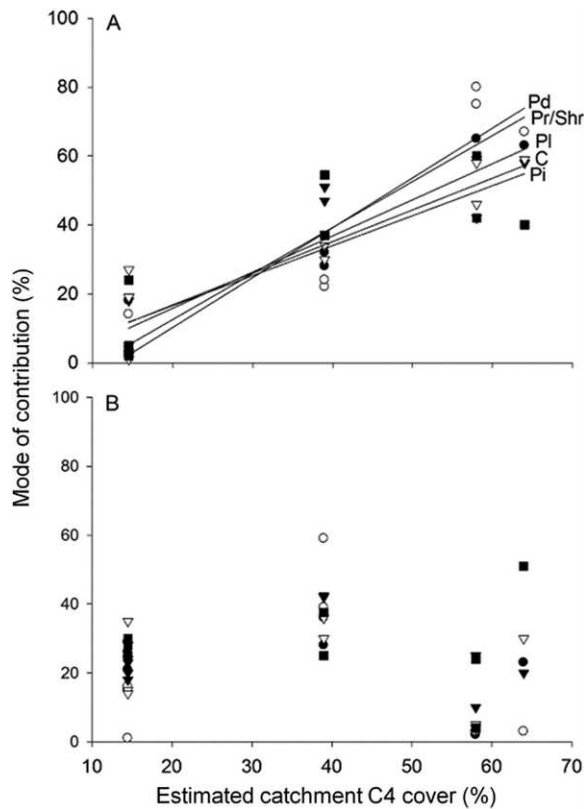


Fig. 5. Relationships between the estimated proportion of C4 vegetation cover in each catchment and the mode of the contribution (based on Bayesian mixing models) of (A) C4 and (B) C3 sources for prawns and shrimps (black circles), phytodetritivorous fish (white circles), planktivorous fish (black triangles), carnivorous fish (white triangles) and piscivorous fish (black squares). Significant relationships are indicated in (A): prawns and shrimps:  $R^2 = 0.93$ ,  $p < 0.0001$ ; phytodetritivorous fish:  $R^2 = 0.92$ ,  $p < 0.0001$ ; planktivorous fish:  $R^2 = 0.82$ ,  $p = 0.0008$ ; carnivorous fish:  $R^2 = 0.83$ ,  $p = 0.0006$ ; piscivorous fish:  $R^2 = 0.70$ ,  $p = 0.0051$ . There was no relationship between C4 cover and the importance of C3 sources of any trophic guild (B).

detritus or algae.

For the Tana estuary, despite the great expanses of C3 mangroves that occur in the estuary, C4 producers were often the most important sources, with contributions as high as 40–59% for carnivorous fish, for example (see Appendix B). This illustrates that it is important to consider the vegetation in the catchment well above the estuaries and deltas as potential sources in stable

isotope studies of estuarine food webs. For example, if catchment vegetation was not considered in the mixing models, high consumer  $\delta^{13}\text{C}$  at the Tana would be interpreted as resulting from a greater incorporation of planktonic algae. This is however not the case as POC in this system is mostly detrital (up to 90%; Bouillon et al. 2009), and due to very high sediment loads aquatic primary production is limited (Robertson and Blaber 1992, Bouillon et al. 2007, Bouillon et al. 2009). Although MPB (characterised by high  $\delta^{13}\text{C}$  (Clementz and Koch 2001)) can be the most important aquatic producers in turbid estuaries (MacIntyre et al. 1996, Underwood and Kromkamp 1999), high consumer  $\delta^{13}\text{C}$  in the Tana, as in the Betsiboka, is also not likely to be a result of a reliance on these algae as the area available for benthic production is limited due to high turbidity, meaning that MPB can only photosynthesise at low tide, but for most of this period they are subjected to photosynthesis-limiting factors such as variations in light, temperature, salinity and to desiccation (Admiraal 1984).

#### Mixing models

Mixing models were useful to identify and quantify the importance of terrestrial material for estuarine consumers. Results agreed well with the type and dominance of terrestrial vegetation, indicating that terrestrial producers are important for estuarine food webs. However, this importance depends on factors such as turbidity and availability of aquatic sources. For example, at the highly turbid C4-dominated Betsiboka, where C3 producers are scarce and waters very turbid, C4 material was the most important contributor to animal nutrition. While the input of nutrients with flood waters can stimulate primary and secondary production (Mortazavi et al. 2000, Hoover et al. 2006), in systems like the Betsiboka, where erosion is high, this input is accompanied by an increase in suspended solids, thus increasing turbidity and limiting aquatic productivity (May et al. 2003, Mead and Wiegner 2010). Hence, organic carbon was mainly derived from erosion from the C4-dominated catchment. At the Tana estuary, where extensive areas of mangrove forest are present and where waters are less turbid, mixing models indicate that consumers rely on a combination of C3, C4 and



planktonic sources.

Again in agreement with the dominant catchment vegetation, C3 producers were important for aquatic consumers from the Zambezi, and were indeed the most important sources for several trophic guilds (see Appendix C). At the C3-dominated Rianila and Ambila, however, a wide range of aquatic producers was available (e.g., periphyton and filamentous green algae) so consumers relied on a combination of sources, and C3 producers were not as important as at the Zambezi estuary, where aquatic sources were less available. This is consistent with the highest importance of imported material for areas where there are large differences in productivity between the donor and recipient habitats and when productivity in the recipient habitat is low (Polis and Hurd 1996, Polis et al. 1997, Cadenasso et al. 2003). Nevertheless, there was evidence for incorporation of C3 material at both the Rianila and Ambila, and there was an increased importance of C3 (Ambila and Rianila) and C4 (Ambila) producers for carnivorous fish. These increases can, at least partially, result from the input of terrestrial material through the transport of terrestrial invertebrates (e.g., ants, spiders, grasshoppers) with the wind and flood waters into the waterways, where they subsidize the diets of carnivorous fish. These invertebrates can be of crucial importance to those fish diets (Nakano and Murakami 2001, Sullivan et al. 2012), and seasonal variations in this importance have been reported for other tropical areas (e.g., Wantzen et al. 2002, Balcombe et al. 2005).

It is however interesting to note that at the Rianila, the importance of C3 producers for phytodetritivorous fish decreased slightly after the wet season, despite the expected transport of material of C3 terrestrial origin with the rain waters. This is probably because at the post-wet season aquatic producers such as periphyton and filamentous green algae were much more abundant. The phytodetritivorous tilapids that occurred at these sites, including *Oreochromis mossambicus*, *Oreochromis niloticus* and *Tilapia rendalli* (see Appendix A) have flexible diets and feed on detritus or algae depending on availability (Lowe-McConnell 2000). So, it is likely that they fed mostly on algae during the post-wet season, when these were readily available, rather than relying on less nutritive terres-

trial detritus, and this led to a decrease in importance of C3 sources.

It is also important to consider that besides terrestrial subsidies, estuaries can also receive inputs from other coastal habitats, as for example seagrass and/or seaweed detritus transported by currents and waves. Although this material was not identified during the study period, it could be important, especially after strong winds (Heck et al. 2008). However, because strong wind events are not regular, because no extensive macrophyte beds are present in the vicinities of the studied estuaries and because sampling was conducted in the inside of the estuaries, these marine subsidies are not likely to be important for the estuarine animal communities studied.

### Conclusion

This large-scale study demonstrates that terrestrial subsidies are important for aquatic food webs in east African estuaries. Carbon of terrestrial origin is transferred through several trophic links, from invertebrates to higher trophic level fish, and its influence is not limited to low trophic level species such as detritivores. Also, while in clear systems, where aquatic producers are abundant, food webs rely on a combination of terrestrial and aquatic sources, in highly turbid systems there is a stronger dependence on organic matter transported by rivers. The ecological health of the overall catchment therefore directly affects the downstream estuaries at the most fundamental level, and activities that alter the turbidity and productivity of rivers and estuaries (e.g., river regulation, removal of riparian vegetation, deforestation and conversion of land to grazing land) affect food webs well beyond the area of impact (Bernardes et al. 2004). This implies that rivers, along with their catchments and estuaries should be managed as open systems.

