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Riverine dominance of a nearshore marine demersal food web: evidence from stable isotope and C/N ratio analysis

A.M. de Lecea, A.J. Smit and S.T. Fennessy

Abstract

The Thukela Bank, KwaZulu-Natal, supports a diverse ecosystem and South Africa's only prawn fishery. Oceanographic studies suggest riverine input is not important for the biology of this system, whereas biological studies suggest the contrary, with prawn catches increasing with increased fluvial run-off. The aim of this study was to determine (i) the importance of riverine and marine organic matter for the Thukela Bank food web; and (ii) whether there are seasonal changes in the Thukela River stable isotope values, and, if so, whether these are reflected in the isotope values of demersal organisms. Estuarine organic matter, sediments and demersal organisms were collected from several sites across the bank in the wet and dry seasons of 2008, 2009 and 2010. Marine particulate organic matter was also collected in 2010 and analysed for δ13C and δ15N, as well as C/N ratios. There were strong seasonal changes in isotopic values of organic matter and fauna, especially faunal δ13C. There was an apparent time-lag in organisms assimilating riverine organic matter isotopic values, with the isotopic signature of demersal organisms reflecting that of riverine organic matter from the previous season, which is likely the result of tissue turnover time. In 2010, Thukela Bank sediment organic matter was of riverine origin and this maintained the demersal food web. We conclude that Thukela River organic matter is an important input to the food web of the Thukela Bank, indicating that any future damming of the catchment area could have serious consequences for this ecosystem.

Introduction

It is well established that rivers play an important role in the local neritic environment by introducing organic matter (OM) and shaping the overall ecology (e.g. Beaulieu 2002; Gillanders and Kingsford 2002). Terrigenous allochthonous material is one of the most important sources of nutrients for primary and secondary productivity in the neritic zone (Polis and Hurd 1996), and contributes to enhancing the overall productivity of these systems (Maslowski 2003). Studies have shown that changes in the riverine input can affect individual species as well as entire communities (Serrano et al. 2010; Olin et al. 2013). A large number of studies worldwide have demonstrated that inshore fisheries are dependent on terrigenous inputs (Darnaude et al. 2004; Darnaude 2005). On the east coast of South Africa, there are inshore fisheries on the Thukela Bank (henceforth referred to as 'the bank'), a shallowwater bank formed by muddy sediment discharges of the Thukela River, extending north- and eastwards across the KwaZulu-Natal (KZN) Bight ('the bight') from the river

mouth (Figure 1). The bank's fisheries include commercial and recreational linefishing and South Africa's only shallow-water penaeid prawn trawl fishery (Fennessy and Groeneveld 1997; Lamberth et al. 2009). Turpie and Lamberth (2010) demonstrated that, during scenarios of low freshwater input from the Thukela River, prawn-trawl catches dropped by up to c. 11%, suggesting that riverine nutrient sources drive secondary productivity and hence influence fisheries yields. De Lecea et al. (2013) concluded that the estuaries were the main biological drivers of the benthic ecosystem of the bight. Similarly, de Lecea et al. (2015) concluded that riverine input played a major role driving the pelagic zooplankton food webs near shore, including in the Thukela Bank area. Lamberth et al. (2009) suggested that any major development that reduces water flow could dramatically reduce linefishery catches on the bank. Consequently, if any future impoundments, such as those suggested by the former South African Department of Water Affairs and Forestry (DWAF 2004) should occur, then there is a need to understand the extent of dependence of organisms on the bank on OM inputs from the Thukela River.

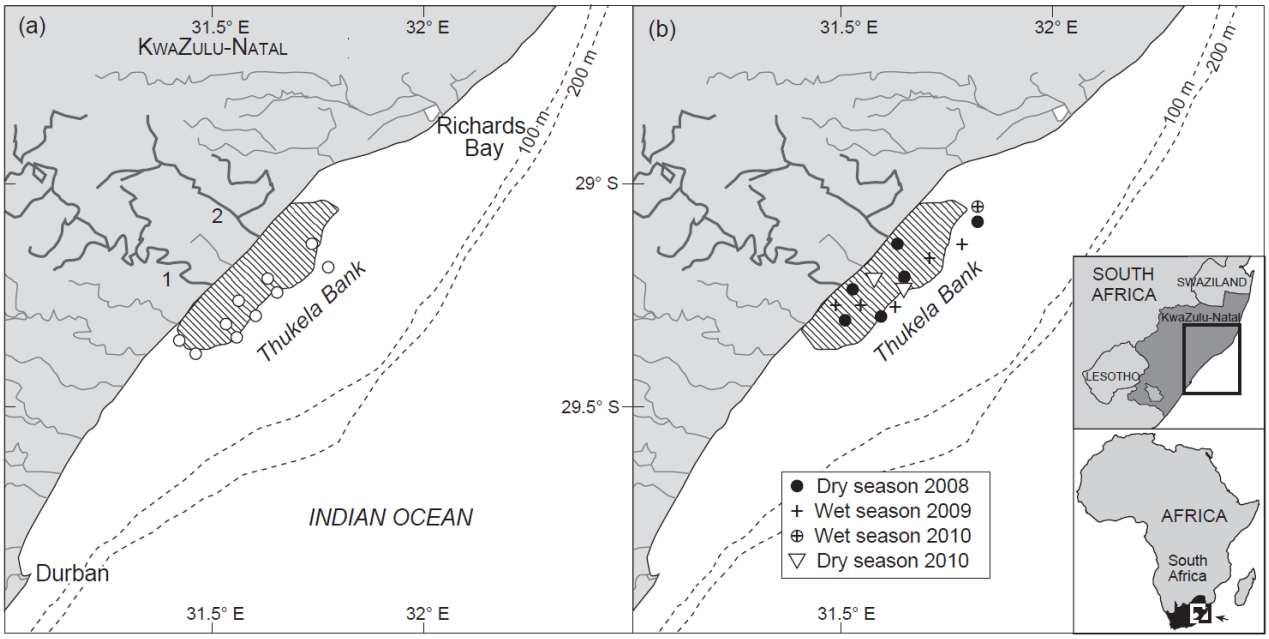

Figure 1: Map of the KwaZulu-Natal Bight showing the Thukela River mouth and the Thukela Bank, as well as (a) sediment stations and (b) trawl sampling locations. The Thukela River (1) and the Matigulu River (2) are shown

