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Post-flood dietary variation in the Mozambique tilapia *Oreochromis mossambicus* in the St Lucia Estuary, South Africa

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ABSTRACT: Although originally endemic to southern Africa, the Mozambique tilapia *Oreochromis mossambicus* is now among the most widely distributed exotic fish species worldwide. It has become the dominant fish species in the St Lucia estuarine lake (South Africa) since the closure of the mouth in 2002 and is therefore a crucial component of the food webs throughout the system. Following a decade-long drought phase, the estuary has received a large amount of freshwater inflow since 2011, resulting in a salinity decrease throughout the system. We compared dietary composition of *O. mossambicus* among 3 sites across a salinity gradient between the hypersaline and diluted stage to determine whether environmental conditions influence the diet of this species. Stable isotope analysis of carbon and nitrogen were used in conjunction with gut content analysis to elucidate dietary composition. A wide range of dietary sources was found during the hypersaline stage, with all sources contributing similar proportions to the diet. However, during the diluted stage that currently prevails in the system, specific dietary sources such as sediment organic matter were more dominant in the diet. Trophic position and salinity showed a significant negative relationship, indicating the adaptability of this species to salinity changes. A high degree of variability in the stomach contents of these fish was identified, with clear differences among sites and between seasons. This is an indication of the trophic plasticity that this species exhibits, which aids its ability to adapt to different environmental conditions and dominate the fish community throughout the St Lucia estuarine system.

KEY WORDS: *Oreochromis mossambicus* · iSimangaliso Wetland Park · Stable isotopes · Diet

INTRODUCTION

Oreochromis mossambicus (Peters, 1852) is endemic to southern Africa, inhabiting coastal lakes, river systems and estuaries from the lower Zambezi River System in Mozambique to the Bushmans River in South Africa (Whitfield & Blaber 1979, Skelton 1993, Whitfield 1998). This species is considered among the most widely distributed exotic fish species across the world, having successfully colonised 90 countries into which it has been introduced (De Silva et al. 2004, Canonico et al. 2005, Casal 2006). This expansion has threatened native fish populations globally (Canonico et al. 2005, Casal 2006). Understanding the dietary response of this species to changes in environmental conditions is thus of crucial importance, not only to ecosystems within its native range, but to all systems where it has been introduced.

The St Lucia Estuary is the most extensive estuarine lake in Africa, forming a vital part of the iSimangaliso (formerly Greater St Lucia) Wetland Park, which is South Africa's first UNESCO World Heritage Site (Taylor 2006). Until recently, the system has experienced an exceptional dry phase, which started in 2002 and ended with the onset of the latest La Niña event in 2011. The St Lucia estuarine system

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experiences a characteristic alternation of wet and dry phases, with each persisting between 4 and 10 yr at a time (Begg 1978). The estuary mouth has also been closed naturally since June 2002, with a brief interruption from March to August 2007 caused by cyclonic activity over the ocean. Since 2002, the area has recorded below average rainfall and thus has received limited freshwater input, with the main source of freshwater being the Mpate River which flows into the Narrows (see Fig. 1). This lack of freshwater inflow has resulted in much of the surface area of the lake exhibiting low water levels (<30 cm) or complete desiccation. All of these conditions have led to the formation of a persistent reverse salinity gradient within the system, with the upper reaches of the estuarine lake exhibiting much higher salinity levels (40–200) than its lower reaches and the mouth region (10–25; Taylor 2006, Carrasco et al. 2012). Salinity is the most important factor affecting fish community structure within the estuarine environment (Blaber & Blaber 1980, Harrison & Whitfield 2006, Whitfield et al. 2006, Vivier et al. 2010). A period of high rainfall started during December 2010/January 2011, resulting in high freshwater inflow into the system and raising water levels and diluting salinities throughout the system.

Since the closure of the mouth in 2002, a ca. 40% loss in fish species richness has occurred throughout the estuarine system (Whitfield 1980, Cyrus et al. 2010, Vivier et al. 2010), with *Oreochromis mossambicus* dominating the fish community (Vivier et al. 2010). Its dominance throughout the system is considered indicative of the extent to which the fish community has been affected, because in the St Lucia system, this species is usually less dominant than other marine associated species (Whitfield & Blaber 1978). The primary reason for this dominance is that under hypersaline conditions, *O. mossambicus* is able to out-compete estuarine species as well as marine species, that use the estuary as nursery area (Whitfield & Blaber 1978). *O. mossambicus* is highly tolerant of a wide range of environmental conditions, surviving in fresh, brackish and marine waters, and is capable of breeding in salinity levels up to 120 (Cyrus & Vivier 2006, Whitfield et al. 2006). This highly fecund species can tolerate temperatures <15 to >40°C (Allanson et al. 1971, Whitfield & Blaber 1979, Behrends et al. 1990, Skelton 1993, Whitfield 1998, Ellender et al. 2008, Doupé et al. 2010). In St Lucia, this species is extremely euryhaline, surviving and breeding successfully in salinities of 70 to 120 in False Bay and parts of the North Lake (Cyrus &Vivier 2006, Whitfield et al. 2006). Skelton (1993) found that *O. mossambicus* is predominantly herbivorous, feeding on algae (especially diatoms) and detritus, with larger individuals occasionally feeding on insects and other invertebrates. This species is an opportunistic forager, feeding on a wide array of dietary components (Bruton & Boltt 1975, Whitfield & Blaber 1979). Epiphytic pennate diatoms are the main dietary food source for this fish, but the availability of this food source is unknown under hypersaline conditions (Vivier et al. 2010). *O. mossambicus* also forms a vital food source for many key species, such as the great white pelican, crocodiles and piscivorous fish and bird species, thus forming an important link in the food webs of this ecosystem (Whitfield 1998, Cyrus & Vivier 2006, Bowker & Downs 2008).

Understanding the trophic links and pathways of organic matter in estuarine food webs has critical impacts on the management of such systems (Stephenson & Lyon 1982). Therefore, information regarding the dietary composition of a critical link in estuarine food webs, such as *Oreochromis mossambicus*, across a salinity gradient is vital. Stable isotope analysis has proven to be an essential companion to gut content analysis, as it provides a better temporal indication of the diet of an organism, rather than a 'snapshot' or temporally biased view which would be obtained from gut content analysis alone (Hesslein et al. 1993, Van der Zanden et al. 1997). Pinnegar & Polunin (1999) have shown that not all dietary material will be well represented in gut contents, whereas isotope analysis will give a more accurate estimate of dietary composition over a longer period of time. This is especially true in fish muscle, where turnover times per day can be as slow as 0.1 to 0.2% (Hesslein et al. 1993). Due to the fact that stable carbon isotopes fractionate very little between energy transfers, they can be confidently used to quantify food sources in aquatic systems (Gannes et al. 1998). Stable nitrogen isotopes are known to fractionate more and are thus used to determine trophic positions of consumers in food webs (DeNiro & Epstein 1978).

Due to climate change, the area around the St Lucia estuarine system is likely to become warmer and wetter as we approach the year 2100 (Været & Sokolic 2008). Understanding how the diet of a dominant fish species within the system may change based on changes in the environmental conditions can be vital in predicting how the system functioning could respond to these natural changes in the future. We therefore aimed to determine whether any evidence exists to suggest that *Oreochromis mossambicus* changes its diet as a result of environmental forcing, in particular the effect of different salinity levels.