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## SUPPLEMENTAL MATERIAL

## APPENDIX A

Table A1. Trophic guild, size range and stable isotope composition (mean  $\pm$  SE) of consumers collected at each site and season. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and molluscs, and carapace width for crabs.  $n$  = Number of samples analysed followed (in brackets) by the number of individuals or range in number of individuals included in each sample. H, herbivore; MPB, microphytobentos feeder; PD, phytodetritivore; O, omnivore; PI, planktivore; C, carnivore; Pi, piscivore; Uk, unknown diet.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$n$
Zambezi						
Pre-Wet ( $n = 50$ )						
Invertebrates ( $n = 17$ )						
Palaemonidae	<i>Macrobrachium rosenbergii</i>	O	120–245	$-21.0 \pm 0.8$	$8.2 \pm 0.2$	6(1–5)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	60–65	$-21.9 \pm 0.7$	$9.2 \pm 0.0$	3(1)
Palaemonidae	<i>Macrobrachium</i> sp. 2	O	50–70	$-20.6 \pm 0.2$	$8.8 \pm 0.5$	2(1)
Palaemonidae	<i>Palaemonetes</i> sp. 1	O	30–35	$-23.5 \pm 0.5$	$7.8 \pm 0.2$	3(3)
Palaemonidae	<i>Palaemonetes</i> sp. 2	O	40–45	$-17.7 \pm 0.4$	$10.7 \pm 0.0$	3(2)
Palaemonidae	NI Palaemonid sp. 1	O	100	$-15.5$	$8.6$	1(1)
Palaemonidae	NI Palaemonid sp. 2	O	50–65	$-20.4 \pm 0.3$	$9.3 \pm 0.1$	4(1)
Penaeidae	<i>Metapenaeus monoceros</i>	O	35–45	$-20.3 \pm 0.1$	$6.6 \pm 0.0$	3(15)
Penaeidae	<i>Metapenaeus stebbingi</i>	O	55–68	$-21.3 \pm 0.3$	$7.3 \pm 0.2$	3(1)
Penaeidae	<i>Penaeus indicus</i>	O/C	50–70	$-21.1 \pm 0.2$	$6.1 \pm 0.1$	3(15)
Penaeidae	<i>Penaeus monodon</i>	O/C	85–110	$-20.9 \pm 0.6$	$8.1 \pm 0.4$	3(3)
Penaeidae	<i>Penaeus semisulcatus</i>	O	60	$-22.7$	$7.0$	1(1)
Portunidae	<i>Scylla serrata</i>	C	65	$-15.6$	$8.2$	1(1)
Portunidae	<i>S. serrata</i>	C	90–110	$-19.2 \pm 0.8$	$7.8 \pm 0.1$	3(1)
Potamididae	<i>Cerithidea decollata</i>	PD	25–28	$-24.4 \pm 0.0$	$4.8 \pm 0.0$	3(3)
Sesarmidae	<i>Chironantes eulimene</i>	H/O	25	$-22.1 \pm 0.1$	$7.9 \pm 0.3$	3(2)
Sesarmidae	<i>Perisesarma guttatum</i>	H/O	17–20	$-21.4 \pm 0.0$	$6.4 \pm 0.1$	3(15)
Fish ( $n = 33$ )						
Ambassidae	<i>Ambassis ambassis</i>	PI	50–100	$-22.8 \pm 0.2$	$9.9 \pm 0.1$	7(5–15)
Carangidae	<i>Parastrumateus niger</i>	PI	130–160	$-18.1 \pm 0.5$	$8.7 \pm 0.2$	3(1)
Carangidae	<i>Caranx ignobilis</i>	Pi	210–300	$-21.4 \pm 0.3$	$10.2 \pm 0.2$	4(1)
Carangidae	<i>Scomberoides commersonianus</i>	Pi	160–200	$-16.7 \pm 0.3$	$12.3 \pm 0.1$	3(1)
Carcharhinidae	<i>Rhizoprionodon acutus</i>	Pi	750–800	$-16.1 \pm 0.2$	$14.4 \pm 0.6$	2(1)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	115–145	$-24.6 \pm 0.5$	$5.8 \pm 0.1$	4(3)
Clariidae	<i>Clarias gariepinus</i>	C	300–350	$-24.3 \pm 0.1$	$8.4 \pm 0.2$	4(1)
Clupeidae	<i>Sardinella albella</i>	PI	150–160	$-17.5 \pm 0.6$	$10.5 \pm 0.2$	3(2)
Cynoglossidae	<i>Cynoglossus</i> sp.	C	180	$-18.3$	$10.6$	1(1)
Cyprinidae	<i>Labeo altivelis</i>	H	155–270	$-19.1 \pm 0.2$	$4.6 \pm 0.1$	4(1–2)
Distichodontidae	<i>Distichodus schenga</i>	O	105–125	$-21.2 \pm 0.0$	$9.0 \pm 0.3$	2(1)
Distichodontidae	<i>Distichodus</i> sp.	O	110–120	$-21.5 \pm 0.4$	$8.7 \pm 0.1$	2(1)
Drepaneidae	<i>Drepane longimana</i>	C	50	$-20.0$	$10.1$	1(1)
Eleotridae	<i>Butis butis</i>	C	100–120	$-22.7 \pm 1.0$	$8.9 \pm 0.3$	3(1)
Engraulidae	<i>Thryssa vitrirostris</i>	PI	80–180	$-17.0 \pm 0.2$	$13.0 \pm 0.1$	6(3–4)
Gobiidae	<i>Glossogobius giuris</i>	C	30	$-23.7$	$7.6$	1(1)
Gobiidae	<i>G. giuris</i>	C	120–250	$-19.2 \pm 0.6$	$8.9 \pm 0.2$	6(1–5)
Haemulidae	<i>Pomadasys argenteus</i>	C	400	$-20.7$	$11.1$	1(1)
Haemulidae	<i>Pomadasys kaakan</i>	C	230	$-23.1$	$9.8$	1(1)
Leiognathidae	<i>Leiognathus equulus</i>	C	70–100	$-22.6 \pm 0.4$	$9.6 \pm 0.2$	4(1)
Mochokidae	<i>Synodontis zambezensis</i>	O	60	$-23.0$	$8.8$	1(1)
Mochokidae	<i>S. zambezensis</i>	O	100–110	$-22.8 \pm 0.6$	$9.7 \pm 0.1$	4(1)
Mugilidae	<i>Liza macrolepis</i>	PD	145–150	$-25.8 \pm 0.3$	$7.6 \pm 0.2$	4(1)
Mugilidae	<i>Valamugil</i> sp.	PD	105–110	$-24.3 \pm 0.5$	$6.9 \pm 0.4$	4(1)
Schilbeidae	<i>Schilbe intermedius</i>	Pi	130–150	$-21.9 \pm 0.5$	$9.8 \pm 0.1$	3(1)
Schilbeidae	<i>Scomber japonicus</i>	Pi	160–235	$-16.7 \pm 0.2$	$12.4 \pm 0.3$	3(1)
Sciaenidae	<i>Atrobucca nibe</i>	C	60–70	$-24.8 \pm 0.2$	$8.0 \pm 0.2$	2(1)
Sciaenidae	<i>A. nibe</i>	C	110–140	$-20.6 \pm 1.1$	$10.7 \pm 0.3$	3(3)
Serranidae	<i>Epinephelus coioides</i>	C	300–410	$-20.7 \pm 0.3$	$11.5 \pm 0.1$	4(1–2)
Sillaginidae	<i>Sillago sihama</i>	C	170–180	$-23.8 \pm 0.2$	$9.2 \pm 0.1$	3(5)
Sillaginidae	<i>S. sihama</i>	C	50–70	$-19.8 \pm 0.4$	$9.6 \pm 0.5$	3(1)
Sparidae	<i>Acanthopagrus berda</i>	C	150–300	$-20.1 \pm 1.2$	$10.0 \pm 0.7$	2(2)
Teraponidae	<i>Terapon jarbua</i>	C	960–150	$-18.2 \pm 0.2$	$11.3 \pm 0.3$	6(2–3)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Post-wet ( <i>n</i> = 85)						
Invertebrates ( <i>n</i> = 15)						
Alpheidae	NI Alpheid	Uk	47-50	-21.4 ± 0.2	6.1 ± 0.1	2(1)
Littorinidae	<i>Littoraria scabra</i>	H	13-16	-19.9 ± 0.1	1.3 ± 0.0	4(5)
Palaemonidae	<i>Macrobrachium rosenbergii</i>	O	60-220	-22.7 ± 0.4	8.1 ± 0.2	6(2-4)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	70	-23.1	8.9	1(1)
Palaemonidae	<i>Macrobrachium</i> sp. 2	O	80-85	-23.2 ± 1.0	8.8 ± 0.3	2(1)
Palaemonidae	<i>Palaemonetes</i> sp. 1	O	30-40	-22.5 ± 0.2	8.8 ± 0.2	3(2)
Penaeidae	<i>Metapenaeus monoceros</i>	O	30-65	-19.8 ± 0.5	7.1 ± 0.1	7(1-6)
Penaeidae	<i>Metapenaeus stebbingi</i>	O	50-60	-25.6 ± 0.3	7.5 ± 0.1	3(1-2)
Penaeidae	<i>Penaeus esculentus</i>	O	75-80	-25.5 ± 0.2	4.9 ± 0.1	3(1)
Penaeidae	<i>Penaeus indicus</i>	O	25-30	-20.1 ± 0.7	7.2 ± 0.1	5(3-4)
Penaeidae	<i>Penaeus semisulcatus</i>	O	70-130	-21.9 ± 0.6	7.9 ± 0.4	4(2)
Portunidae	<i>Scylla serrata</i>	C	100-110	-21.2 ± 0.3	8.2 ± 0.2	4(2)
Potamididae	<i>Cerithidea decollata</i>	PD	20-30	-22.1 ± 0.2	5.7 ± 0.2	4(5)
Sesarmidae	<i>Perisesarma guttatum</i>	H/O	16-23	-20.7 ± 0.1	8.0 ± 0.0	3(2-3)
Sesarmidae	Sesarmid juveniles	H	6-9	-20.1 ± 0.2	5.5 ± 0.1	3(3-4)
Fish ( <i>n</i> = 70)						
Alestidae	<i>Hydrocynus vittatus</i>	Pi	110-305	-22.2 ± 0.4	9.9 ± 0.2	4(1-3)
Ambassidae	<i>Ambassis ambassis</i>	PI	40-140	-22.9 ± 0.4	10.0 ± 0.1	7(2-8)
Atherinidae	<i>Atherinomorus lacunosus</i>	PI	40-45	-24.3 ± 0.1	8.8 ± 0.0	3(6-7)
Carangidae	NI Carangid sp. 1	C	55-85	-17.7 ± 0.2	7.7 ± 0.2	3(2-3)
Carangidae	NI Carangid sp. 2	C	60	-18.2	7.7	1(1)
Carangidae	NI Carangid juvs	C	45	-17.0	7.1	1(1)
Carangidae	<i>Caranx ignobilis</i>	C	45-70	-19.1 ± 0.2	9.7 ± 0.4	4(5)
Carangidae	NI Carangid sp. 3	Pi	120	-21.5	9.6	1(1)
Carangidae	<i>Caranx ignobilis</i>	Pi	140-420	-20.6 ± 0.1	10.4 ± 0.2	6(2-4)
Carangidae	<i>Scomberoides commersonianus</i>	Pi	70-130	-17.8 ± 0.4	11.2 ± 0.1	5(3)
Carangidae	<i>Scomberoides lysan</i>	Pi	100-140	-18.0 ± 0.6	11.0 ± 0.1	3(1)
Chanidae	<i>Chanos chanos</i>	PD	95-200	-24.5 ± 1.3	5.0 ± 0.4	5(1)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	90-120	-21.8 ± 0.3	3.5 ± 0.1	2(7)
Cichlidae	<i>O. mossambicus</i>	PD	140-165	-27.5 ± 0.5	4.9 ± 1.1	2(5)
Cichlidae	NI Cichlid	Uk	80-90	-24.9 ± 1.8	5.8 ± 0.4	3(1-2)
Clariidae	<i>Clarias gariepinus</i>	C	180-195	-24.1 ± 0.3	5.5 ± 0.2	2(1)