Despite this apparent food-web link between terrigenous allochthonous OM and nutrient sources and productivity in the bank region, riverine input into the bight has not been considered as a major factor affecting the region's ecosystem processes (Lutjeharms et al. 2000; Hutchings et al. 2010), but it has been recognised that flooding events have the potential to influence shelf water temporarily (Meyer et al. 2002). It has been accepted that the most important hydrodynamic phenomenon dominating the bight (including the bank), in terms of nutrient input and associated productivity, is an upwelling cell that occurs intermittently, but persistently, in the northern part of the bight where higher concentrations of nutrients are found in association with upwelling events (Meyer et al. 2002). Nevertheless, the Thukela River accounts for more than 35% of the fresh water entering the entire KZN

coastline (Bosman et al. 2007; Hutchings et al. 2010). In addition, the fact that the Thukela Estuary is functionally a river mouth rather than a true estuary indicates that most nutrients/organic matter in its outflow are exported to coastal waters (Lamberth et al. 2009) rather than being trapped and deposited in the estuarine system. Similar suggestions were made by Whitfield (2005), who concluded that, during periods of high-flow conditions, the estuarine zone may be pushed out to sea. Combined with the fact that the bight is oligotrophic (Bustamante et al. 1995; de Lecea and Cooper 2016), this raises the question of whether OM input from the Thukela River and other estuaries within the region could be important for the bight ecosystem. Our study examines the isotopic values of selected marine organisms as well as particulate OM (POM) and OM trapped in the sediments from the Thukela Estuary and the estuary of the nearby, smaller Matigulu River, and from the bank immediately adjacent to those rivers (Figure 1). We used stable isotopes (δ13C and δ15N) and carbon/nitrogen (C/N) elemental ratios to examine the origin of OM in the bank region and to investigate whether there are any seasonal isotopic changes that manifest in the tissues of organisms on the bank. We hypothesised that estuarine OM input, which occurs continuously but with episodic and predominant flood events during the wet austral summer, (i) is a main food source for the benthic food web for both wet and dry seasons and (ii) has strong seasonal differences in its stable isotope composition and C/N ratios. We also hypothesised that (iii) seasonal isotopic changes can be measured in demersal organisms on the bank. Stable isotopes have previously been used successfully to describe the origin of OM in aquatic systems and the food webs associated with them (Lara et al. 2010; Pomerleau et al. 2011; de Lecea et al. 2013; Olin et al. 2013), and have also been used to develop an understanding of seasonality within estuaries (Harmelin-Vivien et al. 2010; Olin et al. 2013). Furthermore, the understanding gained using stable isotope analysis can be strengthened using C/N ratios, because these have the potential to provide information on the origin of OM trapped n sediments (i.e. marine vs terrestrial) (Lamb et al. 2006). The combined use of both datasets can be useful to distinguish further the origin of OM because different plants have very specific isotope value and C/N ratio combinations (Lamb et al. 2006). De Lecea et al. (2013) used this approach to distinguish the origin of OM in the sediments\of the entire KwaZulu-Natal Bight and found the north and south edges of the bight to be dominated by marine POM input, a consequence of the marine oceanographic processes occurring in those regions.

Material and methods

Study site

The Thukela Bank is a mud bank off the Thukela River, located in the north-east of the KZN Bight, that encompasses an area of c. 560 km2 and extends c. 16 km offshore (Fennessy and Groeneveld 1997). (For information on the oceanography of the bight see Lutjeharms et al. 2000.) Linefishing occurs on reefs in the bank region, and the bank supports South Africa's only shallow-water prawn trawl fishery (Fennessy and Groeneveld 1997; Lamberth et al. 2009). The commercial inshore prawn fishery, the location of which includes the Thukela Bank, had an annual average catch (including bycatch) of 397 t, valued at over R 8.5 million (South African rands; 1US$ = R 6.40 [2003 exchange rate]), for the period 1992–2002 (Turpie and Lamberth 2010). The linefishery has a commercial and recreational boat-based

component; the commercial component had average total annual landings of 291 t, valued at R 28.9 million, for the northern part of the bight, including the bank, over the period 1985–2001 (Lamberth et al. 2009). Sediment accumulating on the bank comprises poorly sorted sand close to the Thukela River mouth, with the majority of the bank, from the river mouth to the c. 50 m isobath, formed by mud settling out of the suspended fluvial load (Bosman et al. 2007). A series of fluvially induced processes occur within the bight, dominated by the Thukela River, with an annual flux of 3 865 × 109 m3 and an annual average sediment input into the bight of 6.79 × 106 m3 y–1 (Bosman et al. 2007). Unlike other estuaries in the region, the Thukela is permanently open to the sea (de Lecea and Cooper 2016). The vegetation surrounding the catchment comprises woodlands, coastal forest, montane forest, thicket and grasslands (predominantly C3 plants) (Fairbanks and Benn 2000), but sugarcane monoculture (a C4 plant) is also present in the agriculturally transformed catchment area (Dominy et al. 2001). The smaller Matigulu Estuary has a catchment area of 900 km2 and is fed by the Nyoni and Matigulu rivers (O'Brien et al. 2009). This estuary was chosen for this study due to its proximity to the bank, with its mouth positioned close to the northern end. It is the third-largest source of sediment entering the bight and it has an annual run-off of 201.07 × 106 m3, and a sediment yield of c. 224 440 t y–1 (6.35 × 105 m3) (Cooper 1991) but, unlike the Thukela River estuary, it is not permanently open to the ocean; during periods of low flow (e.g. during the dry season), the mouth can become closed. The KZN region receives c. 1 000–1 200 mm y–1 of rainfall (Day 1981) and has well-defined wet (January–March) and dry (July–September) seasons. The peak of the wet season is in January, with a mean monthly precipitation of 118 mm, whereas August is the driest month (39 mm; Hunter 1988). Thus, in the Thukela River, the highest flow is in February and the lowest in August.