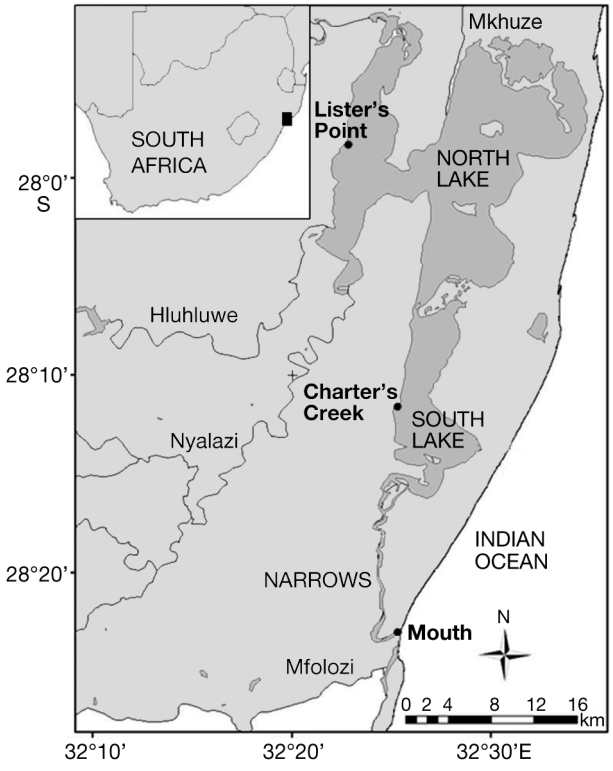

Fig. 1. St Lucia estuarine system, indicating sampling stations (●) and geographic position within South Africa (adapted from Carrasco et al. 2012)

To achieve this, a temporal (seasonal) and spatial comparison was made between the diet of this species during hypersaline conditions and diluted (less saline) conditions.

MATERIALS AND METHODS

Habitat characteristics

A YSI 6029 multi-probe system with 650 MDS data logger was used to measure *in situ* physico-chemical variables such as salinity, temperature, dissolved oxygen, pH and turbidity. Measurements were made at the sediment–water interface at all sites. Seasonal variation in the northern region of KwaZulu-Natal is characterized by wet periods, when rainfall is regular, and dry periods, when rainfall is almost absent. Therefore, sampling was carried out in February 2011 (wet season) and again in May 2011 (dry season), in order to assess the effects of this seasonal variation. Data from this study were then compared with those obtained from an earlier study conducted in 2008/2009 by Carrasco et al. (2012), under prevailing hypersaline conditions. Three representative sites were chosen along the western shore of the estuarine system, each exhibiting varying susceptibility to environmental change: the Mouth, which remains fairly stable in terms of salinity change; Charter's Creek, which is subject to large changes in salinity; and Lister's Point, which exhibits extreme changes in salinity (Fig. 1).

Field sampling and laboratory processing

Isotope material was collected for the fish *Oreochromis mossambicus* as well as any potential food sources which were present at the study sites at the time of sampling. Samples of sediment organic matter (SOM), detritus, microphytobenthos (MPB), particulate organic matter (POM), zooplankton, benthic macrofauna and dominant macroalgae (such as *Cladophora* sp.), as well as fringing vegetation were collected at the 3 study sites, where available.

Fish samples were collected using a cast net with a diameter of 2.44 m, operated from the shore. Hand nets were also used to collect individuals which were able to evade the cast net. A total of 50 *Oreochromis mossambicus* were collected at the 3 study sites during the wet and dry seasons and subsequently frozen (–20°C) prior to laboratory processing. Total length (in mm) for each fish collected was measured. Dorsal muscle samples were extracted from each individual, lipid-treated (Bligh & Dyer 1959) and dried at 60°C for 24 h. Using dorsal or other white muscle tissue for stable isotope analysis limits the variability in $\delta^{15}N$ values which can be associated with other tissue types (Pinnegar & Polunin 1999). A total of 52 fish were collected from the 3 study sites, ranging in size from 30 to 210 mm. Due to the fractionation of the estuarine system and the territorial nature of this fish species, we assumed that the fish sampled at the various sites are from that area of the lake and that there was restricted movement between sites (Turner 1986, Oliveira & Almada 1998).

Zooplankton samples were collected with an epibenthic sled (200 µm mesh, 37 cm diameter). Samples were concentrated onto 20 µm mesh filters, placed into Petri dishes and frozen (–20°C) prior to laboratory processing. In the laboratory, each sample was sorted into the dominant taxa present at the time of collection. Depending on the taxa, 20 to 200 whole individuals were used per replicate. Dominant taxa included the copepods *Pseudodiaptomus stuhlmanni*, *Acartiella natalensis* and *Oithona* sp., as well as the mysid

Mesopodopsis africana. Samples were then defatted for 2 h in a solution of methanol, chloroform and distilled water in the ratio 2:1:0.8, respectively (Bligh & Dyer 1959). Thereafter, samples were treated with 2% HCl to remove any carbonates (Lorrain et al. 2003, Carabel et al. 2006, Søreide et al. 2006) and then rinsed in excess distilled water before being dried at 60°C for 24 h in an air circulated oven.

Benthic macrofauna samples were collected using a Zabalocki-type Ekman grab. Three replicate samples were collected at each site, with each sample comprising 3 grabs. Replicate grabs were 2 to 3 m apart. Samples were emptied into buckets to which water was added and stirred vigorously, thereby suspending benthic invertebrates. The supernatant was washed through a 500 µm sieve. After repeating this process 5 times, any material retained on the sieve was emptied into a plastic jar, while the remaining sediment was washed through a 2000 µm sieve, in order to collect larger and heavier organisms, such as bivalves, gastropods or crustaceans. Samples were subsequently frozen to preserve them for laboratory processing. In the laboratory, the organisms were sorted into their dominant taxa. Single tissue samples were excised from larger bivalves, gastropods and crab specimens. For replication, samples were collected from 3 different individuals. These samples were treated with excess 2% HCl for 24 h in order to remove any shell fragments. Smaller gastropods and polychaetes were used whole. These were also treated with excess 2% HCl for 24 h to dissolve the shells of the gastropods and to ensure that no carbonate material clung to the polychaete appendages. Triplicate samples were prepared where possible, using as many individuals as necessary to achieve the desired weight (0.6 mg) of the sample for analysis.

Detritus material, from the foam layer near the water edge, was collected at each of the study sites when present, and kept frozen at –20°C until laboratory processing. After treating the samples with excess 2% HCl to remove possible biogenic carbonates, the samples were rinsed with distilled water and dried at 60°C for 24 h.

Samples of the dominant macroalgae, such as *Cladophora* sp. and *Ulva* sp., macrophytes and any fringing vegetation were collected, where available. After thoroughly rinsing the samples with distilled water, they were dried at 60°C for 24 h.

POM was sampled by collecting triplicate water samples from each study site. These were then filtered onto pre-combusted (450°C for 6 h) glass fibre filters (GF/F) using a vacuum filtration manifold. Once in the laboratory, filters were treated with excess 2% HCl to remove any inorganic carbon and placed into an air circulated oven at 60°C to dry for a period of 24 h.

Triplicate SOM samples were collected from each of the 3 study sites by removing the surface centimetre of sediment from a 20 mm diameter core and freezing it at –20°C prior to laboratory processing. Cores were collected at distances of 10 to 50 cm apart. Once in the laboratory, each sediment sample was treated with excess 2% HCl for a minimum of 24 h in order to remove any carbonates. Samples were thoroughly rinsed with distilled water and later dried at 60°C for 24 h in an air circulated oven.

MPB samples were collected in triplicate from each site by scraping the upper centimetre of sediment in areas of dense algal coverage, using the same coring method as for SOM collection. The samples were resuspended in filtered estuarine water, stirring them in order to keep the MPB in suspension while the heavier sediment sunk. The supernatant was then filtered onto a pre-combusted (450°C for 6 h) GF/F and frozen at –20°C prior to laboratory analysis. In areas of fine sediment, a method similar to that described by Couch (1989) was used to extract MPB. In the laboratory, the filters were treated with excess 2% HCl to remove any inorganic carbon in the form of calcium carbonate ($CaCO_3$). Filters were then dried again at 60°C for 24 h and frozen at –20°C for storage.