Clariidae	<i>C. gariepinus</i>	C	300-310	-22.0 ± 0.4	6.9 ± 0.2	2(1)
Clupeidae	<i>Hilsa keele</i>	PI	50-110	-17.9 ± 0.1	9.7 ± 0.1	5(2-4)
Clupeidae	<i>Sardinella albella</i>	PI	50	-22.0 ± 0.4	9.3 ± 0.0	2(2)
Clupeidae	<i>S. albella</i>	PI	100-110	-17.5 ± 0.3	9.9 ± 0.1	5(2)
Clupeidae	<i>Spratellomorpha bianalis</i>	PI	40-45	-23.9 ± 0.1	9.0 ± 0.1	4(6-7)
Cynoglossidae	<i>Cynoglossus</i> sp.	C	100-120	-22.4 ± 0.3	9.5 ± 0.0	3(1)
Cyprinidae	<i>Labeo cylindricus</i>	H	90-175	-23.0 ± 0.6	4.9 ± 0.2	3(1-2)
Distichodontidae	<i>Distichodus mossambicus</i>	O	140	-20.8	8.9	1(1)
Drepaneidae	<i>Drepane longimana</i>	C	65-70	-15.8 ± 0.7	10.7 ± 0.1	2(1)
Eleotridae	<i>Eleotris</i> sp.	C	55-82	-20.5 ± 0.4	9.4 ± 0.1	2(1)
Elopidae	<i>Elops machnata</i>	C	150-260	-21.5 ± 0.3	8.9 ± 0.3	5(3-5)
Engraulidae	<i>Engraulis</i> sp.	PI	70-90	-17.6 ± 0.4	11.2 ± 0.1	3(2)
Engraulidae	<i>Thryssa vitrirostris</i>	PI	80	-18.1	9.7	1(1)
Engraulidae	<i>T. vitrirostris</i>	PI	100-110	-17.8 ± 0.5	12.0 ± 0.3	4(2-3)
Gerreidae	<i>Gerres filamentosus</i>	C	80-90	-16.4 ± 0.2	10.6 ± 0.2	3(5)
Gerreidae	<i>G. filamentosus</i>	C	65	-18.8 ± 0.5	11.0 ± 0.0	2(1)
Gobiidae	<i>Glossogobius giuris</i>	C	65	-19.3 ± 0.4	9.6 ± 0.3	2(1)
Gobiidae	<i>G. giuris</i>	C	90-200	-21.6 ± 0.7	8.4 ± 0.2	4(2-4)
Gobiidae	<i>Periophthalmus</i> sp.	C	60-65	-23.0 ± 0.1	9.6 ± 0.1	3(2)
Gobiidae	NI Gobiidae 1	Uk	55-65	-23.1 ± 0.5	8.2 ± 0.2	2(1-2)
Gobiidae	NI Gobiidae 2	Uk	50-60	-23.2 ± 0.4	7.4 ± 0.1	2(1)
Gobiidae	NI Gobiidae 3	Uk	70	-23.6	9.7	1(1)
Haemulidae	<i>Pomadasys argenteus</i>	C	65-100	-18.0 ± 0.4	10.9 ± 0.1	3(2)
Haemulidae	<i>Pomadasys kaakan</i>	C	75-80	-20.1 ± 0.1	10.3 ± 0.2	3(2-3)
Haemulidae	<i>Pomadasys olivaceus</i>	C	75-120	-20.5 ± 0.7	10.6 ± 0.1	3(2)
Hemiramphidae	<i>Hyporhamphus</i> sp.	H/PI	110.0	-20.2 ± 2.0	10.4 ± 0.6	2(1)
Leiognathidae	<i>Leiognathus equulus</i>	C	45-80	-21.7 ± 0.3	10.1 ± 0.1	3(5-8)
Leiognathidae	<i>L. equulus</i>	C	90-110	-19.5	10.7	1(1)
Lobotidae	<i>Lobotes surinamensis</i>	C	120	-19.7	9.6	1(1)
Lobotidae	<i>L. surinamensis</i>	C	250	-16.5	13.1	1(1)
Lutjanidae	<i>Lutjanus argentimaculatus</i>	C	170	-22.1	10.0	1(1)
Lutjanidae	<i>Lutjanus</i> sp.	C	60	-17.9	9.2	1(1)
Mochokidae	<i>Synodontis zambezensis</i>	O	130-140	-22.0 ± 1.0	9.5 ± 0.4	3(1)
Monodactylidae	<i>Monodactylus falciformis</i>	PI	70-75	-23.5 ± 0.1	10.5 ± 0.3	2(1)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Mugilidae	<i>Liza</i> sp.	PD	120–150	-26.8 ± 1.1	6.8 ± 0.3	2(5–6)
Mugilidae	Mugilid juveniles	PD	40–60	-16.8 ± 0.9	7.8 ± 0.3	3(2–3)
Mugilidae	NI Mugilid	PD	170–280	-22.7 ± 0.5	6.6 ± 0.3	4(5)
Mugilidae	<i>Valamugil</i> sp.	PD	100–160	-21.5 ± 0.6	7.9 ± 0.1	5(5–6)
Mullidae	<i>Upeneus</i> sp.	C	55–70	-18.5 ± 0.3	8.2 ± 0.3	2(1)
Mullidae	<i>Upeneus vittatus</i>	C	70–80	-17.4 ± 0.5	8.6 ± 0.2	2(2)
Mullidae	<i>U. vittatus</i>	C	80–110	-17.3 ± 0.4	10.2 ± 0.1	2(3)
Polynemidae	<i>Polydactylus sextarius</i>	C	140–150	-17.3 ± 0.1	11.1 ± 0.1	2(1)
Scatophagidae	<i>Scatophagus tetracanthus</i>	O	30	-22.5	7.7	1(1)
Scatophagidae	<i>S. tetracanthus</i>	O	55–75	-24.5 ± 0.2	9.4 ± 0.2	3(1–2)
Schilbeidae	<i>Schilbe intermedius</i>	Pi	100–280	-20.4 ± 0.2	9.2 ± 0.3	6(1–2)
Sciaenidae	<i>Atrobucca nibe</i>	C	70–80	-24.8 ± 0.2	9.6 ± 0.0	2(3)
Sciaenidae	<i>A. nibe</i>	C	110–200	-21.2 ± 0.4	10.4 ± 0.1	4(2–5)
Sillaginidae	<i>Sillago sihama</i>	C	135–230	-23.1 ± 0.1	9.5 ± 0.1	4(3–6)
Sillaginidae	<i>S. sihama</i>	C	80–110	-19.7 ± 0.4	10.7 ± 0.3	3(1,4)
Sparidae	<i>Acanthopagrus berda</i>	C	90–350	-22.0 ± 0.5	9.5 ± 0.2	3(1,5)
Sphyracnidae	<i>Sphyraena jello</i>	Pi	150	-18.1	10.6	1(1)
Teraponidae	<i>Terapon jarbua</i>	C	60–110	-18.7 ± 0.7	10.2 ± 0.1	3(5–10)
Tetraodontidae	<i>Arothron manilensis</i>	O	70–80	-17.9 ± 0.1	11.1 ± 0.3	2(1)
<b>Betsiboka</b>						
Pre-wet ( <i>n</i> = 85)						
Invertebrates ( <i>n</i> = 28)						
Alpheidae	<i>Alpheus</i> sp.	Uk	50	-12.6	11.4	1(1)
Atyidae	<i>Caridina</i> sp.	H/O	5–10	-11.9 ± 0.0	13.5 ± 0.1	3(15)
Balanidae	<i>Balanus</i> sp.	Pl	7–10	-15.9 ± 0.2	9.9 ± 0.0	3(20)
Grapsidae	<i>Metopograpsus</i> sp.	H	25–40	-14.1 ± 0.8	11.0 ± 0.3	3(1)
Littorinidae	<i>Littoraria scabra</i>	H	15–18	-20.5 ± 0.1	8.9 ± 0.0	3(15)
Matutidae	<i>Matuta</i> sp.	C	70	-12.6	9.9	1(3)
Ocyropodidae	<i>Uca inversa</i>	MPB	14–17	-12.8 ± 0.9	10.0 ± 0.2	3(3)
Ocyropodidae	<i>Uca tetragonon</i>	MPB	20–25	-13.2 ± 0.5	9.3 ± 0.2	3(5)
Ocyropodidae	<i>Uca urvillei</i>	MPB	20–25	-11.7 ± 0.1	7.9 ± 0.0	3(4–5)
Osireidae	<i>Saccostrea cucullata</i>	Pl	20–40	-17.1 ± 0.4	7.1 ± 0.2	6(5)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	70	-14.4 ± 0.5	13.3 ± 0.3	2(1)
Palaemonidae	<i>Macrobrachium</i> sp. 2	O	50–60	-13.1 ± 0.4	13.3 ± 0.2	3(10)
Palaemonidae	NI Palaemonid	Uk	45–50	-14.9 ± 0.2	11.0 ± 0.1	3(1)
Palaemonidae	<i>Palaemonetes</i> sp. 1	O	30–40	-13.5 ± 0.2	12.9 ± 0.1	3(5)
Palaemonidae	<i>Palaemonetes</i> sp. 2	O	34	-17.5	9.9	1(1)
Penaeidae	<i>Metapenaeus monoceros</i>	O	30–40	-12.3 ± 0.2	11.5 ± 0.2	6(15)
Penaeidae	<i>M. monoceros</i>	O	48–70	-15.5 ± 0.4	11.5 ± 0.3	5(2–3)
Penaeidae	<i>Metapenaeus stebbingi</i>	O	40–55	-14.4 ± 0.3	8.7 ± 1.2	2(2)
Penaeidae	<i>Penaeus indicus</i>	O/C	40–70	-13.2 ± 0.4	8.3 ± 0.1	6(2–4)
Penaeidae	<i>P. indicus</i>	O/C	150–170	-14.5 ± 0.3	9.2 ± 0.2	3(5)
Portunidae	<i>Portunus pelagicus</i>	C	55–70	-13.2 ± 1.5	8.6 ± 1.0	2(1)
Portunidae	<i>Scylla serrata</i>	C	60–145	-13.3 ± 0.4	13.1 ± 0.1	5(1–2)
Portunidae	<i>Thalamita crenata</i>	C	40	-13.4 ± 0.1	12.7 ± 0.2	2(1)
Potamididae	<i>Cerithidea decollata</i>	PD	40–50	-18.6 ± 0.1	11.2 ± 0.0	3(15)
Sergestidae	<i>Acetes erythraeus</i>	Pl	20–25	-16.3 ± 0.1	8.5 ± 0.0	3(15)
Sesarmidae	<i>Parasesarma leptosoma</i>	H	15–20	-20.9 ± 0.3	9.2 ± 0.3	3(1)
Squillidae	NI Stomatopoda	C	100–140	-12.1 ± 0.3	8.4 ± 0.7	2(1)
Xanthidae	<i>Eurycarcinus natalensis</i>	C	20–30	-13.0 ± 0.4	13.0 ± 0.0	3(2–3)
<b>Fish (<i>n</i> = 57)</b>						
Ambassidae	<i>Ambassis ambassis</i>	Pl	50–70	-17.7 ± 0.2	11.4 ± 0.3	4(5)
Ariidae	<i>Arius madagascariensis</i>	C	190	-15.9	12.4	1(1)
Belonidae	<i>Strongylura leiura</i>	Pi	355–360	-17.1 ± 0.2	12.0 ± 0.3	3(5)
Carangidae	<i>Alepes djedaba</i>	C	140–300	-16.3 ± 0.2	11.9 ± 0.1	7(1,3)
Carangidae	<i>Carangoides malabaricus</i>	Pi	120–150	-16.4 ± 0.3	12.8 ± 0.1	3(5)
Carangidae	<i>Caranx ignobilis</i>	Pi	140	-14.8	10.2	1(1)
Carangidae	<i>Caranx sexfasciatus</i>	Pi	170–175	-16.3 ± 0.2	12.5 ± 0.4	2(1)
Carangidae	<i>Megalaspis cordyla</i>	Pi	150–230	-16.0 ± 0.1	12.4 ± 0.1	5(1,3,5)
Carangidae	<i>Scomberoides commersonianus</i>	Pi	260–300	-16.2 ± 0.0	13.1 ± 0.2	2(1)
Carangidae	<i>Scomberoides tol</i>	Pi	220	-16.6	11.3	1(1)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	740–720	-15.8 ± 0.7	12.5 ± 0.8	6(1–2)
Clupeidae	<i>Herklotsichthys</i> sp.	Pl	60–80	-17.6 ± 0.6	11.3 ± 0.3	3(3)
Clupeidae	<i>Hilsa kelee</i>	Pl	170–175	-16.7 ± 0.1	9.8 ± 0.0	3(3)
Clupeidae	<i>Sardinella</i> sp.	Pl	150–160	-16.2 ± 0.4	10.2 ± 0.0	3(3)
Eleotridae	<i>Butis butis</i>	C	80	-19.6	11.2	1(1)
Eleotridae	<i>Eleotris acanthopoma</i>	C	80–100	-15.5 ± 0.5	12.5 ± 0.4	6(1)
Engraulidae	<i>Thryssa vitrirostris</i>	Pl	130–135	-15.4 ± 0.0	13.5 ± 0.0	2(1)



Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Gerreidae	<i>Gerres longirostris</i>	C	130–140	-14.4 ± 0.0	10.9 ± 0.0	2(5)
Gobiidae	<i>Periophthalmus</i> sp.	C	58–70	-13.3 ± 0.3	11.7 ± 0.2	5(2–3)
Gobiidae	Ni Gobiidae sp. 1	Uk	90–140	-12.6 ± 0.6	11.5 ± 0.6	3(1)
Gobiidae	Ni Gobiidae sp. 2	Uk	170	-9.7	8.4	1(1)
Gobiidae	Ni Gobiidae sp. 3	Uk	90	-19.4	7.0	1(1)
Haemulidae	<i>Plectorhinchus chubbi</i>	C	90–300	-15.4 ± 0.4	11.7 ± 0.2	5(1)
Haemulidae	<i>Pomadasys maculatus</i>	C	110–150	-15.0 ± 0.1	12.8 ± 0.2	3(5)
Haemulidae	<i>Pomadasys olivaceum</i>	C	100–250	-16.5 ± 0.4	11.9 ± 0.2	4(5)
Leiognathidae	<i>Secutor insidiator</i>	Pl	90–110	-16.6 ± 0.1	12.3 ± 0.0	3(3)
Leiognathidae	<i>Leiognathus equulus</i>	C	100–130	-15.7 ± 0.3	12.3 ± 0.4	5(1)
Leiognathidae	<i>L. equulus</i>	C	70–90	-13.4 ± 0.5	10.1 ± 0.1	2(3)
Lethrinidae	<i>Lethrinus microdon</i>	C	160–200	-16.3 ± 0.3	10.6 ± 0.3	2(3)
Monodactylidae	<i>Monodactylus argenteus</i>	Pl	30–40	-17.0 ± 0.1	11.9 ± 0.0	3(5)
Mugilidae	<i>Liza</i> sp.	PD	150–170	-10.2 ± 0.5	8.3 ± 0.1	2(1)
Mugilidae	<i>Valamugil cunnesius</i>	PD	180–200	-12.6 ± 0.1	13.9 ± 0.0	3(5)
Mugilidae	<i>Valamugil</i> sp.	PD	160	-14.6	10.8	1(1)
Mullidae	<i>Upeneus vittatus</i>	C	100–120	-14.9 ± 0.3	11.6 ± 0.4	5(4–5)
Muraenesocidae	<i>Congresox talabonoides</i>	Pi	1150	-14.9	13.2	1(1)
Polynemidae	<i>Polydactylus sexfilis</i>	C	150–170	-14.8 ± 0.1	12.2 ± 0.0	3(5)
Pristigasteridae	<i>Pellona ditchela</i>	Pl	130–160	-16.7 ± 0.1	11.4 ± 0.1	5(5)
Sciaenidae	<i>Atrobucca nibe</i>	C	130–160	-15.1 ± 0.6	12.1 ± 0.1	3(1)
Sciaenidae	<i>Johnius dorsalis</i>	C	140	-13.6	11.9	1(1)
Sciaenidae	<i>Otolithes ruber</i>	C	290–320	-16.7 ± 0.3	13.5 ± 0.1	3(5)
Scombridae	<i>Rastrelliger kanagurta</i>	Pl	180–230	-17.2 ± 0.1	10.4 ± 0.3	6(1–2)
Serranidae	<i>Epinephelus lanceolatus</i>	Pi	70	-14.3	13.6	1(1)
Serranidae	<i>Epinephelus malabaricus</i>	Pi	210–270	-15.7 ± 0.1	12.8 ± 0.2	3(1)
Sillaginidae	<i>Sillago sihama</i>	C	90–180	-13.8 ± 0.5	12.2 ± 0.2	9(1–3)
Sparidae	<i>Acanthopagrus berda</i>	C	160–190	-17.2 ± 0.3	11.5 ± 0.3	5(1)
Teraponidae	<i>Terapon jarbua</i>	C	120–140	-16.4 ± 0.8	11.6 ± 0.1	5(2–3)
Trichiuridae	<i>Trichiurus lepturus</i>	Pi	600–700	-15.9 ± 0.1	14.0 ± 0.1	3(1)
Post-Wet ( <i>n</i> = 112)						
Invertebrates ( <i>n</i> = 21)						
Balanidae	<i>Balanus</i> sp.	Pl	14–16	-16.7 ± 0.1	9.3 ± 0.2	3(15)
Littorinidae	<i>Littoraria scabra</i>	H	13–14	-22.5 ± 0.1	7.3 ± 0.1	3(15)
Ocyrodidae	<i>Uca inversa</i>	MPB	10–12	-13.8 ± 0.1	10.6 ± 0.1	3(2–3)
Ocyrodidae	<i>Uca tetragonon</i>	MPB	23–25	-15.3 ± 0.5	9.1 ± 0.2	3(10)
Ostreidae	<i>Saccostrea cucullata</i>	Pl	17–24	-17.4 ± 0.2	7.2 ± 0.2	3(10)
Palaemonidae	<i>Macrobrachium</i> sp.	O	20–25	-16.0 ± 0.1	11.2 ± 0.1	3(5)
Penaeidae	<i>Metapenaeus monoceros</i>	O	27–30	-16.2	7.0	1(3)
Penaeidae	<i>M. monoceros</i>	O	35–58	-13.7 ± 0.2	7.6 ± 0.1	4(7–8)
Penaeidae	<i>Metapenaeus stebbingi</i>	O	50–65	-17.7 ± 0.4	8.8 ± 0.4	3(7)
Penaeidae	Penaeid juveniles	PD	12–25	-13.2 ± 0.5	7.6 ± 0.2	3(6–12)
Penaeidae	<i>Penaeus indicus</i>	O	24–25	-14.0 ± 0.2	6.7 ± 0.1	3(5–6)
Penaeidae	<i>P. indicus</i>	O/C	40–60	-16.0 ± 0.6	8.8 ± 0.4	2(3–4)
Penaeidae	<i>P. indicus</i>	O/C	100–170	-16.3 ± 0.1	9.8 ± 0.2	4(6–9)
Penaeidae	<i>Penaeus monodon</i>	O/C	160–210	-18.2 ± 0.9	9.3 ± 0.4	3(2–3)
Penaeidae	<i>Penaeus semisulcatus</i>	O	70–90	-13.4 ± 0.3	8.1 ± 0.1	3(5–6)
Penaeidae	<i>Portunus pelagicus</i>	C	75–140	-15.6 ± 0.2	9.7 ± 0.3	4(1–2)
Portunidae	<i>Scylla serrata</i>	C	110–160	-21.4 ± 0.5	9.4 ± 0.2	3(2)
Potamididae	<i>Cerithidea decollata</i>	PD	20–25	-21.4 ± 0.0	8.3 ± 0.0	3(15)
Sergestidae	<i>Acetes erythraeus</i>	Pl	13–27	-18.2 ± 0.1	8.7 ± 0.3	4(4–5)
Sesarmidae	Sesarmid juveniles	H	4–5	-16.7 ± 0.2	7.7 ± 0.2	3(10)
Sesarmidae	<i>Parasesarma leptosoma</i>	H	14–24	-21.8 ± 0.2	10.3 ± 0.3	7(2–3)
Fish ( <i>n</i> = 90)						
Ambassidae	<i>Ambassis ambassis</i>	Pl	35	-19.6	10.8	1(1)
Ariidae	<i>Arius madagascariensis</i>	C	230–280	-16.9 ± 0.1	12.0 ± 0.1	2(1)
Ariidae	<i>Netuma thalassina</i>	C	160–340	-15.6 ± 0.1	11.8 ± 0.2	5(1)
Ariidae	Ni Ariidae	C	60–160	-16.0 ± 0.1	11.9 ± 0.1	3(5–6)
Belonidae	<i>Strongylura leiura</i>	Pi	390–570	-17.1 ± 0.1	12.5 ± 0.4	3(1–2)
Carangidae	<i>Parastromateus niger</i>	Pl	155–310	-17.1 ± 0.1	11.9 ± 0.3	4(1–2)
Carangidae	Carangid juvenile	C	35	-17.6	7.5	1(1)
Carangidae	<i>Alectis indica</i>	Pi	70–140	-15.3 ± 0.2	10.8 ± 0.1	4(3–6)
Carangidae	<i>Caranx ignobilis</i>	Pi	85–190	-17.9 ± 0.3	10.9 ± 0.1	6(3–14)
Carangidae	<i>Caranx papuensis</i>	Pi	150–170	-13.8 ± 0.6	10.6 ± 0.3	5(3–4)
Carangidae	<i>Caranx sexfasciatus</i>	Pi	110–140	-18.8 ± 0.9	11.0 ± 0.3	3(1)
Carangidae	<i>Megalaspis cordyla</i>	Pi	135–340	-17.1 ± 0.1	11.9 ± 0.1	13(1–4)
Carangidae	<i>Scomberoides commersonianus</i>	Pi	180–420	-19.4 ± 0.9	11.5 ± 0.3	5(1–2)
Carangidae	<i>Scomberoides tol</i>	Pi	170–270	-16.7 ± 0.2	11.2 ± 0.3	5(3–4)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Carangidae	<i>Trachinotus africanus</i>	Pi	135–180	-13.4 ± 1.0	7.8 ± 0.5	3(1–2)
Carangidae	<i>Ulua mentalis</i>	Pi	140–145	-16.3 ± 0.1	10.4 ± 0.2	3(1)
Carcharhinidae	<i>Rhizoprionodon acutus</i>	Pi	320–1200	-15.2 ± 0.1	13.5 ± 0.3	7(1)
Chirocentridae	<i>Chirocentrus dorab</i>	Pi	340–500	-17.1 ± 0.0	11.8 ± 0.3	3(2)
Cichlidae	<i>Oreochromis niloticus</i>	PD	125–130	-24.3 ± 1.1	7.6 ± 0.2	3(2)
Clupeidae	<i>Hilsa kelee</i>	PI	155–160	-18.6 ± 0.3	10.3 ± 0.1	3(3)
Clupeidae	<i>Sauvagella madagascariensis</i>	PI	20–45	-18.8 ± 0.1	10.4 ± 0.1	6(7)
Cynoglossidae	<i>Paraplagusia bilineata</i>	C	85–200	-15.1 ± 0.1	11.5 ± 0.3	4(2–3)
Drepanidae	<i>Drepane longimana</i>	C	85–250	-15.6 ± 0.6	13.3 ± 0.2	5(1;3–4)
Drepanidae	<i>Elops machnata</i>	C	160–280	-18.0 ± 0.2	9.4 ± 0.2	3(1–2)
Engraulidae	<i>Engraulis</i> sp.	PI	45–110	-18.2 ± 0.2	11.9 ± 0.1	10(2–7)
Engraulidae	<i>Stolephorus indicus</i>	PI	65–140	-16.3 ± 0.6	11.6 ± 0.1	4(6)
Engraulidae	<i>Thryssa vitrirostris</i>	PI	70–115	-16.6 ± 0.4	12.3 ± 0.2	3(3–8)
Gerreidae	<i>Gerres filamentosus</i>	C	80–160	-15.7 ± 0.5	10.5 ± 0.2	5(3–8)
Gerreidae	<i>Gerres longirostris</i>	C	105–155	-15.0 ± 0.2	9.9 ± 0.3	4(2–3)
Gobiidae	<i>Acentrogobius nebulosus</i>	C	68	-15.0	10.0	1(1)
Gobiidae	<i>Glossogobius giuris</i>	C	130	-21.6	9.8	1(1)
Gobiidae	<i>Periophthalmus</i> sp.	C	70–80	-17.0 ± 0.6	14.4 ± 0.3	3(2)
Gobiidae	NI Gobiidae sp. 1	Uk	95–150	-11.1 ± 0.3	5.6 ± 0.4	4(5–7)
Gobiidae	NI Gobiidae sp. 2	Uk	80	-10.6	8.0	1(1)
Gobiidae	NI Gobiidae sp. 3	Uk	280	-11.5	8.4	1(1)
Haemulidae	<i>Pomadasys kaakan</i>	C	460–500	-15.7 ± 0.5	13.1 ± 0.1	2(1)
Haemulidae	<i>Pomadasys kaakan</i>	C	125–230	-16.4 ± 0.1	10.9 ± 0.2	4(2–3)
Haemulidae	<i>Pomadasys maculatus</i>	C	100–210	-17.2 ± 0.3	11.4 ± 0.2	7(1–6)
Hemiramphidae	<i>Hemiramphus far</i>	PI	200–240	-13.9 ± 0.5	7.8 ± 0.3	2(4)
Hemiramphidae	<i>Hyporhamphus</i> sp.	H/PI	85–140	-16.6 ± 0.2	11.0 ± 0.1	5(3–4)
Hemiramphidae	<i>Hyporhamphus</i> sp.	H/PI	320–450	-18.0 ± 0.1	9.6 ± 0.1	3(1–2)
Kyphosidae	<i>Neoscorpis lithophilus</i>	O	140	-16.8	12.8	1(1)
Leiognathidae	<i>Secutor insidiator</i>	PI	60–65	-17.1 ± 0.1	11.7 ± 0.1	3(3)
Leiognathidae	<i>Leiognathus equulus</i>	C	100–160	-14.4 ± 0.6	10.3 ± 0.2	4(3–9)
Leiognathidae	<i>L. equulus</i>	C	25–40	-19.2 ± 1.0	10.8 ± 0.1	3(3–10)
Leiognathidae	<i>Gazza minuta</i>	Pi	100–110	-17.2 ± 0.0	12.3 ± 0.1	3(6)
Lethrinidae	<i>Lethrinus harak</i>	C	205–215	-15.2 ± 0.3	11.0 ± 0.2	3(1)
Lethrinidae	<i>Lethrinus mahsena</i>	C	180–280	-15.3 ± 0.2	11.7 ± 0.2	3(1–3)
Lethrinidae	<i>Lethrinus microdon</i>	C	125–135	-17.6 ± 0.3	8.7 ± 0.1	3(1–2)
Lethrinidae	<i>L. microdon</i>	C	180–230	-16.3 ± 0.2	11.2 ± 0.3	2(1)
Lobotidae	<i>Lobotes surinamensis</i>	C	125–145	-18.0 ± 0.5	8.1 ± 0.2	5(1–2)
Lutjanidae	<i>Lutjanus bohar</i>	C	100–155	-18.3 ± 1.3	9.6 ± 0.5	3(1)
Lutjanidae	<i>Lutjanus gibbus</i>	C	210	-16.2	12.5	1(1)
Lutjanidae	<i>Lutjanus rivulatus</i>	C	190–220	-15.8 ± 0.1	12.8 ± 0.1	4(2–5)
Lutjanidae	<i>Lutjanus russelli</i>	C	140–155	-17.0 ± 0.5	9.4 ± 0.1	3(2–3)
Monodactylidae	<i>Monodactylus falciformis</i>	PI	130–150	-15.2 ± 2.1	11.2 ± 0.5	3(7)
Mugilidae	<i>Liza</i> sp.	PD	110–190	-13.1 ± 0.6	7.1 ± 0.4	9(1–6)
Mugilidae	<i>Mugil cephalus</i>	PD	135–140	-16.4 ± 0.6	8.0 ± 0.2	2(1)
Mugilidae	NI Mugilid	PD	160–170	-17.2 ± 0.5	8.5 ± 0.1	3(3)
Mullidae	<i>Upeneus</i> sp.	C	50–55	-17.5 ± 0.1	6.8 ± 0.2	3(4–5)
Mullidae	<i>Upeneus vittatus</i>	C	50–70	-17.1 ± 0.1	8.0 ± 1.2	2(2)
Mullidae	<i>U. vittatus</i>	C	100–135	-16.1 ± 0.2	10.9 ± 0.3	3(4)
Muraenesocidae	<i>Muraenesox bagio</i>	Pi	650–1100	-15.9 ± 0.3	12.7 ± 0.3	3(3–4)
Platycephalidae	<i>Platycephalus indicus</i>	C	260–570	-20.5 ± 0.5	10.6 ± 0.3	3(1–2)
Polynemidae	<i>Polydactylus sexfilis</i>	C	95–145	-16.1 ± 0.6	11.9 ± 0.1	5(2–3)
Pristigasteridae	<i>Pellona ditchela</i>	PI	100–140	-16.1 ± 0.6	11.6 ± 0.4	3(6)
Psettodidae	<i>Psettodes erumei</i>	C	220–270	-16.5 ± 0.4	11.2 ± 0.2	5(1)
Sciaenidae	<i>Johnius dorsalis</i>	C	105–115	-16.6 ± 0.3	11.9 ± 0.2	5(5–7)
Sciaenidae	<i>Otolithes ruber</i>	C	145–260	-17.5 ± 0.2	12.7 ± 0.2	5(4–6)
Scombridae	<i>Rastrelliger kanagurta</i>	PI	170–200	-17.3 ± 0.3	9.7 ± 0.2	4(3)
Scombridae	<i>Scomberomorus commerson</i>	Pi	600–620	-16.9 ± 0.0	11.3 ± 0.1	2(1)
Scombridae	<i>Scomberomorus plurilineatus</i>	Pi	450	-17.6	13.3	1(1)
Scombridae	<i>Scomberomorus</i> sp.	Pi	135–340	-16.8 ± 0.1	11.6 ± 0.2	6(3–4)
Serranidae	<i>Cephalopholis argus</i>	Pi	140–160	-15.9 ± 0.1	11.9 ± 0.4	2(1)
Serranidae	<i>Epinephelus malabaricus</i>	Pi	150–290	-16.3 ± 0.5	11.8 ± 0.5	3(2–4)
Serranidae	<i>E. malabaricus</i>	Pi	370–500	-15.9 ± 0.1	13.4 ± 0.1	3(1)