Sample collection

Multiple field samples were collected over the course of several smaller studies. Collectively they provided a suite of sample types and seasons that facilitated a broader view of the biological functioning of the bight. However, the sampling effort was not equal between seasons (see Appendix 1 for further details). Demersal organisms were collected on four occasions, twice during the wet season (January 2009 and 2010) and twice during the dry season (August 2008 and 2010). Samples were collected from one-hour demersal trawls towed at a speed of 2.5 knots, with 50 mm stretched mesh in the codend, conducted using commercial trawlers; the FV *Ocean Surf* (2008 dry season) and the FV *Ocean Spray* (in all other seasons) (the trawling procedure is detailed in Fennessy [2016]). Trawl locations were chosen to coincide with the prawn trawling grounds on the bank (Figure 1). Species to be collected were pre-selected based on their likely frequency of occurrence (as anticipated by STF from prior experience of the fishery) and were stored and prepared according to de Lecea et al. (2011). A total of 11 species were collected in sufficient numbers per season/year to permit comparisons, namely seven teleosts (*Atrobucca nibe, Cynoglossus attenuatus, C. lida, Johnius dorsalis (dussumieri), Otolithes ruber, Pomadasys olivaceum* and *Saurida undosquamis*) and four decapods (*Metapenaeus monoceros, Penaeus indicus, Portunus hastatoides* and *P. sanguinolentus*) (Appendix 1). Particulate organic matter (POM) samples were collected from the Thukela Estuary and Matigulu Estuary mouths during the last two hours of an outgoing spring low tide to ensure that riverine and not marine POM was

collected. Three replicates of surface POM were collected on three occasions (each separated by about two weeks) in each of the wet and dry seasons in 2008, 2009 and 2010. Samples were collected in acid-washed 500-ml bottles and placed on ice in a dark coolbox for later laboratory processing within six hours of collection. Simultaneously, replicate sediment samples were collected by scraping the upper 2 cm of sediment, collected using a modified van Veen grab, into plastic jars. Marine POM samples were collected using a Sea-Bird 911+ CTD with 12 PVC Niskin bottles of 5 litres each attached to a rosette. The CTD was deployed from the research vessel RS *Algoa* during a synoptic survey of the bight that was conducted in both seasons of 2010, and sampling localities closely coincided with the 2010 trawl localities (Figure 1). Simultaneously, marine sediment samples were collected using a modified van Veen grab, which was used to collect sediment/benthos samples for a different concurrent study (MacKay et al. 2016). A subsample of sediments was collected immediately from the top 2 cm layer at each site, placed in a sealed bag and frozen at −20 °C.

Sample preparation and stable isotope analysis

Demersal organisms were only partially defrosted prior to tissue sampling to keep leaching of cell contents to a minimum (de Lecea et al. 2011). For teleosts, muscle was collected from the caudal peduncle on the left side of the body. For decapods, muscle tissue collection was more varied; for the Natantia, the shell was first removed from the abdominal segment from where tissue was sampled, whereas for the Brachyura, adductor leg muscle tissue from inside the carapace was harvested. Care was taken to ensure that non-muscular tissue (skin, bone, exoskeleton, intestine) was excluded from the samples. Lipid extraction or lipid collection models were not applied, following Boecklen et al. (2011), who found insufficient variation (0.64‰) in δ13C of lipid-extracted and non-extracted muscle and bone tissue to justify the increased variation in δ15N values that usually occurs as a result of lipid extraction. In addition, de Lecea and de Charmoy (2015) demonstrated that the current mathematical isotope correction models available in the literature did not work with all the species in the bight. Muscle-tissue samples were placed immediately in an air-circulating oven and dried at 60 °C for 48 h, then homogenised and weighed into tin capsules (SANTI® Analytical, Teufen, Switzerland); c. 1.00 mg dry mass was required to yield sufficient δ15N and δ13C for analysis. For POM, water volumes of 500 ml (see Appendix 1) were filtered through precombusted (4 h at 450 °C) 40 mm diameter Whatman GF/F filters. Filters containing OM were then frozen at −20 °C and stored. Prior to analysis, the samples were acidified with a 2% HCl solution to prevent inorganic CaCO3 affecting organic δ13C values (Lorrain et al. 2003), rinsed with Milli-Q water and oven-dried at 65 °C. The samples were analysed at the IsoEnvironmental isotope facility at Rhodes University, Grahamstown, South Africa, using an ANCA-SL elemental analyser coupled to a Europa Scientific 20-20 isotope ratio mass spectrometer (IRMS) (Sercon). Each batch of 96 combustions contained 34 known standards, 29 of which were beet sugar and ammonium sulphate (in-house standards) and 5 of which were certified protein standard casein (calibrated against International Atomic Energy Agency [IAEA] standards IAEA-CH-6 and IAEA-N-1). The analytical precision of the instrument used for muscle tissue was 0.09‰ for 15N/14N and 0.08‰ for 13C/12C and, for OM filters, the precision was 0.07‰ for 15N/14N and 0.11‰ for 13C/12C. Sediment samples were placed in an air-circulation oven at 50 °C for 24 h, ground to ensure homogenisation,