Stable isotope analysis

Once dry, sediment samples were milled and placed into Eppendorf microcentrifuge tubes, while filters were placed into tin foil envelopes. Animal, plant and algal tissues were ground into a homogenous mixture using a sterilized mortar and pestle, after which they were weighed in 5 × 8 mm tin capsules. For animal tissues, 0.6 mg of the homogenised tissue was weighed and packaged for isotope analysis. Plant and algal tissues required a larger sample to attain a signature and thus 2.0 mg of homogenised tissue was used. All samples were then sent to the Stable Light Isotope Unit, Department of Archaeology, University of Cape Town, South Africa, where they were analysed using a Thermo Finnigan Flash EA 1112 series elemental analyser equipped with a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer. Ratios were expressed as the parts per thousand deviation from the standard (atmospheric nitrogen for nitrogen and Vienna Pee Dee Belemnite for carbon) in delta (δ) notation according to:

$$\delta X = [(R_{Sample}/R_{Standard}) - 1] \times 1000 \quad (1)$$

where $X = {}^{13}C$ or ^{15}N and R = corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Based on the valine internal standard, a precision of 0.03 and 0.05‰ was attained with this method for carbon and nitrogen, respectively.

Dietary composition and trophic positioning

Gut content analysis was conducted on each of the tilapia specimens collected to gain a better perspective of the short-term dietary composition for the species. Specimens were gutted, and the entire gut was preserved in 10% phloxin-stained formalin solution prior to laboratory analysis. Each gut was analysed under a dissecting microscope, and the contents were identified as far as possible. Visible material was classified into the most likely dietary sources. Two methods were employed to quantify the contents following Hyslop (1980). A numerical abundance method was used for all dietary items which could be counted (zooplankton and other invertebrates), while an occurrence method was used to assess the proportion of fish which consumed specific dietary items. Where dietary items could not be counted, such as detritus and macroalgae, the proportion of the total gut content was estimated on a counting grid and expressed as a percentage.

Trophic position was calculated using the following formula outlined by Post (2002):

$$\text{Trophic position} = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta_n \quad (2)$$

where $\delta^{15}N_{consumer}$ is the nitrogen isotope signature of the fish and $\delta^{15}N_{base}$ is that of the food base chosen based on its relative position to the consumer, λ refers to the trophic level of the base ($\lambda = 1$ for primary producers), and Δ_n is the average trophic enrichment of nitrogen (3.4‰). This provided an estimate of how far the consumer is from the trophic base, which was selected separately for each site and season.

Statistical analysis

Statistical analyses were performed using IBM SPSS Statistics version 19 for Windows. Stable carbon and nitrogen isotope ratios of all possible food sources were analysed using a 2-way analysis of variance (ANOVA) in order to determine potential differences between the sources in the wet and dry seasons, and among the study sites. Tukey's HSD post hoc comparisons were performed to determine specific differences between sources. Data were checked for normality, and the residuals of the ANOVA were checked for homoscedasticity to ensure that the assumptions of the test were met. Although the assumption of homoscedasticity was not met for any of the data, Zar (1996) stated that ANOVA is robust enough to overcome this.

Following Parnell et al. (2010), Stable Isotope Analysis in R (SIAR) version 4.0 was used to create a mixing model, based on the standard corrected carbon and nitrogen ratios, in order to determine the likely contribution of each potential food item to the diet of *Oreochromis mossambicus* at the 3 study sites during the wet and dry season. A trophic enrichment factor, using values of 3.4‰ for $\delta^{15}N$ and 1‰ for $\delta^{13}C$ (Smit 2001, Carrasco et al. 2012), was incorporated in the model. A standard deviation of 1‰ was used for both carbon and nitrogen signatures, to remove any bias in the variability of trophic fractionation among the sources (Caut et al. 2009, Inger et al. 2010). All possible dietary items collected at the sampling sites during the different seasons were used to run the models. Where samples were not collected, this source was excluded from the model, as no signature was available.

The Primer (version 6) multivariate statistics package (Clarke & Gorley 2006) was used to test for dietary differences among the 3 sampling sites based on the gut contents. An analysis of similarity (ANOSIM) was performed, and a non-metric multidimensional scaling (NMDS) plot of the data from all 3 sampling locations, taking both the wet and dry season into account, was constructed. The ANOSIM calculates a global R value using randomization to determine the average of the ranked dissimilarities within and among groups. An R value of 1 indicates the greatest dissimilarity possible, and a value of 0 indicates no dissimilarity. A 1-way ANOSIM was used to test for differences among the different sampling sites. The data were log transformed in order to minimise the effect of dietary items that were dominant, thus accounting for total dietary composition. A Bray-Curtis similarity coefficient was used to calculate the similarity of the data among sites. This similarity matrix was then used to create the NMDS plots, using 100 iterations in order to generate the most likely outcome. A 2-dimensional plot was generated from the output of the analysis. Clusters were identified by eye based on proximity and indicated on the figure.

A linear regression was performed on the $\delta^{15}N$ and $\delta^{13}C$ signatures of *Oreochromis mossambicus*

against the measured lengths of the fish sampled, in order to determine whether there was a significant relationship between fish size and the relative isotope ratios. The assumption of normality of data was checked prior to running the test, and it was satisfied. A linear regression was also performed on the calculated trophic level of *O. mossambicus* and the physico-chemical parameters which were measured at the sampling sites, in order to test whether these affect the trophic level of the fish at the sampling sites. The assumptions of this test were also met.

RESULTS

Physico-chemical characteristics of study sites

From the physico-chemical data (Fig. 2), it is evident that the condition of the system has changed between the hypersaline stage in 2009 and the diluted stage in 2011. The salinity at the Mouth remained more stable over both periods, with values remaining in a narrow range around 10 to 15. During the hypersaline period, the salinity at Charter's Creek was 53.6 in the dry season (Carrasco et al. 2012), compared to 16.4 for the dry season during the diluted period. Salinities of 44.7 and 57.2 for the wet and dry season, respectively, were recorded at Lister's Point during the diluted period. During the hypersaline period, salinities of 141 and 85.5 were recorded for the wet and dry season, respectively, which gives an indication of the extreme nature of this area.

During the diluted stage, temperature ranged from 22.1°C at Lister's Point in the wet season to 31.3°C during the dry season. Turbidity was highest at Charter's Creek in the dry season (106 NTU) and lowest at the Mouth during the wet season (7.8 NTU). Depth ranged from 0.15 m at Charter's Creek in the dry season to 0.46 m at the Mouth in the wet season. These conditions were markedly different from those recorded by Carrasco et al. (2012) for the hypersaline stage (Fig. 2).