Siganidae	<i>Siganus sutor</i>	H	100–180	-14.4 ± 0.9	7.5 ± 0.3	5(2–4)
Sillaginidae	<i>Sillago sihama</i>	C	135–160	-13.2 ± 0.5	11.3 ± 0.1	3(5)
Sillaginidae	<i>S. sihama</i>	C	65–105	-13.9 ± 0.3	9.7 ± 0.1	3(2–3)
Sparidae	<i>Crenidens crenidens</i>	H	125–155	-17.1 ± 0.3	5.6 ± 0.1	2(1)
Sparidae	<i>Acanthopagrus berda</i>	C	115–130	-21.2 ± 0.1	8.4 ± 0.1	3(1–2)
Sphyraenidae	<i>Sphyraena chrysaenia</i>	Pi	200–220	-16.9 ± 0.0	11.2 ± 0.2	2(1)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Sphyrinaeidae	<i>Sphyrina jello</i>	Pi	200–600	-15.7 ± 0.6	11.7 ± 0.5	5(1–3)
Teraponidae	<i>Terapon jarbua</i>	C	85–210	-16.1 ± 0.2	10.9 ± 0.2	5(3–11)
Teraponidae	<i>Terapon theraps</i>	C	45–50	-17.4	9.8	1(2)
Teraponidae	<i>T. theraps</i>	C	85–140	-16.3 ± 0.2	11.3 ± 0.1	3(1–2)
Tetraodontidae	<i>Arothron</i> sp.	O	43	-16.7	10.8	1(1)
Trichiuridae	<i>Trichiurus lepturus</i>	Pi	450–650	-16.1 ± 0.2	13.0 ± 0.1	3(3–4)
NI Teleost	NI Teleost #1	Uk	200–210	-13.6 ± 0.1	10.7 ± 0.1	3(2)
NI Teleost	NI Teleost #2	Uk	140	-16.9	11.5	1(1)
Rianila						
Pre-Wet ( <i>n</i> = 47)						
Invertebrates ( <i>n</i> = 12)						
Atyidae	<i>Caridina</i> sp.	H/O	5–6	-16.7 ± 0.6	5.9 ± 0.1	3(5)
Isopoda	NI Isopoda	Uk	8	-18.7 ± 0.7	6.8 ± 0.2	4(1)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	45–50	-22.2 ± 0.1	8.1 ± 0.2	3(3)
Palaemonidae	<i>Macrobrachium</i> sp. 2	O	55	-22.9 ± 1.6	8.4 ± 0.4	2(5)
Palaemonidae	<i>Macrobrachium</i> sp. 3	O	80–100	-25.9 ± 0.4	8.6 ± 0.2	3(5)
Palaemonidae	<i>Palaemonetes</i> sp. 1	O	20–25	-21.3 ± 0.2	8.1 ± 0.0	3(10)
Palaemonidae	<i>Palaemonetes</i> sp. 2	O	15–20	-18.6 ± 0.7	7.8 ± 0.4	2(1)
Penaeidae	<i>Metapenaeus monoceros</i>	O	30–35	-22.7 ± 1.1	5.7 ± 0.6	3(2)
Penaeidae	<i>Metapenaeus stebbingi</i>	O	35–40	-21.6 ± 0.4	6.4 ± 0.1	2(2)
Penaeidae	<i>M. stebbingi</i>	O	55–65	-25.0 ± 0.4	7.2 ± 0.1	4(2–3)
Sesarmidae	<i>Chiromantes eulimene</i>	H/O	10–30	-22.2 ± 0.5	5.7 ± 0.1	4(3)
Varunidae	<i>Varuna</i> sp.	H	50–55	-18.3	5.5	1(1)
Fish ( <i>n</i> = 35)						
Ambassidae	<i>Ambassis natalensis</i>	Pi	40–50	-20.9 ± 0.4	8.6 ± 0.0	2(3)
Anchariidae	<i>Gogo brevibarbis</i>	C	160–170	-18.2 ± 0.5	11.2 ± 0.3	4(1)
Carangidae	<i>Alepes djedaba</i>	C	105–160	-19.6 ± 0.4	10.3 ± 0.2	5(1–2)
Carangidae	NI Carangid	Pi	150	-24.6	9.6	1(1)
Carangidae	<i>Caranx ignobilis</i>	Pi	150–260	-20.9 ± 0.2	10.0 ± 0.2	4(1)
Carangidae	<i>Caranx papuensis</i>	Pi	150–250	-23.8 ± 0.4	9.8 ± 0.1	3(1)
Chaniidae	<i>Channa maculata</i>	Pi	300	-23.2	10.1	1(1)
Cichlidae	<i>Oreochromis niloticus</i>	PD	190	-23.8	5.4	1(1)
Cichlidae	<i>Tilapia rendalli</i>	PD	35–55	-20.4 ± 0.2	7.3 ± 0.3	3(1)
Cichlidae	<i>Tilapia zillii</i>	PD	110–160	-19.8 ± 1.1	7.4 ± 0.6	4(1)
Cichlidae	<i>Paretroplus polyactis</i>	O	80–90	-18.4 ± 0.1	8.3 ± 0.0	2(1)
Cichlidae	<i>P. polyactis</i>	Un	180–210	-27.7 ± 1.8	9.8 ± 0.1	4(1)
Cichlidae	NI Cichlidae sp. 1	Uk	95–110	-17.0 ± 0.1	8.3 ± 0.1	2(2)
Cichlidae	NI Cichlidae sp. 2	Uk	90–100	-23.3 ± 0.7	7.0 ± 0.2	4(1)
Eleotridae	<i>Eleotris</i> sp.	C	45–155	-20.6 ± 0.6	7.4 ± 0.3	6(1–2)
Gerreidae	<i>G. filamentosus</i>	C	75–80	-15.4 ± 0.4	8.6 ± 0.3	2(1)
Gerreidae	<i>Gerres filamentosus</i>	C	100	-22.5 ± 1.5	11.4 ± 0.5	2(1)
Gerreidae	<i>Gerres longirostris</i>	C	150–250	-22.4 ± 1.1	10.0 ± 0.1	4(1)
Gerreidae	<i>Gerres methueni</i>	C	130–140	-17.2 ± 0.4	9.9 ± 0.6	2(1)
Gobiidae	<i>Glossogobius giuris</i>	C	55–180	-19.0 ± 0.3	7.8 ± 0.2	10(1–2)
Gobiidae	NI Gobiidae sp. 1	Uk	10–15	-20.2 ± 0.4	7.9 ± 0.0	3(5)
Gobiidae	NI Gobiidae sp.2	Uk	25–30	-15.7 ± 0.4	8.0 ± 0.1	4(5)
Leiognathidae	<i>Secutor insidiator</i>	Pi	70–90	-18.0 ± 0.0	11.7 ± 0.1	4(1)
Leiognathidae	<i>Gazza minuta</i>	Pi	100–110	-18.0 ± 0.0	11.6 ± 0.0	2(1)
Leiognathus	<i>Leiognathus equulus</i>	C	95	-20.8	9.0	1(1)
Mugilidae	<i>Liza macrolepis</i>	PD	170	-18.8	7.0	1(1)
Mugilidae	<i>Valamugil</i> sp.	PD	150–180	-19.8 ± 0.1	6.8 ± 0.0	3(4–5)
Platycephalidae	<i>Platycephalus indicus</i>	C	240	-19.9	9.1	1(1)
Polynemidae	<i>Polydactylus plebeius</i>	C	310	-16.8	12.1	1(1)
Scatophagidae	<i>Scatophagus tetracanthus</i>	O	290	-29.9	4.0	1(1)
Sciaenidae	<i>Atrubucca nibe</i>	C	150–200	-17.9 ± 0.3	11.2 ± 0.1	3(5)
Sciaenidae	<i>Otolithes ruber</i>	C	210–230	-17.6 ± 0.1	12.4 ± 0.0	3(2)
Serranidae	<i>Epinephelus malabaricus</i>	Pi	300–307	-20.9 ± 0.8	11.3 ± 0.3	2(1)
Sillaginidae	<i>Sillago sihama</i>	C	130–190	-18.6 ± 0.9	11.6 ± 0.0	2(2)
Sparidae	<i>Rhabdosargus thorpei</i>	C	400–500	-23.8 ± 0.3	10.3 ± 1.3	2(1)
Post-Wet ( <i>n</i> = 49)						
Invertebrates ( <i>n</i> = 9)						
Amphipoda	Amphipoda sp. 1	Uk	1–2	-21.4 ± 0.1	5.7 ± 0.0	3(20)
Amphipoda	Amphipoda sp. 2	Uk	4–5	-21.4 ± 0.2	5.5 ± 0.0	3(20)
Amphipoda	Amphipoda sp. 3	Uk	9–10	-22.4 ± 0.1	6.1 ± 0.0	3(60)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	36–40	-21.5 ± 0.1	6.9 ± 0.0	2(5)
Palaemonidae	<i>Palaemonetes</i> sp. 1	O	20–25	-21.3 ± 0.1	6.7 ± 0.1	3(5)
Palaemonidae	<i>Palaemonetes</i> sp. 2	O	10–12	-18.9 ± 0.0	7.6 ± 0.0	2(5)
Palaemonidae	<i>Palaemonid</i> sp. 1	O	50–55	-18.6 ± 0.4	8.3 ± 0.0	2(1)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Sesarmidae	<i>Chromantes eulimene</i>	H/O	20–25	-22.8 ± 0.2	5.8 ± 0.1	3(4)
Decapoda	Crab megalopa	PI	2–3	-21.9 ± 0.4	5.1 ± 0.2	4(3)
Fish ( <i>n</i> = 40)						
Ariidae	<i>Netuma thalassina</i>	C	230–520	-17.4 ± 0.4	11.6 ± 0.1	4(1)
Atherinidae	<i>Atherinomorus lacunosus</i>	PI	45–55	-19.8 ± 0.4	9.4 ± 0.2	3(2–3)
Belonidae	<i>Strongylura leiura</i>	Pi	320–400	-17.2 ± 0.3	11.7 ± 0.3	2(1)
Carangidae	<i>Alepes djedaba</i>	C	120–140	-17.5 ± 0.2	10.4 ± 0.0	3(4)
Carangidae	<i>Carangoides malabaricus</i>	Pi	120	-17.5	10.2	1(1)
Carangidae	<i>Caranx ignobilis</i>	Pi	110–120	-18.9 ± 0.2	9.5 ± 0.1	3(2–3)
Carangidae	<i>C. ignobilis</i>	Pi	220–260	-21.7 ± 0.3	10.1 ± 0.1	3(3–4)
Carangidae	<i>Caranx papuensis</i>	Pi	115–120	-20.1 ± 1.0	9.5 ± 0.3	2(1)
Carangidae	<i>Caranx</i> sp.	Pi	45–50	-18.8 ± 0.0	7.8 ± 0.0	3(6)
Carangidae	<i>Ulua mentalis</i>	Pi	125	-17.3	10.4	1(1)
Channidae	<i>Channa maculata</i>	Pi	180–230	-23.4 ± 1.5	9.1 ± 0.2	3(1)
Cichlidae	<i>Oreochromis niloticus</i>	PD	135–160	-17.4 ± 0.4	5.7 ± 0.1	3(5)
Cichlidae	<i>Tilapia zillii</i>	PD	120–145	-17.2 ± 0.2	4.0 ± 0.4	2(1)
Cichlidae	<i>Paretroplus polyactis</i>	O	120–270	-23.2 ± 0.2	8.7 ± 0.3	6(1;4)
Cichlidae	<i>Ptychochromis oligacanthus</i>	O	155	-20.2	8.0	1(1)
Cynoglossidae	<i>Cynoglossus</i> sp.	C	170	-16.1	10.4	1(1)
Drepanidae	<i>Drepane longimana</i>	C	168	-19.0	11.2	1(1)
Gerreidae	<i>Gerres filamentosus</i>	C	45–55	-17.7 ± 0.2	7.2 ± 0.2	2(2–3)
Gerreidae	<i>G. filamentosus</i>	C	115–175	-22.3 ± 0.3	9.1 ± 0.4	5(3–5)
Gerreidae	<i>Gerres methueni</i>	C	120–210	-21.9 ± 0.7	8.9 ± 0.3	3(2–3)
Gobiidae	<i>Glossogobius giuris</i>	C	45	-19.6	7.5	1(1)
Gobiidae	<i>G. giuris</i>	C	230–290	-22.5 ± 0.4	8.6 ± 0.1	2(2–3)
Haemulidae	<i>Pomadasys maculatus</i>	C	140–160	-21.3 ± 0.4	9.5 ± 0.2	3(2)
Leiognathidae	<i>Leiognathus equulus</i>	C	90	-25.6	10.4	1(1)
Mugilidae	<i>Liza macrolepis</i>	PD	160–170	-19.0 ± 0.2	6.4 ± 0.2	3(3)
Mugilidae	<i>Valamugil</i> sp.	PD	120–170	-19.2 ± 0.4	6.0 ± 0.1	3(3)
Mullidae	<i>Upeneus vittatus</i>	C	115–120	-18.2 ± 0.1	11.3 ± 0.0	2(1)
Osphroneminae	<i>Osphronemus goramy</i>	O	220	-25.2	6.9	1(1)
Planktivores	<i>Ambassis natalensis</i>	PI	65–75	-20.1 ± 0.9	8.1 ± 0.1	3(2–3)
Platycephalidae	<i>Platycephalus indicus</i>	C	240–250	-17.1 ± 0.2	10.7 ± 0.1	3(1)
Polynemidae	<i>Polydactylus plebeius</i>	C	140–170	-18.5 ± 0.2	10.1 ± 0.2	3(2–3)
Scatophagidae	<i>Scatophagus tetracanthus</i>	O	180	-28.0	8.3	1(1)
Sciaenidae	<i>Johnius dorsalis</i>	C	120–160	-17.9 ± 0.1	11.4 ± 0.1	3(9)
Sciaenidae	<i>Otolithes ruber</i>	C	180–190	-17.5 ± 0.1	11.1 ± 0.0	3(3)
Scombridae	<i>Rastrelliger kanagurta</i>	PI	140–170	-18.2 ± 0.3	9.0 ± 0.1	5(1)
Scombridae	<i>Scomberomorus</i> sp.	Pi	250–260	-17.8 ± 0.1	11.1 ± 0.2	3(1)
Sillaginidae	<i>Sillago sihama</i>	C	155–180	-20.1 ± 1.3	8.3 ± 1.1	3(4)
Sparidae	<i>Rhabdosargus thorpei</i>	C	170	-20.7	7.0	1(1)
Sphyraenidae	<i>Sphyraena chrysotaenia</i>	Pi	210	-17.7	12.0	1(1)
Synodontidae	<i>Saurida tumbil</i>	Pi	190–230	-17.3 ± 0.2	10.7 ± 0.1	3(2–3)
Ambila						
Pre-wet ( <i>n</i> = 25)						
Invertebrates ( <i>n</i> = 13)						
Amphipoda	Gammarid amphipods sp. 1	Uk	4–5	-18.0	6.6	1(10)
Amphipoda	Gammarid amphipods sp. 2	Uk	8–10	-22.5	6.0	1(10)
Majidae	NI Majidae	Uk	2	-17.4	5.0	1(3)
Mytilidae	Mytilidae sp. 1	PI	10–14	-23.9 ± 0.3	3.5 ± 0.2	4(15)
Mytilidae	Mytilidae sp. 2	PI	8–12	-23.9 ± 0.1	3.6 ± 0.1	4(15)
Naticidae	<i>Neverita didyma</i>	C	28–31	-25.3 ± 0.1	6.5 ± 0.1	4(5)
Palaemonidae	NI Palaemonid sp. 1	O	75–98	-24.5 ± 0.8	7.5 ± 0.2	2(1)
Palaemonidae	NI Palaemonid sp. 2	O	94–97	-20.0 ± 0.5	8.2 ± 0.4	3(1)
Palaemonidae	<i>Macrobrachium</i> sp.	O	50–55	-23.0 ± 0.3	6.6 ± 0.2	3(3)
Palaemonidae	<i>Palaemonetes</i> sp.	O	10–20	-22.7 ± 0.1	5.6 ± 0.0	3(15)
Penaeidae	<i>Metapenaeus monoceros</i>	O	100–105	-20.0 ± 0.7	7.4 ± 0.3	3(1)
Potamididae	<i>Terebralia palustris</i>	MPB	25–30	-12.1 ± 0.0	3.0 ± 0.1	3(15)
Varunidae	<i>Varuna</i> sp.	H	50–65	-20.8 ± 0.6	6.9 ± 0.5	2(3)
Fish ( <i>n</i> = 12)						
Ambassidae	<i>Ambassis natalensis</i>	PI	35	-19.9	8.5	1(1)
Ambassidae	<i>A. natalensis</i>	PI	55–70	-24.4 ± 0.0	8.8 ± 0.1	3(2)
Carangidae	<i>Alepes djedaba</i>	C	140–155	-20.8 ± 1.5	9.3 ± 0.2	2(1)
Channidae	<i>Channa maculata</i>	Pi	200–265	-22.6 ± 0.7	8.1 ± 0.2	4(1)
Cichlidae	NI Cichlid	PD	170	-16.4	4.6	1(1)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	100–150	-20.5 ± 0.2	6.2 ± 0.1	4(2–3)
Cichlidae	<i>Paretroplus polyactis</i>	O	170–200	-18.4 ± 1.4	8.4 ± 0.0	2(1)
Cichlidae	<i>Ptychochromis grandidieri</i>	O	100–125	-15.1 ± 0.8	8.2 ± 0.1	3(2)



Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Gerreidae	<i>Gerres longirostris</i>	C	110–130	$-15.3 \pm 1.2$	$9.4 \pm 0.1$	4(3)
Gerreidae	<i>Gerres methueni</i>	C	60–80	-15.9	9.3	1(4)
Gobiidae	<i>Glossogobius giuris</i>	C	20–25	$-16.4 \pm 0.9$	$7.0 \pm 0.2$	3(2–3)
Gobiidae	<i>G. giuris</i>	C	90–120	$-21.1 \pm 0.7$	$8.2 \pm 0.5$	3(2)
Platycephalidae	<i>Platycephalus indicus</i>	C	180–200	$-19.6 \pm 0.1$	$8.7 \pm 0.0$	2(2)
Post-wet ( <i>n</i> = 43)						
Invertebrates ( <i>n</i> = 18)						
Amphipoda	Gammarid amphipods sp. 1	Uk	4–5	$-16.4 \pm 0.6$	$4.9 \pm 0.2$	3(30)
Amphipoda	Gammarid amphipods sp. 2	Uk	10	-23.5	6.3	1(10)
Atyidae	NI Atyidae	H/O	5–10	$-19.7 \pm 0.2$	$5.3 \pm 0.1$	5(10–30)
Atyidae	<i>Caridina</i> sp.	H/O	15	-23.1	5.8	1(2)
Corixidae	NI Corixidae	O	6	-27.4	5.3	1(5)
Ephemeroptera	Mayfly larvae	C	10	-20.1	7.0	1(1)
Isopoda	Isopods sp. 1	Uk	7–10	$-19.3 \pm 0.2$	$7.0 \pm 0.1$	2(4)
Isopoda	Isopods sp. 2	Uk	3	$-19.3 \pm 0.0$	$5.0 \pm 0.1$	2(10)
Isopoda	Isopods sp. 3	Uk	3	$-19.4 \pm 0.4$	$6.8 \pm 0.4$	2(30)
Mytilidae	Mytilidae sp. 2	Pl	15–20	$-23.7 \pm 0.3$	$4.1 \pm 0.1$	3(30)
Naticidae	<i>Neverita didyma</i>	C	20–22	$-25.5 \pm 0.2$	$6.5 \pm 0.2$	3(3)
Odonata	Dragonfly larvae	C	10	$-23.0 \pm 0.3$	$7.5 \pm 0.3$	2(1)
Palaemonidae	<i>Macrobrachium</i> sp.	O	33–50	$-22.8 \pm 0.5$	$7.5 \pm 0.0$	3(1–2)
Palaemonidae	<i>Palaemonetes</i> sp.	O	30–35	$-23.6 \pm 0.5$	$6.4 \pm 0.1$	3(5)
Penaeidae	<i>Metapenaeus monoceros</i>	O	60–65	$-19.9 \pm 0.2$	$5.7 \pm 0.0$	3(15)
Portunidae	<i>Scylla serrata</i>	C	100	-20.5	7.1	1(1)
Potamididae	<i>Terebralia palustris</i>	MPB	25–30	$-8.4 \pm 0.7$	$3.3 \pm 0.1$	4(5–7)
Varunidae	<i>Varuna</i> sp.	H	20–45	$-21.1 \pm 0.4$	$6.7 \pm 0.4$	4(1)
Fish ( <i>n</i> = 24)						
Ambassidae	<i>Ambassis natalensis</i>	Pl	15–25	$-23.8 \pm 0.7$	$7.7 \pm 0.1$	5(2;12–13)
Ambassidae	<i>A. natalensis</i>	Pl	60–75	$-17.3 \pm 0.3$	$9.2 \pm 0.1$	3(7–8)
Atherinidae	<i>Atherinomorus lacunosus</i>	Pl	40–55	$-23.5 \pm 0.4$	$9.1 \pm 0.1$	3(8)
Carangidae	<i>Caranx papuensis</i>	Pi	80–160	$-19.1 \pm 0.2$	$8.2 \pm 0.1$	4(1–2)
Channidae	<i>Channa maculata</i>	Pi	100–110	$-21.9 \pm 0.3$	$7.9 \pm 0.0$	2(1)
Channidae	<i>C. maculata</i>	Pi	190–350	$-20.5 \pm 0.8$	$9.1 \pm 0.2$	4(2–3)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	70–165	$-19.2 \pm 0.3$	$5.5 \pm 0.3$	6(1–3)
Cichlidae	<i>Oreochromis niloticus</i>	PD	90	-21.2	6.4	1(1)
Cichlidae	<i>O. niloticus</i>	PD	130	-15.0	6.8	1(1)
Cichlidae	<i>Tilapia zillii</i>	PD	210	-19.3	6.5	1(1)
Cichlidae	<i>Paretroplus polyactis</i>	O	60–70	$-26.1 \pm 0.0$	$9.7 \pm 0.3$	2(2)
Cichlidae	<i>P. polyactis</i>	Uk	85–220	$-22.1 \pm 1.0$	$7.9 \pm 0.2$	4(3–5)
Cichlidae	<i>Ptychochromis grandidieri</i>	O	45–65	$-15.5 \pm 1.1$	$8.3 \pm 0.7$	2(2)
Cichlidae	<i>P. grandidieri</i>	O	75–135	$-18.2 \pm 0.3$	$7.2 \pm 0.3$	5(8–10)
Cichlidae	NI Cichlid 1	Uk	60–70	$-8.1 \pm 0.4$	$8.7 \pm 0.4$	3(1)
Cichlidae	NI Cichlid 2	Uk	110–155	$-19.6 \pm 1.0$	$6.1 \pm 0.5$	2(2)
Cichlidae	NI Cichlid 3	Uk	55–90	$-25.2 \pm 1.1$	$7.7 \pm 0.1$	2(3–4)
Cichlidae	NI Cichlid 4	Uk	55–65	$-23.3 \pm 0.1$	$7.1 \pm 0.1$	3(3)
Clupeidae	<i>Sauvagella madagascariensis</i>	Pl	35–60	$-25.6 \pm 1.0$	$8.4 \pm 0.1$	5(1)
Eleotridae	<i>Eleotris</i> sp.	C	60–80	$-19.8 \pm 0.5$	$7.5 \pm 0.0$	3(3)
Gerreidae	<i>Gerres filamentosus</i>	C	105	-16.2	8.7	1(1)
Gobiidae	<i>Glossogobius giuris</i>	C	45–100	$-19.9 \pm 0.4$	$7.8 \pm 0.1$	3(6–9)
Gobiidae	<i>G. giuris</i>	C	200–300	$-19.1 \pm 0.5$	$8.4 \pm 0.1$	3(4–7)
Teraponidae	<i>Terapon jarbua</i>	C	95	-17.4	9.0	1(1)
Tana ( <i>n</i> = 59)						
Invertebrates ( <i>n</i> = 28)						
Alpheidae	NI Alpheid 1	Uk	5–10	$-13.0 \pm 0.5$	$12.4 \pm 0.2$	2(2–3)
Alpheidae	NI Alpheid 2	Uk	10–17	$-15.3 \pm 0.1$	$11.8 \pm 0.2$	4(3–5)
Amphipoda	NI Gammarids sp. 1	Uk	3–5	$-15.2 \pm 0.3$	$9.5 \pm 0.1$	2(30)
Amphipoda	NI Gammarids sp. 2	Uk	10	$-14.6 \pm 0.3$	$10.7 \pm 0.4$	3(10)
Amphipoda	NI Gammarids sp. 3	Uk	10	-22.6	9.3	1(10)
Balanidae	<i>Balanus</i> sp.	Pl	15–17	$-18.4 \pm 0.1$	$12.0 \pm 0.0$	3(10)
Littorinidae	<i>Littoraria scabra</i>	H	4–6	$-22.3 \pm 0.3$	$1.8 \pm 0.6$	4(3)
Ocyrodidae	<i>Ocyrode ceratophthalmus</i>	C	27–35	$-14.8 \pm 0.0$	$12.0 \pm 0.1$	2(1)
Ocyrodidae	<i>Ocyrode madagascariensis</i>	C	12	$-18.0 \pm 0.6$	$9.9 \pm 0.2$	2(1)
Ocyrodidae	<i>Ocyrode</i> sp.	C	3–7	$-13.0 \pm 0.3$	$11.5 \pm 0.1$	2(1)
Ocyrodidae	<i>Uca</i> sp.	MPB	3	$-16.2 \pm 0.5$	$10.2 \pm 0.1$	3(3)
Ocyrodidae	<i>Uca urvillei</i>	MPB	25	$-15.6 \pm 0.5$	$9.4 \pm 0.2$	3(3)
Palaemonidae	<i>Macrobrachium</i> sp. 1	O	100	$-21.1 \pm 0.4$	$11.6 \pm 0.1$	2(1)
Palaemonidae	<i>Macrobrachium</i> sp. 2	O	45–50	$-18.6 \pm 0.1$	$12.6 \pm 0.1$	3(10)
Palaemonidae	NI Caridean	O	40–45	$-17.6 \pm 0.2$	$11.7 \pm 0.0$	3(15)
Penaeidae	<i>Metapenaeus monoceros</i>	PD	20–25	$-12.2 \pm 0.4$	$12.8 \pm 0.1$	4(5)