acidified using 2% HCl solution to isolate the OM within the sediments, rinsed with Milli-Q water and returned to the oven for desiccation. Samples were processed in the archaeometry laboratory at the University of Cape Town. They were combusted in a Flash EA 1112 series elemental analyser (Thermo Finnigan); the gases were passed to a Delta Plus XP IRMS (Thermo Electron) via a Conflo III gas control unit (Thermo Finnigan). A proteinaceous gel produced by Merck (Darmstadt), was used as a standard and was calibrated against the IAEA standards. The analytical precision of the instrument was 0.06‰ for 15N/14N and 0.06‰ for 13C/12C. Isotope ratios obtained from both instruments are given in the standard δ-notation for element *X* (Epstein et al. 1953): d*X*(‰) = [(*R*sample − *R*standard)/*R*standard − 1] × 1 000 (1) where *R* is the ratio of 15N:14N or 13C:12C in the sample (*R*sample) and in the standard (*R*standard), expressed relative to the international standard (Sulzman 2007). *Statistical analysis and mixing models* For the samples collected in 2010, the Bayesian mixing model MixSir (version 1.0.4 with uninformative priors; Moore and Semmens 2008) was used to determine the proportional contribution of marine and riverine OM to the sediments of the bank and the contribution of OM and/ or sediment OM in the diet of demersal organisms. For sediment OM origin, mixing models were used to elucidate the role of riverine input, using riverine and marine POM isotope values as 'source' and marine sediments OM isotope values as 'consumer' with no applied fractionation factors. In the second case, in order to determine the origin of the OM that maintains the demersal organisms of the bank, Thukela and Matigulu riverine POM, as well as marine and sediment OM, were set as 'sources' in the mixing model, while the demersal organisms were set as the 'consumers'. These organisms would not be feeding directly on the OM trapped in the sediments, and hence the trophic position calculated for each species by de Lecea et al. (2013), along with the one-step fractionation factors of 0.4‰ (SD 1.3) for 13C and 3.4‰ (SD 1) for 15N (Post 2002), were used to estimate appropriate enrichment factors. In both mixing-model cases, the maximum importance ratio was below 0.001, suggesting that the models were effective in estimating the true posterior density (Moore and Semmens 2008). Results for MixSIR are presented as the median and the 5th and 95th confidence intervals. Non-mixing model statistics were calculated using R 2.12.0 (R Development Core Team 2010). The dataset collected for 2010 POM stable isotope values and C/N ratios was analysed using a Kruskal–Wallis non-parametric test comparing Site (Matigulu, Thukela or marine) and Origin (marine vs riverine). A two-way ANOVA was used to compare the isotope values and C/N ratio from the Thukela and Matigulu estuaries. Ordinarily riverine and marine sediments are not likely to be found together and as such riverine and marine sediment OM were not compared. It was decided that because there were only three years' worth of data collected (Appendix 1) the best approach was to compare the wet and dry seasons (2008, 2009 and 2010) for the riverine OM and the isotope values and C/N ratios of organisms. Because the data were non-parametric, a Welch *t*-test was used. Ocean Data View 4 was used to produce bottom-contour maps using the GPS coordinates, marine sediment C/N ratios and sediment mixing model results.

Results

Isotopic variables and C/N ratios (2010)

There were significant δ13C signature differences in both seasons when comparing POM by site (Matigulu, Thukela and marine), and origin (marine vs riverine) (Table 1, Figure 2). Marine sediment δ13C values were also significantly different to both riverine and marine POM values (Figure 2; Table 1). Marine sediment C/N ratios were significantly different from marine POM C/N ratios (Figure 2; Table 1) in the wet season, but not from riverine POM C/N ratios for either season. Values from marine sediments collected closer to the Matigulu Estuary mouth showed a lower C/N ratio, while those marine sediments originating from closer to the Thukela Estuary mouth were generally higher (Figure 3a, b). The mixing models confirmed that the bank sediments in both seasons in 2010 were composed mainly of riverine OM

Table 1: Comparative Kruskal–Wallis results for dry and wet seasons (a) comparing POM values by site (i.e. Matigulu, Thukela or marine) and origin (marine vs estuarine), and (b) comparing estuarine and marine POM isotopic signature, respectively, against marine sediment isotopic signature

Season	Variable	χ^2	df	*p*	Season	Variable	χ^2	df	*p*
(a) Dry		*Site*			(b) Dry		*Marine OM vs marine sediment*		
	$\delta^{15}N$	1.422	2	0.49		$\delta^{15}N$	1.03	1	0.31
	$\delta^{13}C$	7.2	2	0.03*		$\delta^{13}C$	6.6	1	0.01**
	C/N ratio	5.42	2	0.06		C/N ratio	2.67	1	0.1
		Origin					*Estuarine OM vs marine sediment*		
	$\delta^{15}N$	1.07	1	0.3		$\delta^{15}N$	0.04	1	0.84
	$\delta^{13}C$	5.4	1	0.02*		$\delta^{13}C$	11	1	0.0009***
	C/N ratio	1.67	1	0.2		C/N ratio	0.09	1	0.76
Wet		*Site*			Wet		*Marine OM vs marine sediment*		
	$\delta^{15}N$	1.42	2	0.49		$\delta^{15}N$	1.44	1	0.23
	$\delta^{13}C$	7.2	2	0.03*		$\delta^{13}C$	5.34	1	0.02*
	C/N ratio	5.42	2	0.07		C/N ratio	5.34	1	0.02*
		Origin					*Estuarine OM vs marine sediment*		
	$\delta^{15}N$	1.07	1	0.32		$\delta^{15}N$	0.13	1	0.72
	$\delta^{13}C$	5.4	1	0.02*		$\delta^{13}C$	8	1	0.005**
	C/N ratio	1.67	1	0.2		C/N ratio	0.89	1	0.35

*$p < 0.05$, **$p \leq 0.01$, ***$p < 0.001$

(Figure 3c, d), with the lowest values occurring north of the Matigulu Estuary.