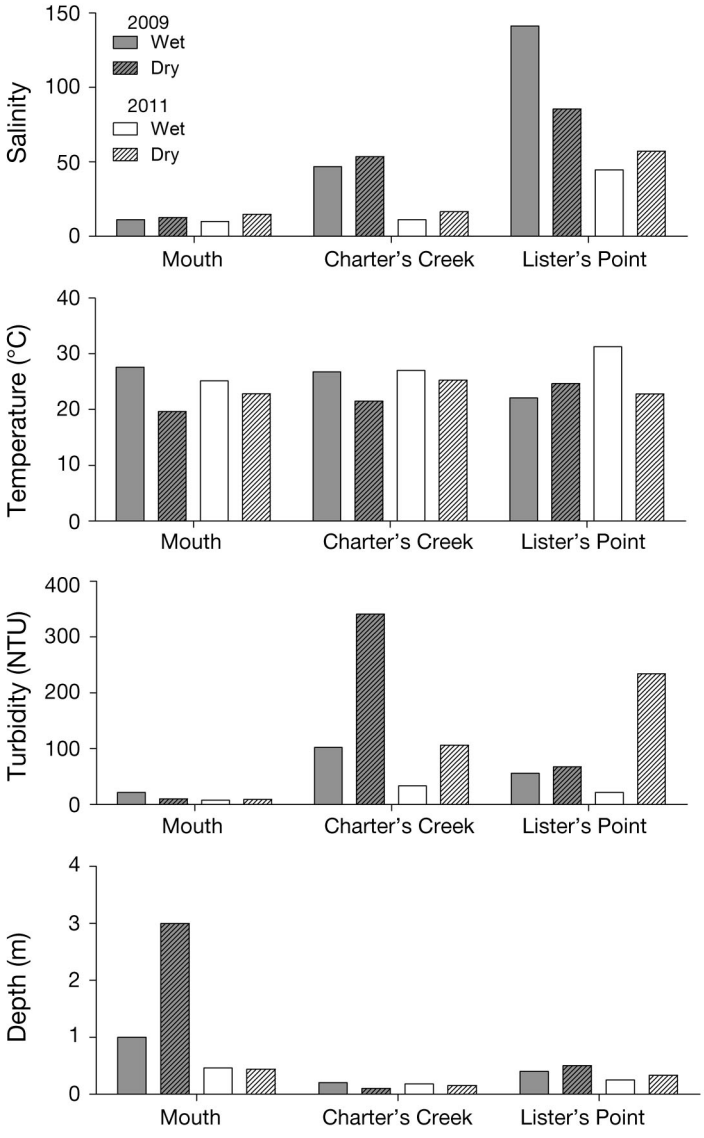

Fig. 2. Physico-chemical parameters for the wet and dry seasons at the 3 study sites (Mouth, Charter's Creek and Lister's Point), during the current diluted phase (white bars) and the previous hypersaline stage (grey bars). Data for hypersaline stage from Carrasco et al. (2012)

Temporal and spatial variation in stable isotope signatures of dietary sources

Mouth

We found a significant difference in the $\delta^{13}C$ signatures of the source items between the wet and dry season ($F = 12.7$, $p = 0.001$). However, no significant difference was evident in the $\delta^{15}N$ signatures between the seasons ($F = 2.20$, $p = 0.001$). The different sources were significantly different from each other in both their $\delta^{15}N$ ($F = 10.3$, $p = 0.001$) and $\delta^{13}C$ signatures ($F = 19.3$, $p = 0.001$). The $\delta^{13}C$ signatures of the sources showed a wide range, with values between −32.8‰ for POM and −15.4‰ for detritus. The $\delta^{15}N$ signatures also varied greatly, with values ranging from 2.3‰ for detritus to 12.8‰ for *Mesopodopsis africana* (Table 1).

Table 1. Mean ± SD stable isotope ratios of carbon and nitrogen, mean C:N ratio, and sample sizes of *Oreochromis mossambicus* and dietary sources for the 3 sampling sites in the St Lucia Estuary during both the wet and dry season

	Mouth								Charter's Creek								Lister's Point							
	Wet				Dry				Wet				Dry				Wet				Dry			
Dietary items	$\delta^{13}C$	$\delta^{15}N$	C:N	n	$\delta^{13}C$	$\delta^{15}N$	C:N	n	$\delta^{13}C$	$\delta^{15}N$	C:N	n	$\delta^{13}C$	$\delta^{15}N$	C:N	n	$\delta^{13}C$	$\delta^{15}N$	C:N	n	$\delta^{13}C$	$\delta^{15}N$	C:N	n
Acartiella natalenis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−19.6±0.1	6.4±0.1	4.7	2	–	–	–	–
Assiminea cf. *capensis*	–	–	–	–	–	–	–	–	–	–	–	–	−14.5±0.1	9.7±0.1	4.3	3	–	–	–	–	–	–	–	–
Bivalves	–	–	–	–	–	–	–	–	–	–	–	–	−19.1±0.6	8.2±0.5	3.9	6	–	–	–	–	–	–	–	–
Cladophora sp.	–	–	–	–	–	–	–	–	−22.3±0.3	6.8±0.2	38.9	6	–	–	–	–	−20.6±0.2	5.5±0.0	9.7	3	–	–	–	–
Detritus	−25.1±3.1	2.6±0.3	26.2	3	–	–	–	–	−15.7±0.0	9.7±0.3	23.1	3	−15.3±0.2	8.5±0.5	17.2	3	–	–	–	–	−19.4±0.1	4.4±0.3	6.2	3
Fringing vegetation	–	–	–	–	–	–	–	–	–	–	–	–	−14.0±0.1	7.8±0.6	31.7	–	–	–	–	–	–	–	–	–
Grass	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−12.4±0.1	7.2±0.4	11.7	3	–	–	–	–
Macroalgae	–	–	–	–	–	–	–	–	–	–	–	–	−11.9±1.4	10.4±0.6	20.3	9	–	–	–	–	–	–	–	–
Mesopodopsis africana	−29.2±0.1	12.6±0.3	3.7	3	−25.2±0.3	10.1±0.0	4.5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Microphyto-benthos	−20.4±0.4	4.0±0.6	6.9	3	−13.5±0.1	8.6±0.3	7.3	3	−23.1±0.4	2.0±0.5	7.5	3	–	–	–	–	–	–	–	–	–	–	–	–
Nereid polychaete	–	–	–	–	–	–	–	–	–	–	–	–	−15.8±0.2	12.5±0.2	4.2	3	–	–	–	–	–	–	–	–
Oithona sp.	–	–	–	–	–	–	–	–	–	–	–	–	−25.0±0.1	7.1±0.0	4.9	2	–	–	–	–	–	–	–	–
Oreochromis mossambicus	−23.9±06	6.9±1.4	3.2	7	−22.7±2.9	6.9±0.8	3.1	9	−15.8±0.6	6.0±0.9	3.3	12	–	–	–	8	−22.6±3.5	5.6±1.0	3.2	7	−18.1±0.2	4.0±0.3	3.3	9
Particulate organic matter	−32.5±0.4	7.9±0.5	5.7	3	−16.4±0.3	2.8±0.2	5.3	3	−23.3±0.3	3.3±0.3	4.9	2	−18.5±0.0	3.8±0.3	7.0	3	−21.1±0.0	4.8±0.5		2	−22.3±0.2	2.4±0.2	6.6	3
Pseudodiaptomus stuhlmanni	−27.8±0	10.8±0	5.2	1	−29.3±0.1	8.1±0.0	5.4	2	–	–	–	–	–	–	–	–	−20.6±0.1	5.4±0.1	5.7	3	–	–	–	–
Reeds	−28.6±0.1	1.9±0.4	11.9	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Salmacoma littoralis	–	–	–	–	–	–	–	–	−17.6±0.3	9.6±0.1	3.7	3	–	–	–	–	–	–	–	–	–	–	–	–
Sediment organic matter	–	–	–	–	–	–	–	–	−17.5±0.6	4.6±0.9	7.7	3	−17.8±0.5	4.6±0.7	7.8	3	−17.0±0.5	4.5±0.5	8.0	3	−17.6±0.2	4.1±0.0	7.0	3
Solen cylindraceus	–	–	–	–	–	–	–	–	−17.8±0.1	8.0±0.1	3.5	3	–	–	–	–	–	–	–	–	–	–	–	–
Submerged vegetation	–	–	–	–	−18.6±0.5	8.1±0.4	14.2	3	–	–	–	–	–	–	–	–	–	–	–	–	−13.3±0.2	7.3±0.2	19.4	3
Varuna litterata	−20.4±2.6	10.3±0.3	3.4	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