Table A1. Continued.

Family	Species	Diet	Size	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>
Penaeidae	<i>M. monoceros</i>	O	40–45	$-12.7 \pm 1.0$	$8.3 \pm 0.9$	3(2)
Penaeidae	<i>M. monoceros</i>	O	65–70	$-20.6 \pm 0.3$	$11.1 \pm 0.3$	2(1)
Penaeidae	<i>Penaeus indicus</i>	O/C	70–75	$-18.3 \pm 0.2$	$10.1 \pm 0.2$	3(3)
Penaeidae	<i>P. indicus</i>	O/C	75–120	$-18.4 \pm 0.4$	$9.6 \pm 0.2$	4(3)
Penaeidae	<i>Penaeus monodon</i>	C	55–65	$-18.5 \pm 0.1$	$11.0 \pm 0.3$	3(3)
Penaeidae	Penaeidae postlarvae	PI	13–14	$-19.4 \pm 0.3$	$9.9 \pm 0.2$	3(5)
Polychaeta	NI Polychaeta	C	9	-17.1	12.3	1(5)
Portunidae	<i>Scylla serrata</i>	C	130–140	$-18.9 \pm 2.0$	$12.2 \pm 0.4$	2(1)
Potamididae	<i>Terebralia palustris</i>	MPB	20–25	$-18.9 \pm 0.1$	$8.2 \pm 0.1$	3(5)
Sergestidae	<i>Acetes erythraeus</i>	PI	13–16	$-19.3 \pm 0.1$	$10.8 \pm 0.1$	3(15)
Sesamidae	<i>Sesarma meinerti</i>	H	8	$-13.9 \pm 0.7$	$11.6 \pm 0.4$	3(5)
Tanaidacea	NI Tanaids	Uk	3	-13.7	9.6	1(30)
Fish ( <i>n</i> = 29)						
Ambassidae	<i>Ambassis ambassis</i>	PI	35–40	$-24.0 \pm 0.6$	$10.3 \pm 0.1$	4(3–4)
Ambassidae	<i>A. natalensis</i>	PI	45–55	$-17.7 \pm 0.3$	$12.5 \pm 0.2$	3(3–4)
Ariidae	<i>Galeichthys feliceps</i>	C	65–100	$-18.4 \pm 0.6$	$13.1 \pm 0.2$	1(1)
Ariidae	<i>G. feliceps</i>	C	200–300	$-17.1 \pm 0.1$	$13.3 \pm 0.2$	2(3)
Carangidae	Carangid juveniles	C	35–45	$-19.1 \pm 0.4$	$11.2 \pm 0.2$	3(3)
Cichlidae	<i>Oreochromis mossambicus</i>	PD	70–100	$-27.5 \pm 0.8$	$8.5 \pm 1.4$	3(1)
Clariidae	<i>Clarias gariepinus</i>	C	180	-15.9	12.6	1(1)
Claroteidae	<i>Clarotes laticeps</i>	C	360	-20.4	10.2	1(1)
Clupeidae	<i>Herklotsichthys quadrimaculatus</i>	PI	65–85	$-17.7 \pm 0.1$	$14.2 \pm 0.1$	3(15)
Clupeidae	<i>Sardinella albella</i>	PI	55–58	$-17.5 \pm 0.2$	$12.0 \pm 0.0$	2(1)
Cynoglossidae	<i>Paraplagusia bilineata</i>	C	94	-17.8	12.9	1(1)
Engraulidae	<i>Engraulis</i> sp.	PI	35–38	$-20.7 \pm 0.1$	$13.7 \pm 0.0$	2(1)
Engraulidae	<i>Thryssa vitrirostris</i>	PI	45–50	$-18.1 \pm 0.1$	$13.7 \pm 0.3$	2(3)
Engraulis	<i>Engraulis</i> sp.	PI	57–60	$-17.1 \pm 0.4$	$12.3 \pm 0.4$	3(1)
Gobiidae	NI Gobiidae	Uk	45	-20.6	12.9	1(1)
Haemulidae	<i>Pomadasys olivaceum</i>	C	120–145	$-19.2 \pm 0.4$	$12.9 \pm 0.1$	3(1)
Leiognathidae	<i>Leiognathus equulus</i>	C	20–25	$-18.0 \pm 0.3$	$12.5 \pm 0.2$	6(3–5)
Lutjanidae	Lutjanidae juvenile	C	75	-17.4	12.9	1(1)
Lutjanidae	<i>Lutjanus bohar</i>	C	280	-18.8	13.2	1(1)
Megalopidae	<i>Megalops cyprinoides</i>	C	160	-18.7	12.8	1(1)
Megalopidae	<i>M. cyprinoides</i>	C	320	-23.3	10.0	1(1)
Mugilidae	Mugilid juveniles	PD	25–28	$-18.1 \pm 0.2$	$10.4 \pm 0.2$	3(3)
Mugilidae	NI Mugilid sp. 1	PD	60–65	$-17.2 \pm 0.0$	$12.6 \pm 0.1$	2(2)
Mugilidae	NI Mugilid sp. 2	PD	65–85	$-13.6 \pm 0.2$	$11.8 \pm 0.2$	3(4–6)
Mugilidae	<i>Valamugil seheli</i>	PD	35–50	$-15.6 \pm 0.3$	$11.0 \pm 0.3$	3(5)
Sciaenidae	<i>Johnius dorsalis</i>	C	95–100	$-16.7 \pm 0.2$	$13.1 \pm 0.1$	3(5)
Sillaginidae	<i>Sillago sihama</i>	C	75–120	$-16.0 \pm 0.6$	$13.4 \pm 0.2$	4(3)
Tetraodontidae	<i>Chelonodon patoca</i>	O	30–37	$-17.9 \pm 0.3$	$12.6 \pm 0.1$	3(2)
Unknown	Fish larvae	PI	6–7	$-18.8 \pm 0.2$	$9.8 \pm 0.2$	3(3–4)