The main biological drivers in the wet and dry seasons of 2010

Because the OM collected in both seasons had clearly distinct isotopic values, it was possible to set it as a source for the mixing model, together with the marine sediment OM. This enabled measurement of which of these OM sources the organisms were (indirectly) dependent on. It is important to note that, in most cases, the organisms in this study would not have directly consumed OM or the OM in the sediments, in most cases, but rather would have obtained it by secondary (or tertiary) predation or by scavenging (i.e. OM would be passed through the food chain via an intermediate trophic level, e.g. benthic macrofauna). Mixing model results indicated that during the wet season the main biological driver for the decapod *P. sanguinolentus* and the teleosts *A. nibe*, *C. attenuatus* and *J. dorsalis* originated from the marine sediment OM (>90%) (Table 2), which, as mentioned, was composed mainly of riverine OM. The OM sources for the teleosts *O. ruber*, *P. olivaceus* and *S.*

undosquamis were a mixture of marine POM and marine sediment OM, with *O. ruber* obtaining most of its OM from a food web supported by the OM in the sediments, whereas *Pomadasys olivaceus* and *S. undosquamis* obtained most of their OM from marine-derived sources (Table 2). In the dry season the situation was similar, with decapod species depending mainly on OM originally derived from the sediments (Table 2). However, unlike the wet season, most of the teleost species appeared to obtain their OM from a mixture of organisms feeding either on sediment OM or marine POM, with sediment-derived OM being slightly more important. The exceptions were *C. attenuatus* and *J. dorsalis*, which were highly dependent on OM derived from the sediments, whereas *C. lida* was dependent mostly on OM derived from marine POM (Table 2). As with the wet season, *S. undosquamis* obtained most of its OM through preying on organisms that depended mainly on marine POM, with sediment OM playing a minor role (Table 2).

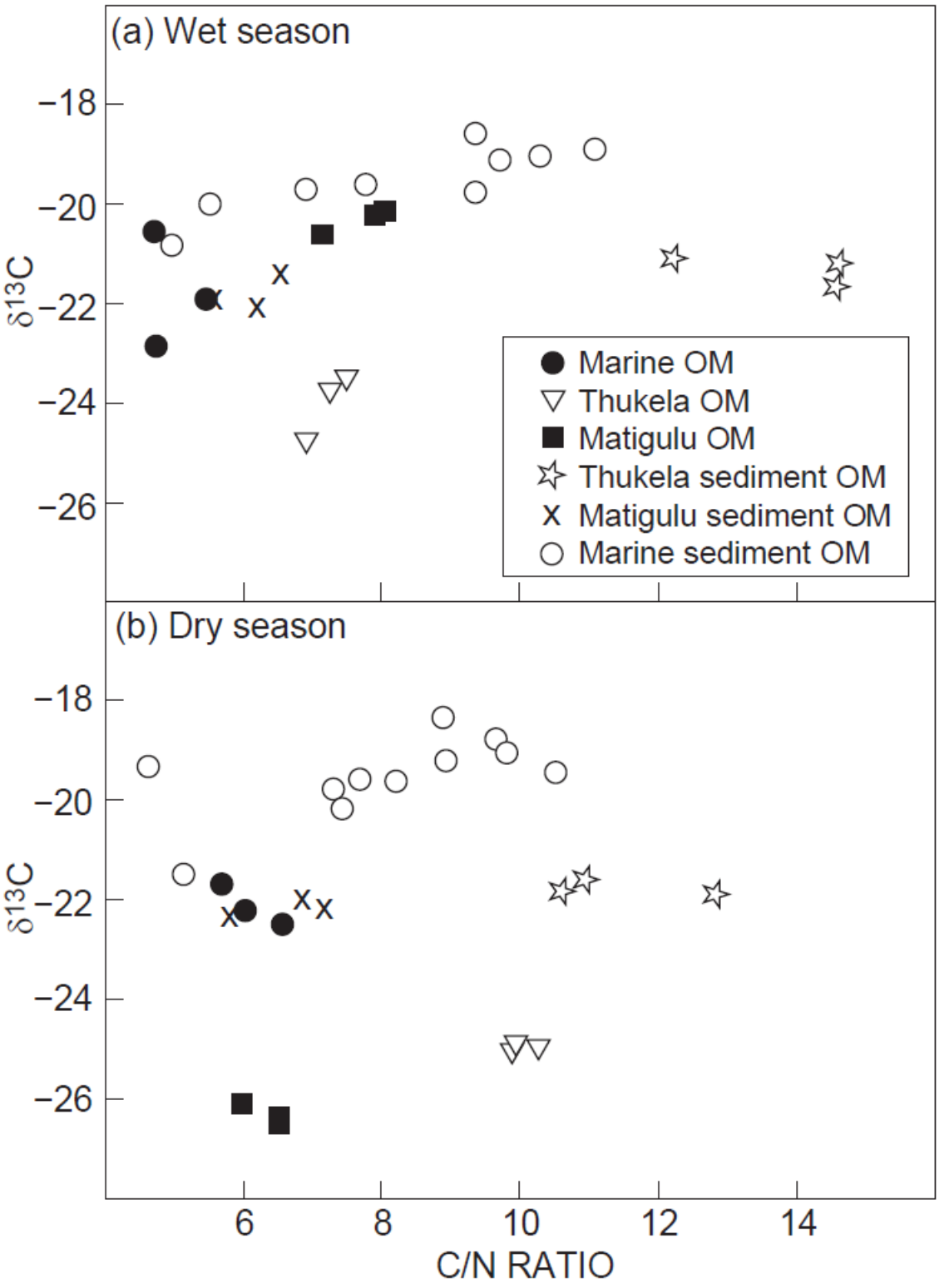

Figure 2: $\delta^{13}C$ and C/N ratio values for different sources of OM and sediments collected from the Matigulu and Thukela estuaries and the Thukela Bank (= marine) for (a) wet and (b) dry seasons