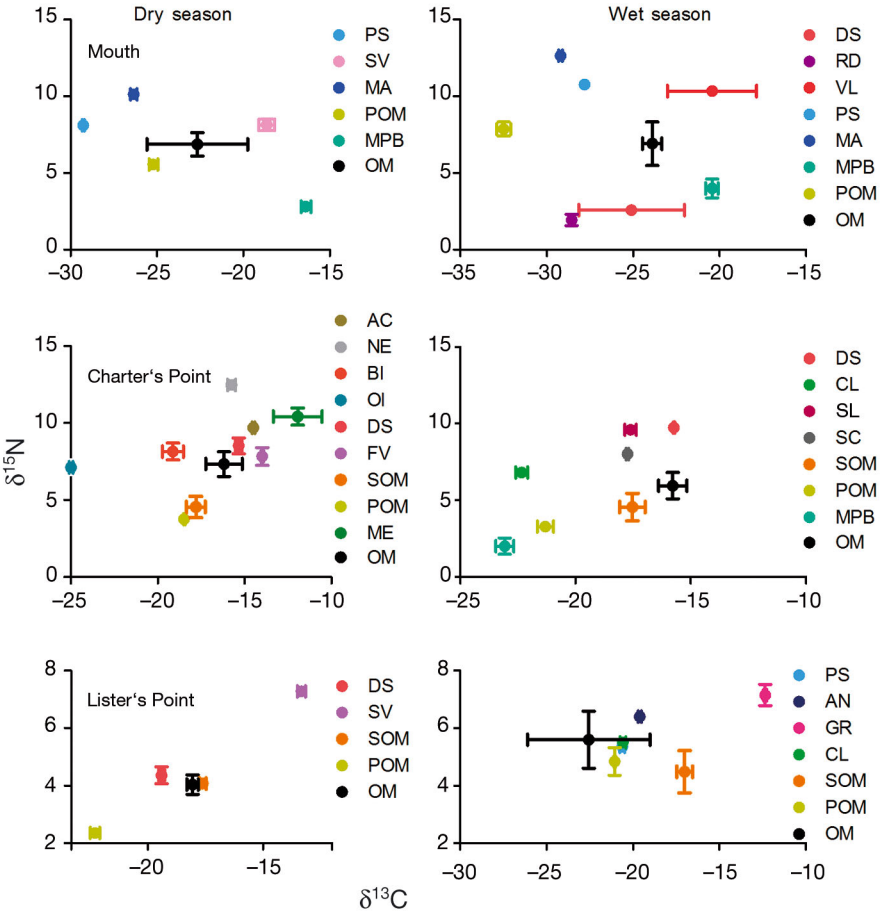

Fig. 3. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ signatures of *Oreochromis mossambicus* and the different food sources during the wet and dry seasons at the 3 sampling sites. *O. mossambicus* signatures were corrected for trophic enrichment using standard fractionation values of 3.4 for $\delta^{15}N$ and 1 for $\delta^{13}C$. Note different axis scales. Codes for dietary items: AC, *Assiminea* cf. *capensis*; AN, *Acartiella natalensis*; BI, bivalves; CL, *Cladophora* sp.; DS, detritus; FV, fringing vegetation; GR, grass; MA, *Mesopodopsis africana*; ME, macroalgae; MPB, microphytobenthos; NE, nereid polychaetes; OI, *Oithona* sp.; OM, *O. mossambicus*; POM, particulate organic matter; PS, *Pseudodiaptomus stuhlmanni*; RD, reeds; SC, *Solen cylindraceus*; SL, *Salmacoma littoralis*; SOM, sediment organic matter; SV, submerged vegetation; VL, *Varuna litterata*

Charter's Creek

The results of the 2-way ANOVA indicated no significant difference between the $\delta^{15}N$ (F = 0.1, p = 0.749) and $\delta^{13}C$ (F = 2.51, p = 0.119) signatures between the wet and dry seasons. However, most sources significantly differed in both their $\delta^{15}N$ (F = 23.5, p < 0.05) and $\delta^{13}C$ (F = 32.5, p < 0.05) signatures. Where sources were statistically similar (p > 0.05), they were combined to give a group signature. This was the case for the bivalves, which incorporated *Solen cylindraceus* and *Brachidontes virgiliae*, and the macroalgae, which included *Cladophora* sp. and *Ulva* sp. The $\delta^{15}N$ signatures ranged from 1.6‰ for MPB to 12.6‰ for the nereid polychaetes (Fig. 3, Table 1). The $\delta^{13}C$ signature values ranged from −25.6‰ for detritus to −11.9‰ for the macroalgae group (Fig. 3, Table 1).

Lister's Point

We found a significant difference in the $\delta^{13}C$ (F = 7.76, p = 0.008) and $\delta^{15}N$ (F = 14.3, p = 0.001) signature values between the wet and dry seasons. Significant differences were also found between the different sources for both $\delta^{13}C$ (F = 13.8, p = 0.001) and $\delta^{15}N$ (F = 53.7, p = 0.001). The $\delta^{13}C$ of the sources ranged from −22.5‰ for POM to −12.3‰ for the submerged grass (Fig. 3, Table 1). The $\delta^{15}N$ signature values had a smaller range, between 2.3‰ for POM and 7.6‰ for the submerged grass (Fig. 3, Table 1).

Temporal and spatial variation in *Oreochromis mossambicus* signatures and trophic positioning

The C:N ratios of *O. mossambicus* were consistently low, with all values falling in the 3.0 to 3.4 range. We found a significant difference in $\delta^{13}C$ signatures of *O. mossambicus* among the 3 study sites (F = 19.3, p = 0.001), but the $\delta^{13}C$ signatures were not significantly different between seasons (F = 1.65, p = 0.227) or between the different sized individuals (F = 1.62, p = 0.215). The $\delta^{15}N$ signatures were also significantly different among the 3 study sites (F = 18.6, p = 0.001). Similar to $\delta^{13}C$, no significant difference was evident in the $\delta^{15}N$ signatures between the wet and dry seasons (F = 0.578, p = 0.464) or between the differently sized individuals (F = 0.966, p = 0.556).

At Lister's Point, there was a significant negative relationship between the size of the fish sampled and both their $\delta^{13}C$ (regression: R^2 = 0.44, p = 0.003, n = 16) and $\delta^{15}N$ signatures (R^2 = 0.49, p = 0.002, n = 16). At Charter's Creek, we noted a significant positive

relationship between fish size and $\delta^{13}C$ signatures (R^2 = 0.198, p = 0.049, n = 20), and a significant, albeit very weak, relationship between the $\delta^{15}N$ signatures and the size of the fish sampled (R^2 = 0.043, p = 0.043, n = 20). No significant relationships between fish size and $\delta^{13}C$ (R^2 = 0.06, p = 0.76, n = 16) and $\delta^{15}N$ (R^2 = 0.24, p = 0.26, n = 16) signatures were found at the Mouth. From a seasonal perspective, we identified a significant negative relationship between both carbon (R^2 = 0.54, p = 0.006, n = 12) and nitrogen (R^2 = 0.35, p = 0.041, n = 12) signatures and the size of the fish collected at Charter's Creek during the wet season. No significant relationships were identified at either of the other sites.

Trophic position was significantly different among the 3 sampling sites (F = 32.74, p = 0.001), but not between the wet and dry season at each site (p = 0.001). Trophic position was significantly related to salinity (R^2 = 0.56, p < 0.05, n = 52) and turbidity (R^2 = 0.29, p < 0.05, n = 52) among the 3 sampling sites. Both relationships indicate a negative impact on the trophic positioning of *Oreochromis mossambicus*, with position decreasing with an increase in salinity or turbidity. Together, salinity and turbidity accounted for most of the variability in trophic position among the sites. Temperature and depth were not significantly related to trophic position.

Dietary composition: gut contents

At the Mouth, a high degree of similarity was evident between the dietary composition of *Oreochromis mossambicus* during the wet and dry seasons. The most common gut contents were detrital matter, contributing 77 to 80%, and sand grains, contributing 12 to 14% of the gut contents (Fig. 4). Fish sampled during the dry season exhibited a higher proportion of sand material compared to those sampled during the wet season. During the wet season, fish consumed macroalgae, which contributed 7% of the total gut contents. Shell fragments were found in the gut contents of fish sampled in the dry season but were absent in those collected during the wet season. Fish scales, ostracods, diatoms, copepods (*Acartiella natalensis*) and plant matter were found in the gut contents of fish in both the wet and dry seasons (Table 2). The bivalve *Brachidontes virgiliae* was found in the stomach contents of fish collected in the wet season, but was absent during the dry season (Table 2). Macroalgae were detected in the gut contents of the largest individuals, but only during the dry season. Fish scales were only identified in the larger individuals collected in both the wet and dry seasons.