## APPENDIX B

Table B1. Bayesian isotope mixing model (SIAR) results (mode of percentage contribution followed by 95% credibility intervals) for the contribution of the different classes of producers for the different consumer trophic guilds collected at the C4-dominated sites of Betsiboka and Tana. SD  $\delta^{13}\text{C}$  and SD  $\delta^{15}\text{N}$  are the residual error, i.e., the variability in  $\delta^{13}\text{C}/\delta^{15}\text{N}$  (in ‰) that can not be explained by diet alone. For the Betsiboka, only  $\delta^{13}\text{C}$  was used as  $\delta^{15}\text{N}$  of the different producers was similar. For the Tana, models were based on both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . C3, C3 producers; C4, C4 producers.

Producer class	Betsiboka Pre-Wet	Betsiboka Post-Wet	Tana
Prawns/shrimps			
C3	2 (0–15)	2 (0–22)	23 (16–32)
C4	80 (71–85)	65 (57–78)	63 (53–72)
Plankton	21 (0–27)	33 (1–41)	13 (2–25)
SD $\delta^{13}\text{C}$ (‰)	1.0 (0.5–1.6)	1.5 (0.9–2.1)	2.9 (1.9–4.2)
SD $\delta^{15}\text{N}$ (‰)			0.1 (0.0–1.3)
Phytodetritivorous fish			
C3	3 (0–18)	3 (0–19)	3 (0–14)
C4	80 (61–91)	75 (61–84)	67 (56–78)
Plankton	8 (0–34)	21 (0–35)	29 (12–41)
SD $\delta^{13}\text{C}$ (‰)	2.3 (1.4–4.3)	2.0 (1.4–3.1)	1.2 (0.0–2.7)
SD $\delta^{15}\text{N}$ (‰)			0.1 (0.0–1.6)
Planktivores			
C3	25 (16–35)	10 (2–35)	20 (12–29)
C4	59 (51–66)	42 (35–60)	58 (51–65)
Plankton	14 (0–32)	46 (5–63)	22 (9–33)
SD $\delta^{13}\text{C}$ (‰)	0.1 (0.0–0.5)	0.9 (0.0–1.3)	0.1 (0.0–1.1)
SD $\delta^{15}\text{N}$ (‰)			0.1 (0.0–1.4)
Carnivores			
C3	4 (0–25)	5 (0–31)	30 (23–36)
C4	58 (53–73)	46 (41–65)	59 (54–64)
Plankton	40 (2–46)	50 (4–59)	11 (2–20)
SD $\delta^{13}\text{C}$	1.1 (0.7–1.6)	1.5 (1.1–1.8)	0.1 (0.0–1.0)
SD $\delta^{15}\text{N}$			0.1 (0.0–1.0)
Piscivores			
C3	24 (14–33)	4 (0–32)	51 (28–68)
C4	60 (54–68)	42 (36–62)	40 (21–53)
Plankton	15 (0–31)	55 (7–64)	4 (0–35)
SD $\delta^{13}\text{C}$	0.0 (0.0–0.5)	1.1 (0.1–1.4)	0.4 (0.0–5.3)
SD $\delta^{15}\text{N}$			0.7 (0.0–6.8)

APPENDIX C

Table C1. Bayesian isotope mixing model (SIAR) results (mode of percentage contribution followed by 95% credibility intervals) for the contribution of the different classes of producers for the different consumer trophic guilds collected at the C3-dominated sites of Zambezi, Rianila and Ambila. When distribution of consumers was bimodal, results are presented for each group separately. SD  $\delta^{13}\text{C}$  and SD  $\delta^{15}\text{N}$  are the residual error, i.e., the variability in  $\delta^{13}\text{C}/\delta^{15}\text{N}$  (in ‰) that can not be explained by diet alone. For the Zambezi, only  $\delta^{13}\text{C}$  was used as  $\delta^{15}\text{N}$  of the different producers was similar. For the Rianila and Ambila, models were based on both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . C3, C3 producers; C4, C4 producers; FGA, filamentous green algae; macroalgae are *Enteromorpha* sp. and *Chaetomorpha* sp.

Producer class	Zambezi		Rianila		Ambila	
	Pre-Wet	Post-Wet	Pre-Wet	Post-Wet	Pre-Wet	Post-Wet
Prawns/shrimps						
C3	28 (19–46)	36 (21–54)	29 (10–55)	32 (18–45) 17 (3–27)	21 (4–34)	26 (13–40)
C4	32 (24–51)	28 (11–45)	2 (0–17)	1 (0–14) 8 (0–21)	2 (0–16)	18 (0–28)
Plankton	40 (2–56)	36 (2–66)	36 (3–53)	5 (0–22) 10 (0–21)	26 (6–40)	24 (3–38)
Benthic algae			5 (0–20)	8 (0–16) 7 (0–16)	2 (0–20)	9 (0–29)
FGA1			6 (0–37)	13 (0–33) 17 (0–28)	3 (0–22)	
FGA2				2 (0–22) 14 (0–26)		
Epiliths				14 (0–31) 17 (1–30)		
Epiphytes					19 (0–36)	23 (2–40)
<i>R. maritima</i>			2 (0–13)	1 (0–12) 11 (0–22)		
Macroalgae					15 (0–26)	
SD $\delta^{13}\text{C}$ (‰)	1.5 (0.0–2.1)	2.0 (0.1–2.7)	1.9 (0.1–2.9)	0.1 (0.0–1.0) 0.2 (0.0–1.6)	1.4 (0.0–2.5)	1.4 (0.0–3.1)
SD $\delta^{15}\text{N}$ (‰)			1.0 (0.7–1.5)	0.1 (0.0–1.6) 0.1 (0.0–1.6)	0.8 (0.1–1.5)	0.1 (0.0–1.2)
Phytodetritivores						
C3	59 (45–69)	39 (18–58)	29 (11–50)	15 (3–25)	16 (0–28)	1 (0–16)
C4	22 (9–33)	24 (2–42)	3 (0–27)	2 (0–16)	2 (0–21)	14 (0–34)
Plankton	22 (0–43)	38 (2–77)	18 (0–39)	5 (0–16)	19 (0–32)	27 (4–44)
Benthic algae			1 (0–10)	14 (6–21)	3 (0–23)	28 (2–42)
FGA1			3 (0–27)	17 (1–34)	3 (0–25)	
FGA2				14 (0–28)		
Epiliths				17 (1–32)		
Epiphytes					19 (1–38)	29 (4–51)
<i>R. maritima</i>			28 (9–39)	5 (0–18)		
Macroalgae					20 (1–37)	
SD $\delta^{13}\text{C}$ (‰)	0.4 (0.0–1.4)	2.8 (0.3–0.3)	2.2 (0.9–3.8)	1.0 (0.6–1.9)	0.3 (0.0–4.2)	1.3 (0.0–3.1)
SD $\delta^{15}\text{N}$ (‰)			0.8 (0.5–1.2)	0.1 (0.0–0.5)	0.3 (0.0–5.2)	0.9 (0.0–1.9)
Planktivores						
C3	28 (15–33) 56 (40–62)	54 (46–63) 31 (23–34)	24 (8–37)	20 (8–31)	18 (0–36)	23 (9–36)
C4	65 (52–70) 37 (21–43)	30 (22–39) 64 (57–68)	18 (0–32)	3 (0–17)	2 (0–20)	5 (0–21)
Plankton	6 (0–31) 4 (0–37)	14 (0–31) 6 (0–19)	4 (0–23)	11 (0–21)	21 (2–39)	26 (3–42)
Benthic algae			10 (0–29)	13 (4–21)	2 (0–22)	4 (0–24)
FGA1			20 (0–36)	18 (0–30)	2 (0–24)	
FGA2				11 (0–26)		
Epiliths				17 (0–29)		
Epiphytes					20 (0–40)	31 (12–55)
<i>R. maritima</i>			19 (1–35)	2 (0–16)		
Macroalgae					5 (0–29)	
SD $\delta^{13}\text{C}$ (‰)	0.1 (0.0–1.0)	0.4 (0.0–1.0)	0.1 (0.0–1.6)	1.2 (0.7–2.2)	1.6 (0.0–28.3)	3.2 (1.6–5.3)
SD $\delta^{15}\text{N}$ (‰)	0.1 (0.0–1.2)	0.1 (0.0–0.6)				
SD $\delta^{15}\text{N}$ (‰)			2.1 (0.9–7.1)	0.1 (0.0–0.7)	0.2 (0.0–2.9)	0.1 (0.0–0.7)



Table C1. Continued.

Producer class	Zambezi		Rianila		Ambila	
	Pre-Wet	Post-Wet	Pre-Wet	Post-Wet	Pre-Wet	Post-Wet
<b>Carnivores</b>						
C3	36 (18–51)	30 (15–46)	15 (0–33)	28 (13–44)	14 (0–26)	35 (23–43)
C4	30 (12–46)	34 (19–50)	2 (0–18)	1 (0–15)	19 (2–33)	27 (10–50)
Plankton	35 (3–69)	35 (5–66)	25 (2–46)	6 (0–33)	4 (0–24)	2 (0–20)
Benthic algae			30 (15–46)	17 (10–26)	20 (0–31)	19 (0–40)
FGA1			12 (0–36)	3 (0–28)	19 (0–31)	
FGA2				2 (0–20)		
Epiliths				2 (0–22)		
Epiphytes					5 (0–26)	2 (0–20)
<i>R. maritima</i>			1 (0–12)	1 (0–11)		
Macroalgae					10 (0–23)	
SD $\delta^{13}\text{C}$	2.0 (0.1–2.7)	1.9 (0.1–2.4)	2.1 (0.5–2.9)	2.2 (1.7–2.9)	2.2 (1.3–3.8)	1.2 (0.2–2.3)
SD $\delta^{15}\text{N}$			1.4 (1.1–1.8)	1.2 (0.4–1.7)	1.5 (0.9–2.3)	0.1 (0.0–1.2)
<b>Piscivores</b>						
C3	49 (33–55)	25 (16–42)	25 (4–41)	16 (2–27)	28 (13–46)	30 (19–43)
	26 (12–31)			34 (16–54)		
C4	42 (27–49)	37 (28–55)	2 (0–19)	9 (0–23)	3 (0–25)	24 (5–41)
	67 (53–73)			1 (0–15)		
Plankton	10 (0–37)	38 (2–55)	28 (4–47)	17 (1–24)	13 (0–27)	17 (0–27)
	8 (0–33)			16 (0–32)		
Benthic algae			19 (2–31)	13 (5–21)	5 (0–26)	18 (0–36)
				3 (0–15)		
FGA1			13 (0–39)	14 (0–26)	13 (0–30)	
				5 (0–30)		
FGA2				12 (0–24)		
				2 (0–19)		
Epiliths				11 (0–24)		
				5 (0–28)		
Epiphytes					15 (0–31)	12 (0–28)
<i>R. maritima</i>			1 (0–13)	8 (0–20)		
				1 (0–12)		
Macroalgae					1 (0–14)	
SD $\delta^{13}\text{C}$	0.2 (0.0–1.3)	1.4 (0.0–2.0)	1.6 (0.0–2.6)	0.5 (0.0–0.8)	1.5 (0.0–4.9)	1.3 (0.0–2.5)
	0.1 (0.0–1.1)			0.5 (0.0–2.5)		
SD $\delta^{15}\text{N}$			0.6 (0.4–1.0)	0.5 (0.0–1.0)	0.2 (0.0–2.0)	0.1 (0.0–1.1)
				0.2 (0.0–2.3)		