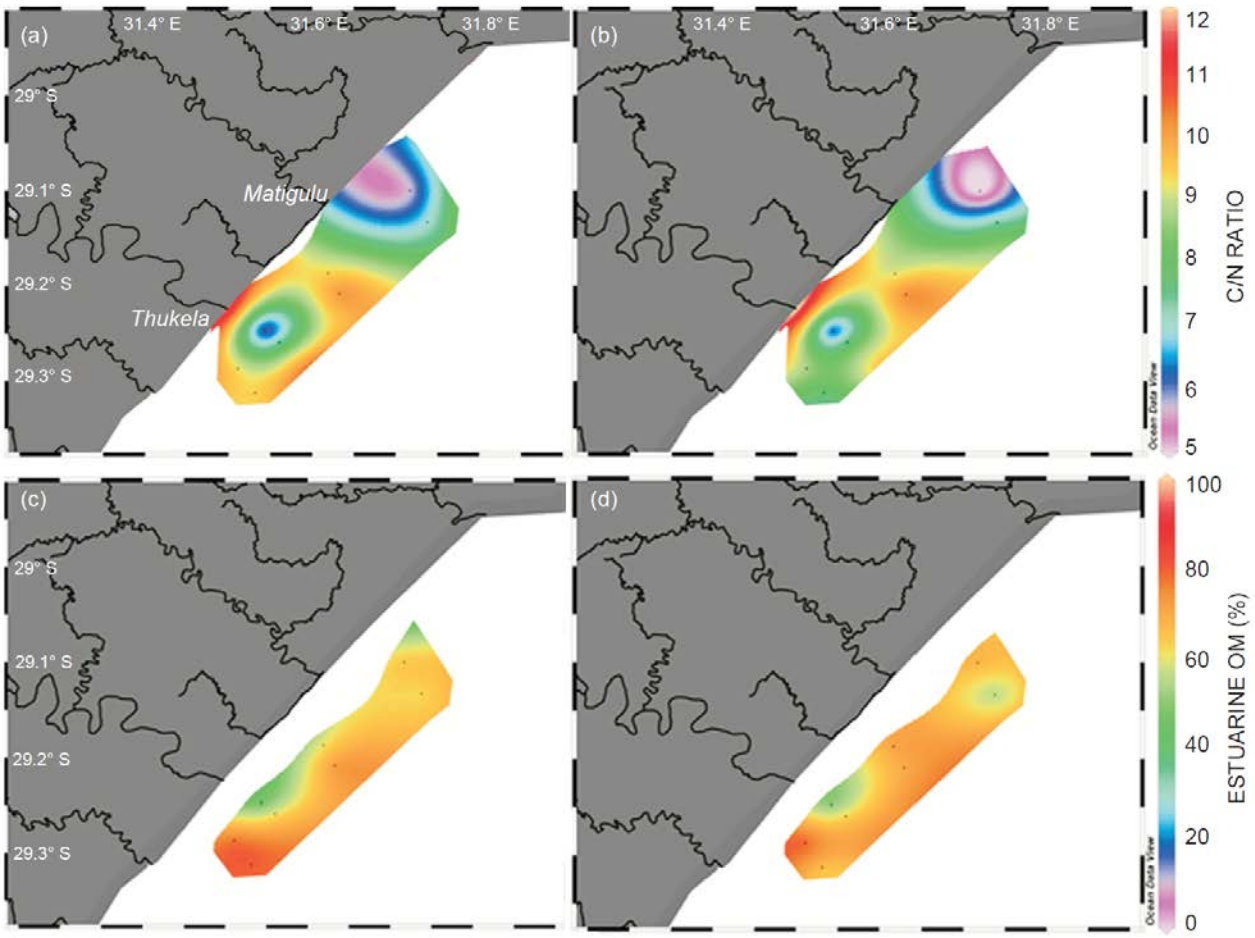

Figure 3: (a, b) C/N ratio and (c, d) mixing model results for marine and estuary mouth sediment stations for the (a, c) wet and (b, d) dry seasons in 2010. Mixing model results show origin of OM (%) in marine sediments

Investigation of seasonal differences in riverine OM and animal tissue isotopic and C/N ratios

Riverine OM isotope values differed statistically between seasons for all years for the Thukela Estuary, with samples collected during the wet season being 13C-enriched and 15N-depleted compared to those of the dry season (Table 3). Neither Thukela nor Matigulu estuary OM showed statistically significant seasonality in C/N ratios (Table 3; Welch *t*-test, $p > 0.05$). However, there were significant differences in C/N ratios between the two estuaries (two-way ANOVA: df = 1, SS = 7.85, MS = 7.85, $F = 4.59$, $p < 0.05$). In 2010, some of the organisms showed clear seasonal feeding habits (Table 2); thus it is expected that this should manifest in the organisms' isotopic values. Of the 11 demersal species collected in this study, two species, *A. nibe* and *P. olivaceus*, were significantly enriched in δ15N in the wet season compared to the dry season (Table 3). On the other hand, seven species were significantly enriched in 13C during the dry season (Table 3), with another two being more enriched but not significantly different. Five out of 11 organisms had significant differences in C/N ratios between the wet and dry seasons (Table 3).

Discussion

The aim of this study was to clarify the role played by the Thukela River in introducing OM into the nearby Thukela Bank ecosystem. It was found that, in both seasons (wet and dry) in 2010, riverine OM was the dominant OM input (>60%) into the bank sediments. Mixing models revealed that organisms in the wet season were dependent on the OM of the bank. In the dry season, sediment OM (and, by implication, riverine OM) remained the most important driver for nine of the 11 species studied, but unlike in the wet season, marine POM also played an important role for the teleosts, perhaps highlighting a more opportunistic feeding behaviour and/or greater reliance on pelagic food webs.

Table 2: Bayesian mixing model results for organisms (i.e. consumers) and OM sources (particulated and accumulated in the sediments) (i.e. food sources) collected in the wet and dry seasons of 2010, showing which source of OM is the main driver of the food web on the Thukela Bank. Median and 5th and 95th confidence intervals are shown