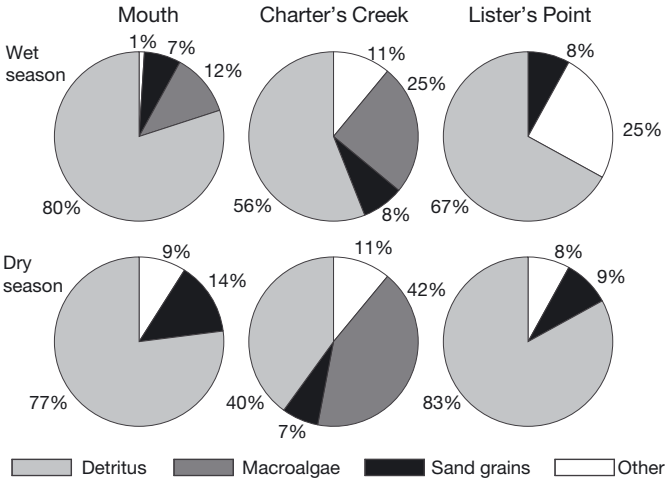

Fig. 4. Major dietary items found in the gut contents of *Oreochromis mossambicus* collected at 3 different sampling sites in the St Lucia Estuary during the wet and dry seasons. Details on the 'Other' category are given in Table 1

The greatest variation in gut content composition was found at Charter's Creek, with a large difference in the number of dietary components between the wet and dry season (Table 2). Detrital matter was found to be the most dominant food source during the wet season, whereas macroalgae were dominant in the dry season, contributing 42% of the gut contents. Fish scales, amphipods and sand grains were identified in conjunction with the plant matter from the fish sampled during the wet season. The dry season exhibited a markedly different result, with a greater degree of variety in the gut contents of these fish. Copepods (*Acartiella natalensis*), gastropod snails (*Assiminea* cf. *capensis*), ostracods, diatoms, fish bones and scales, sand grains and plant matter were identified from the gut contents of the fish sampled during this season (Table 2). During the dry season, a small proportion of the collected fish (22%) contained only zooplankton in the gut. These fish were also the smallest individuals collected at the site. Fish scales were again only identified in the gut contents of the larger individuals. The bivalve *Solen cylindraceus* was only identified in the gut contents of fish collected in the dry season (Table 2).

Lister's Point showed a similar trend to that observed at the Mouth, with a high degree of similarity between the dietary composition of fish sampled in the wet and dry seasons. Here, the dominant food item found in the guts was detritus, which was found in high concentrations during both wet and dry sea-

Table 2. Mean ± SD number of individuals found in the gut contents of *Oreochromis mossambicus* at the different sites during the wet and dry season with all items falling into the 'Other' category in Fig. 4. Numbers in parentheses indicate occurrence frequency in percentages. na: not applicable; for these dietary items that could not be counted (e.g. detritus), the proportion of the total gut content was estimated. (–): not found. n: number of tilapia sampled

Dietary item	Mouth		Charter's Creek		Lister's Point	
	Dry season n = 9	Wet season n = 6	Dry season n = 9	Wet season n = 10	Dry season n = 9	Wet season n = 7
Assiminea cf. *capensis*	–	–	2.50 ± 2.14 (89)	5.50 ± 2.98 (80)	–	–
Acartiella natalensis	–	–	1.00 ± 0.00 (11)	–	–	30.14 ± 21.95 (100)
Amphipoda	1.75 ± 0.96 (44)	1.00 ± 0.00 (33)	1.67 ± 0.58 (33)	9.00 ± 0.00 (10)	–	–
Brachidontes virgiliae	3.75 ± 1.83 (89)	–	2.63 ± 1.60 (89)	–	–	–
Cladocera	–	–	–	–	–	25.29 ± 23.26 (100)
Detritus	na (100)	na (100)	na (100)	na (100)	na (100)	na (100)
Diatoms	1.00 ± 0.00 (11)	1.00 ± 0.00 (17)	–	2.50 ± 0.71 (20)	1.80 ± 0.84 (56)	–
Sipuncula	2.75 ± 2.06 (44)	1.75 ± 0.96 (67)	1.00 ± 0.00 (22)	1.83 ± 0.75 (60)	4.80 ± 5.17 (56)	1.00 ± 0.00 (14)
Fish egg	–	–	1.00 ± 0.00 (11)	1.50 ± 0.71 (20)	–	5.67 ± 2.52 (43)
Fish scales	1.80 ± 0.84 (56)	2.50 ± 0.71 (33)	1.00 ± 0.00 (11)	1.33 ± 0.52 (60)	1.50 ± 0.58 (44)	3.80 ± 0.84 (71)
Foraminifera	–	–	–	–	2.00 ± 1.29 (78)	–
Insect wing	–	–	–	–	–	1.00 ± 0.00 (14)
Macroalgae	na (22)	–	na (100)	na (90)	–	–
Nematoda	1.00 ± 0.00 (33)	2.00 ± 0.00 (17)	1.00 ± 0.00 (33)	2.50 ± 1.29 (40)	1.67 ± 1.15 (33)	1.00 ± 0.00 (14)
Ostracoda	9.56 ± 3.94 (100)	4.25 ± 2.75 (67)	–	1.00 ± 0.00 (20)	–	15.86 ± 15.06 (100)
Pseudodiaptomus stuhlmanni	–	–	–	–	–	–
Solen cylindraceus	–	–	1.50 ± 1.00 (44)	–	–	–
Sand grains	na (100)	na (100)	na (100)	na (100)	na (100)	na (100)
Shell fragments	4.25 ± 1.67 (89)	1.00 ± 0.00 (17)	na (11)	–	–	–
Tanaid	–	–	–	11.00 ± 0.00 (10)	–	–

sons, contributing 67 and 83% of the total content, respectively. During the wet season, zooplankton such as the copepod *Acartiella natalensis* and cladocerans were found in 100% of the guts analysed. Ostracods were also identified from all the guts analysed (Table 2). Both of these taxa were completely absent from the gut contents during the dry season. Fish scales, copepods (*A. natalensis*), ostracods, detritus and diatoms were all identified from the gut contents of fish collected during the wet season, while foraminiferans, diatoms, detritus, sand grains and fish scales were identified from fish collected during the dry season (Table 2).

The results of the ANOSIM indicate a significant difference in the dietary composition among the different sampling locations (R = 0.761 p = 0.001). The NMDS procedure was considered to be sufficiently described in 2 dimensions with a stress value of 0.14 (Clarke & Warwick 2001). From Fig. 5, it is evident that the fish collected from the Mouth separated from those collected at Charter's Creek, but were more similar to the individuals from Lister's Point. The fish

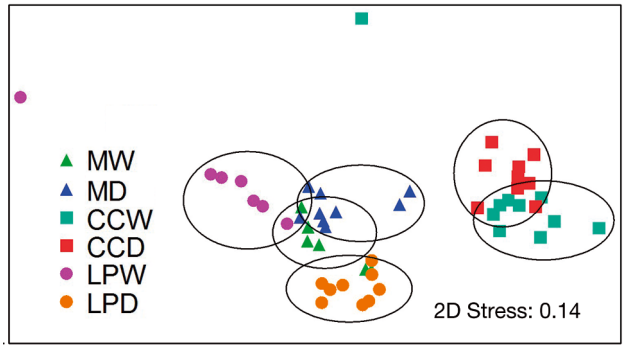

Fig. 5. *Oreochromis mossambicus*. Non-metric multidimensional scaling (NMDS) plot of the log-transformed gut content data from 3 sampling locations in the St Lucia Estuary. M: Mouth, CC: Charter's Creek, LP: Lister's Point, W: wet season, D: dry season

from Charter's Creek clustered separately from both the Lister's Point and Mouth individuals based on the composition of their gut contents. We also noted separation, with little overlap in clusters, between the