Species	Description	Marine OM	Thukela OM	Matigulu OM	Marine sediment OM
		Wet season			
Portunus sanguinolentus	Decapod	0.01 (0.00–0.05)	0.01 (0.00–0.04)	0.01 (0.00–0.04)	0.96 (0.92–0.99)
Atrobucca nibe	Teleost	0.04 (0.00–0.97)	0.01 (0.00–0.06)	0.02 (0.00–0.08)	0.91 (0.00–0.98)
Cynoglossus attenuatus	Teleost	0.01 (0.00–0.03)	0.01 (0.00–0.02)	0.01 (0.00–0.02)	0.98 (0.94–1.00)
Johnius dorsalis	Teleost	0.04 (0.00–0.98)	0.01 (0.00–0.04)	0.01 (0.00–0.03)	0.93 (0.00–0.99)
Otolithes ruber	Teleost	0.64 (0.53–0.77)	0.01 (0.00–0.04)	0.03 (0.00–0.20)	0.31 (0.05–0.45)
Pomadasys olivaceus	Teleost	0.27 (0.02–0.31)	0.01 (0.00–0.04)	0.05 (0.00–0.17)	0.64 (0.58–0.86)
Saurida undosquamis	Teleost	0.74 (0.62–0.84)	0.01 (0.00–0.05)	0.06 (0.00–0.20)	0.17 (0.02–0.35)
		Dry season			
Metapenaeus monoceros	Decapod	0.01 (0.00–0.04)	0.01 (0.00–0.02)	0.01 (0.00–0.03)	0.95 (0.94–0.99)
Panaeus indicus	Decapod	0.01 (0.00–0.08)	0.01 (0.00–0.04)	0.01 (0.00–0.04)	0.95 (0.88–0.98)
Portunus sanguinolentus	Decapod	0.01 (0.00–0.02)	0.00 (0.00–0.02)	0.00 (0.00–0.02)	0.96 (0.94–0.98)
Atrobucca nibe	Teleost	0.45 (0.01–0.94)	0.01 (0.00–0.03)	0.01 (0.00–0.03)	0.53 (0.01–0.94)
Cynoglossus attenuatus	Teleost	0.01 (0.00–0.02)	0.01 (0.00–0.02)	0.01 (0.00–0.01)	0.97 (0.96–0.97)
Cynoglossus lida	Teleost	0.95 (0.01–0.99)	0.01 (0.00–0.02)	0.00 (0.00–0.01)	0.01 (0.00–0.97)
Johnius dorsalis	Teleost	0.02 (0.00–0.95)	0.01 (0.00–0.04)	0.01 (0.00–0.03)	0.92 (0.01–0.97)
Otolithes ruber	Teleost	0.48 (0.42–0.56)	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.51 (0.43–0.58)
Pomadasys olivaceus	Teleost	0.45 (0.39–0.51)	0.00 (0.00–0.01)	0.00 (0.00–0.01)	0.54 (0.49–0.61)
Saurida undosquamis	Teleost	0.67 (0.38–0.97)	0.01 (0.00–0.04)	0.01 (0.00–0.04)	0.31 (0.01–0.60)

Origin of OM in the sediments and marine POM seasonality

Isotopic δ13C values indicated that the marine sediment OM was distinct from both the marine and riverine OM sampled from the water column. Sediment OM must originate from either the marine or terrestrial environment. It is plausible, however, that the stable isotope values of the marine sediment OM represent mainly terrestrial plant detritus, with some marine phytoplankton accumulating and mixing in the sediments. In this regard, Goñi et al. (1998) found that, in marine areas with several OM inputs, the isotopic signature of the marine sediments did not represent one particular source, but a mixture of all sources. There was strong seasonality in the isotopic values of OM collected from the Thukela River mouth, with 15N significantly enriched and 13C significantly depleted in the dry season, in comparison with the wet season. Seasonality in riverine isotopic values is common on account of the highly dynamic nature of estuaries (Faye et al. 2011), including in tropical and subtropical estuaries where wet and dry seasons are well defined (Olin et al. 2012). The relatively depleted OM 13C values in both seasons were likely due to the presence of C3 plant detritus from the Thukela River, where C3 plants grow in 75% of the catchment area (Harrison et al. 2001). The δ13C of C3 plants ranges from −22‰ to −33‰, and that of C4 plants ranges from −9‰ to −16‰ (Huang et al. 2000), whereas for both C3 and C4 plants

δ15N ranges from −7‰ to 7‰ (Kelly 2000). The majority of C/N ratios estimated in our study ranged between 8 and 10. As with δ13C, these values do not fully represent either marine or riverine OM. Marine phytoplankton C/N ratios are usually <5 due to the high levels of nitrogen accumulated in phytoplankton cells, whereas C/N ratios of terrestrial plants are usually ≥11 (Lamb et al. 2006). Hence our results might indicate a mixture of marine and terrestrial OM, in accordance with the findings of Ogrinc et al. (2005). However, given that bacterial degradation of terrestrial material in marine sediments can cause a lowering of C/N ratios to values similar to those obtained in our study (Thornton and McManus 1994), it is considered likely that, although some mixing of marine and riverine OM may occur, the major source of OM to the bank is of riverine origin. Mixing models strengthened this notion by indicating that, although there was a mixture of marine and riverine OM, the majority of OM accumulated in the sediments was of riverine origin.

Identification of the OM driving the food web of the Thukela Bank

A short literature review was undertaken to assess the diets of the organisms sampled for this study, the majority of which are known to feed on epibenthic organisms (Appendix 2). The mixing model results agree largely in that most species sampled in this study depended on the OM accumulating in the sediments, which suggests that macrobenthos (not sampled here) may play an important role in this food web. However, there were some exceptions – *O. ruber*, *P. olivaceus* and *S. undosquamis* – which were instead highly dependent on marine POM in both seasons. *Atrobucca nibe* were also highly dependent on marine POM in the dry season but not in the wet, seemingly changing their feeding mode according to the season, a strategy that has been well described in other studies (Polis et al. 1995). Overall the main OM source driving the food web was the marine sediment OM, which, as discussed above, was mainly of riverine origin. This was followed in the dry season by marine POM becoming an important dietary supplement for a number of species.

Organism seasonal stable isotope values and C/N ratios

Isotopic signatures in both OM and in organism tissue reflected a well-defined seasonal change. The upwelling cell in the northern part of the bight is not seasonal (Lutjeharms et al. 1989; Hutchings et al. 2010), and hence, unless there is another source of seasonal OM onto the bank that was not accounted for, it is likely that the Thukela and Matigulu River were the sources.