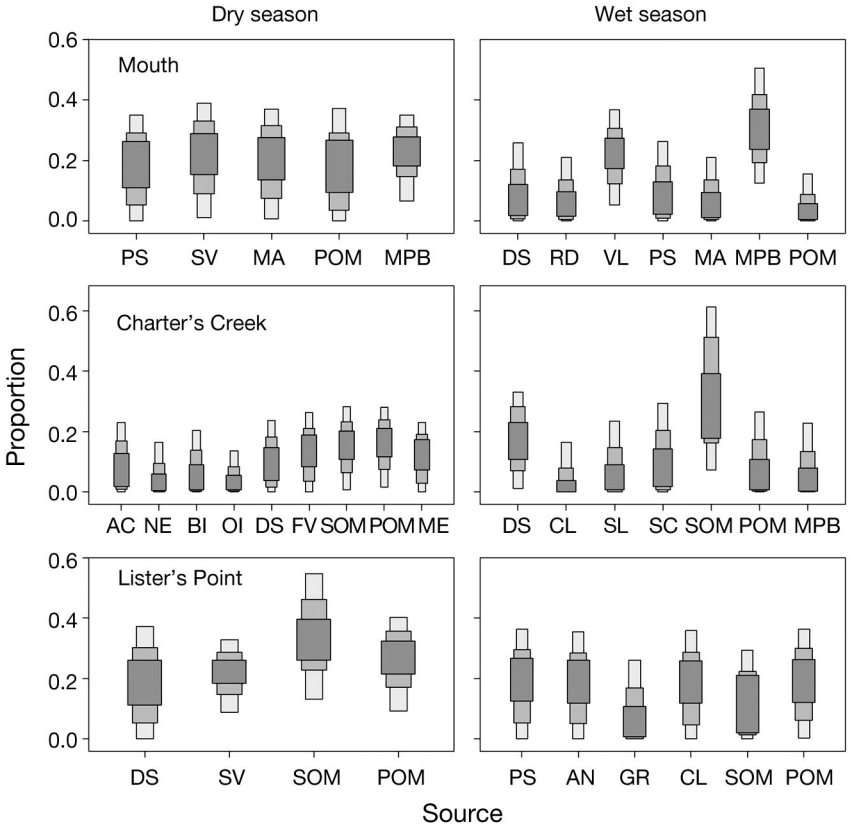

Fig. 6. Contribution of dietary items to the diet of *Oreochromis mossambicus* at the 3 sampling sites during the wet and dry seasons (based on Stable Isotope analysis in *R* mixing models). For each item, 95, 75 and 25% credibility intervals are plotted (light, medium and dark grey, respectively). Codes for dietary items as in Fig. 3

fish collected in the wet and dry seasons. The Lister's Point specimens were distinctly separate from a seasonal perspective, with the clusters for the wet and dry seasons exhibiting no overlap (Fig. 5).

Dietary contribution: stable isotopes

At the Mouth, all dietary items contributed a similar proportion to the diet of up to 40% during the dry season (Fig. 6). MPB showed a slightly higher proportion, contributing between 10 and 35% of the total diet during this season. A similar pattern was observed for the wet season, when 2 main items appeared to play a greater role in the diet of *Oreochromis mossambicus*. *Varuna litterata*, a crab found here during the wet season, contributed between 5 and 35% of the total diet. MPB was again important, contributing the highest proportion to the diet, up to 50%. All other dietary items contributed similar proportions of up to 25% of the total diet (Fig. 6).

At Charter's Creek, all dietary items contributed similar proportions to the diet of *Oreochromis mossambicus* during the dry season, with most contributing up to 20% of the diet (Fig. 6). Nereid polychaetes and the copepod *Oithona* sp. were of lesser importance, contributing <18%. SOM and POM were the only items contributing higher proportions, up to 28% of the diet. The results from the wet season differed drastically. SOM was a dominant food source, contributing up to 62% of the diet. Detritus was also dominant, contributing up to 35% of the diet. All other food items contributed minor amounts (up to 20%) to the total diet (Fig. 6).

At Lister's Point, SOM and POM were identified as the dominant food items for tilapia during the dry season, potentially contributing up to 55 and 40% of the total diet, respectively (Fig. 6). Detritus contributed up to 37% of the total diet. Submerged vegetation was also important, contributing up to 35% to the total diet. During the wet season, however, all dietary items contributed similar proportions to the diet (up to 30%), and no single food source appeared to play a dominant role in the diet. Grass and SOM were the 2 sources of least importance, contributing less than 30% to the diet (Fig. 6).

DISCUSSION

Previous studies conducted in the St Lucia system during the hypersaline period recorded salinities substantially higher than those recorded during the current study; this was particularly evident at Charter's Creek and at Lister's Point (Whitfield et al. 2006, Carrasco et al. 2012). These high salinities are indicative of the freshwater deprivation and persistent reverse salinity gradient which was present at that time. Although this reverse salinity gradient is still present, the heavy rainfall and consequent freshwater inflow during the wet season of 2010/2011 caused substantial dilution, with a marked decrease in the salinity at all sampling stations (e.g. Charter's Creek was almost 75% less saline than during the study of

Carrasco et al. 2012). At the Mouth, however, there has been little effect in terms of salinity, with levels remaining between 9 and 15 (Carrasco & Perissinotto 2012, present study). At Lister's Point, salinity levels of over 140 were recorded during the hypersaline stage (Carrasco & Perissinotto 2012). Levels in this region are now within the range of 40 to 60, i.e. almost 60% less saline than the hypersaline stage (Fig. 2). From these figures it is evident that the system is in general much less saline than it has been for the past 8 to 9 yr (Whitfield & Taylor 2009).

In terms of dietary composition, Carrasco et al. (2012) found that in the St Lucia system, *Oreochromis mossambicus* had a diverse diet, feeding on a variety of different food items. They also documented that there was generally no dominant food source for this species, with all dietary constituents contributing similar proportions to the diet at both the Mouth and Charter's Creek. In contrast, our study indicates that, under certain conditions, this species will target a specific food source, which will then constitute the majority of its diet. This was evident at Lister's Point during the dry season, where *O. mossambicus* consumed SOM as its main food source, with this source constituting up to 55% of its total diet. At Charter's Creek during the wet season, the diet was again dominated by 2 food sources, SOM (up to 62%) and detritus (up to 35%). The gut content analysis gave a different picture, with detritus being the dominant food source at all sites during both wet and dry seasons. Algal sources were also found to be dominant at Charter's Creek, but this was not reflected in the mixing models. At Lister's Point, both the gut contents and mixing models indicated that these fish have a more varied diet during the wet season, with a wider variety of sources than those recorded in the dry season. Inconsistencies between gut content analysis and mixing model results may occur because fish were feeding in different areas compared to where the sampling was carried out and thus not all food source signatures were obtained. Because the mixing models give a more long-term average of the dietary intake, it could also be possible that the results from these analyses represent relics from the weeks before sampling occurred, thus not reflecting the recent addition of some sources to the diet. This may have been the case at Charter's Creek, as plant/algal matter was the dominant food item from the gut contents of *O. mossambicus* during both seasons, which was not reflected in the mixing models. Gut contents did indicate a shift in food preference, with smaller individuals feeding on zooplankton and larger individuals consuming sources such as fish and higher proportions of detritus, which is concordant with reports by Whitfield (1998) and Skelton (1993). Considering both the gut contents and mixing model results, it is still evident that *O. mossambicus* changes its diet both seasonally and spatially. Diets did differ among the sampling sites as well as between seasons. These findings highlights the importance of combining isotope and gut content analyses to obtain an accurate picture of the diet of these fish.

Previous studies have reported that *Oreochromis mossambicus* preferentially feeds on plant/algal material and detritus (De Silva et al. 1984, Skelton 1993, Doupé et al. 2010). Our results contradict these findings to some extent, providing evidence that this fish also feeds on benthic invertebrates and zooplankton, thus suggesting a more omnivorous diet. The occurrence of zooplankton in the gut contents of fish at Lister's Point during the wet season coincides with a bloom event which occurred here prior to sampling (N. K. Carrasco pers. obs.). Zooplankton samples collected at the time of sampling indicate a concentration of around 600 000 ind. m^{-3}, which is higher than average for this site (Carrasco et al. 2010). Both the gut contents and mixing models indicated a shift in diet to incorporate this abundant food source, which is indicative of the opportunistic nature of *O. mossambicus*. Differently aged individuals of this species are known to feed on different food sources, with adults feeding preferentially on detritus and juveniles feeding more readily on benthic microfauna and zooplankton (Bruton & Boltt 1975, Whitfield & Blaber 1978). This was supported by the results of our study, which showed that smaller individuals at Charter's Creek and Lister's Point had zooplankton in their gut contents, which was absent from the larger individuals. Pennate diatoms were thought to be the most important food sources during hypersaline conditions (Vivier et al. 2010), but this was not supported by the results of our study either. The high concentrations of silt and sand grains in the guts support the observations of Piet & Guruge (1997), who showed that *O. mossambicus* is found in close proximity to the substrate when actively feeding. The presence of fish scales in the gut contents of the larger specimens supports previous observations that this species feeds on other fish species, as well as its own young (Whitfield 1998). Doupé et al. (2009) provided field and laboratory evidence showing that *O. mossambicus* is capable of predatory behaviour, actively feeding on other native fish species, with larger individuals capturing more prey species. This could have great impacts for a system such as the

St Lucia Estuary, which these fish inhabit, and could affect the already heavily impacted population structure of other native fish species.

The regression analysis provided an interesting outcome, particularly for Lister's Point, where a significant relationship between the size of the fish and the $\delta^{15}N$ signatures was obtained. Skelton (1993) indicated that juvenile tilapia are known to congregate in shoals in shallower water. Therefore, it is likely that juveniles feed on different food sources, compared to their adult counterparts, as supported by other authors (e.g. Bruton & Boltt 1975, Whitfield & Blaber 1978). At Lister's Point, there is a very gentle gradient in the substrate at the edge of the water, resulting in a broad region of very shallow water (up to 20 cm deep) along the banks. This provides a refuge for juvenile tilapia and could explain the relationship between fish size and $\delta^{15}N$ signatures. At Charter's Creek, there is also an extensive area of shallow water along the bank region, but the relationship between the size and $\delta^{13}C$ signatures of the fish sampled here indicates that these fish may be feeding in different areas. It is well-established that nitrogen signatures can be used to determine the relative trophic position of consumers (e.g. DeNiro & Epstein 1978). The regression analysis performed on the trophic position of this species indicated that at higher salinities, *Oreochromis mossambicus* feeds at a lower trophic level, when compared to lower-salinity areas. This was evident, as the mean trophic level at Lister's Point was found to be lower than at both Charter's Creek and the Mouth. Salinity has been shown to affect trophic positioning within a food web (Post et al. 2000, Govender et al. 2011).

Balcombe et al. (2005) showed that fish species native to Australia tend to switch their diets depending on season, with the dry and wet period having significantly different diets due to changes in availability of food sources. Doupé et al. (2010) showed through experimental feeding of *Oreochromis mossambicus* that plant sources were not sufficient to sustain its metabolic requirements and that only fish fed a protein source were able to maintain body weights during the experiments. Thus, it was suggested that despite this fish being predominantly herbivorous, it requires some form of protein in its diet in order to survive (Bowen 1979, Doupé et al. 2010). Our results suggest that alternative food sources, such as bivalves and zooplankton, may be important in the diet of *O. mossambicus* in the St Lucia Estuary. Maddern et al. (2007) and Doupé et al. (2010) showed that fish exposed to different environmental conditions exhibit some degree of trophic plasticity, with *O. mossambicus* in different systems feeding on different dietary sources. Tilapias are in general able to adapt to changes in environmental conditions through changes in their life history traits, as well as through facultative feeding (Maitipe & De Silva 1985, McKaye et al. 1995). Our study also shows that seasonal effects can cause a change in the diet of this fish; this was particularly evident at Lister's Point, as environmental conditions at this site can vary greatly between the wet and dry season.

Other invasive fish species, such as the round goby *Neogobius melanostomus*, have been shown to exhibit similar properties with respect to their diet, in areas that they have invaded. Corkum et al. (2004) outlined that this goby has a varied diet which consists of zooplankton, benthic invertebrates and molluscs. They also showed that this species undergoes an ontogenetic shift in diet, with adults becoming molluscivores. This is similar to *Oreochromis mossambicus,* which experiences a shift in diet from zooplankton and benthic invertebrates during juvenile stages to a diet dominated by detritus and macroalgae as adults (Whitfield 1998). Brush et al. (2012) also showed that the diet of the round goby differed spatially and temporally, as well as with body size. The reason for its invasion success can thus be attributed to its broad diet, as well as its ability to survive a wide range of environmental conditions (Corkum et al. 2004). Gido & Franssen (2007) showed that fish such as blue tilapia *O. aurens* succeed as an invasive species in Central America due to their feeding preferences. These fish are omnivorous and have the ability to feed on lower-quality trophic sources, which are easily available in the habitats into which they have been introduced, thus aiding in invasion success (Gido & Franssen 2007). In Australia, the ability and success of *O. mossambicus* to invade native river systems can in part be attributed to its dietary characteristics (Leveque 2002, Doupé & Burrows 2008). Leveque (2002) also suggested that the success of tilapia species in Africa and throughout the world can be attributed to their broad diet and their tolerance of a wide variety of environmental conditions. The invasion success of *O. mossambicus* has had detrimental impacts on the native fish and other fauna in numerous places including Australia, the southern USA and Madagascar (McKaye et al. 1995, Leveque 2002, Canonico et al. 2005, Gido & Franssen 2007, Maddern et al. 2007, Doupé & Burrows 2008). The dominance of this species in the St Lucia Estuary can thus be attributed to the broad dietary preferences of these fish, which is vital in a system where food availability varies greatly.

One of the most pivotal requirements for future studies of this nature is the quantification of the different food sources in order to determine the relative abundances at different sites during the wet and dry seasons. This will provide an estimate of the availability of these sources, which can also help to establish potential electivity indexes for the fish species at different periods. Forage ratio and Ivlev's electivity index are 2 methods which can be used to quantify food selection and have been modified to take into account food availability (Jacobs 1974).

In conclusion, we have shown that *Oreochromis mossambicus* in the St Lucia Estuary exhibits some degree of trophic plasticity, as it has the ability to alter its diet according to the prevailing conditions. During hypersaline conditions, these fish fed on a variety of different sources, which included both plant/algal and animal material. However, there were no dominant sources, with all dietary constituents contributing similar proportions. This study revealed that there is some variability in this occurrence, with fish feeding predominantly on specific sources which thus dominate their diets during the less saline period. This variability was supported by both the mixing models and the gut content analysis. The main reason for this dominance is that these food items are likely more abundant in the less saline conditions. The isotope analysis also indicated variation in the trophic positioning of differently sized individuals, where there are suitable habitats for juveniles to use as refuges (e.g. shallow water shore regions). The analysis of the trophic positioning of *O. mossambicus* also revealed that salinity and turbidity are the driving factors responsible for the trophic position of this species in the system, either directly by influencing the fish themselves or indirectly by affecting their dietary sources. The hypothesis that there would be dietary variation between the hypersaline and diluted stages is therefore supported, as is the hypothesis that fish size can determine dietary composition. Overall, the success of this species and its subsequent dominance of the estuarine system can be attributed not only to its remarkable tolerance of salinity variations, but also to its ability to alter its diet accordingly.

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