Table 3: Welch *t*-test results comparing the combined wet and dry seasons of 2008, 2009 and 2010 in terms of mean isotope and C/N ratio values for estuarine POM and Thukela Bank organisms

	Value tested	*t*	df	*p*		Mean (SD) Wet	Mean (SD) Dry
POM (Thukela Estuary)	$\delta^{15}N$	2.75	19.47	0.01	**	3.32 (1.73)	5.69 (1.77)
	$\delta^{13}C$	−4.82	10.10	0.00	***	−21.48 (1.93)	−24.75 (0.57)
	C/N	−0.01	15.18	0.99		8.47 (1.10)	8.48 (2.48)
POM (Matigulu Estuary)	$\delta^{15}N$	0.23	16.19	0.82		3.96 (3.09)	4.19 (1.69)
	$\delta^{13}C$	−1.28	22.31	0.21		−22.18 (1.41)	−23.19 (2.60)
	C/N	0.48	23.88	0.64		7.59 (0.68)	7.76 (1.08)
Atrobucca nibe	$\delta^{15}N$	−2.97	9.80	0.01	**	11.78 (0.32)	11.44 (0.08)
	$\delta^{13}C$	−0.86	10.98	0.41		−16.84 (0.31)	16.94 (0.13)
	C/N	−0.14	10.63	0.89		3.22 (0.09)	3.22 (0.03)
Cynoglossus attenuatus	$\delta^{15}N$	0.44	32.65	0.67		11.56 (0.35)	11.51 (0.33)
	$\delta^{13}C$	1.51	32.99	0.14		−16.13 (0.30)	−15.98 (0.31)
	C/N	−0.43	32.94	0.67		3.18 (0.05)	3.17 (0.06)
Cynoglossus lida	$\delta^{15}N$	−1.11	12.78	0.29		11.65 (0.12)	11.48 (0.46)
	$\delta^{13}C$	−2.17	10.10	0.05		−16.23 (0.20)	−16.66 (0.56)
	C/N	3.24	12.99	0.01	**	3.14 (0.03)	3.30 (0.16)
Johnius dorsalis	$\delta^{15}N$	2.04	33.67	0.06		11.98 (0.31)	12.25 (0.50)
	$\delta^{13}C$	3.30	36.90	0.00	***	−16.73 (0.38)	−16.31 (0.42)
	C/N	0.13	33.53	0.90		3.27 (0.06)	3.27 (0.10)
Otolithes ruber	$\delta^{15}N$	0.38	44.23	0.70		12.23 (0.38)	12.29 (0.61)
	$\delta^{13}C$	1.94	47.36	0.06		−16.62 (0.45)	−16.38 (0.42)
	C/N	0.33	48.22	0.74		3.29 (0.19)	3.31 (0.18)
Pomadasys olivaceus	$\delta^{15}N$	−2.21	30.55	0.03	*	12.57 (0.39)	12.26 (0.44)
	$\delta^{13}C$	3.59	34.74	0.00	***	−16.67 (0.29)	−16.24 (0.44)
	C/N	−2.10	24.82	<0.05	*	3.28 (0.16)	3.17 (0.14)
Saurida undosquamis	$\delta^{15}N$	−0.38	16.55	0.71		12.12 (0.45)	11.84 (0.62)
	$\delta^{13}C$	2.62	9.41	0.03	*	−16.88 (0.46)	−16.31 (0.33)
	C/N	−5.09	20.17	<0.01	***	3.27 (0.10)	3.08 (0.09)
Metapeneaus monoceros	$\delta^{15}N$	−0.51	16.73	0.62		10.90 (0.44)	10.83 (0.32)
	$\delta^{13}C$	4.66	31.85	0.00	***	−16.99 (0.34)	−16.30 (0.54)
	C/N	−0.37	28.84	0.71		3.27 (0.10)	3.22 (0.05)
Penaeus indicus	$\delta^{15}N$	−0.97	28.92	0.34		10.75 (0.21)	10.63 (0.51)
	$\delta^{13}C$	3.19	9.58	0.01	**	−16.77 (0.64)	−16.06 (0.31)
	C/N	−4.38	18.16	<0.01	***	3.31 (0.05)	3.21 (0.07)
Portunus hastatoides	$\delta^{15}N$	−0.10	11.31	0.92		10.56 (0.58)	10.53 (0.37)
	$\delta^{13}C$	2.86	9.91	0.02	*	−17.60 (0.46)	−17.14 (0.23)
	C/N	−0.82	11.95	0.43		3.42 (0.14)	3.38 (0.10)
Portunus sanguinolentus	$\delta^{15}N$	1.97	35.89	0.06		10.89 (0.39)	11.12 (0.33)
	$\delta^{13}C$	4.59	30.81	0.00	***	−16.75 (0.61)	−16.02 (0.35)
	C/N	−2.38	31.99	0.02	*	3.45 (0.21)	3.32 (0.13)

*$p < 0.05$, **$p \leq 0.01$, ***$p < 0.001$

Seasonal changes in organism isotopic response were the converse of changes in OM isotopic signature; OM was 13C-enriched in the wet season compared to the dry season, whereas organisms were 13C-enriched in the dry season. This may reflect a time-lag due to the fact that OM accumulates in the sediments and is consumed by organisms lower in the food web, which in turn are consumed by organisms at higher trophic levels, such as those in our study. In addition, time-lags in an organism's tissue reflecting the isotopic signature of its food are common on account of the period of time that organism tissue takes to reach equilibrium with that of the diet (Vanderklift and Ponsard 2003). Hence it is likely that a time-lag occurred in the assimilation by organism tissue of the isotopic signature of the OM released by the Thukela River. Overall there was some congruence between seasonal changes in OM and organism isotope values if isotopic incorporation times are taken into account. The time required for the δ15N value in an organism's tissue to reach equilibrium with the diet may differ from that for δ13C values (Olive et al. 2003). Furthermore, it has been demonstrated that isotopic equilibrium between predator muscle tissue and that of the diet in the wild is limited due to seasonal changes or changes in prey item composition (Sweeting et al. 2005).

In the current study, it appears that 13C from the diet was assimilated faster in the muscle tissue than 15N, because δ13C values showed a clear seasonality for most species, whereas this was not the case for δ15N values. This could be because nitrogen isotopic values vary for a number of reasons, including different forms of nitrogen excretion (Minagawa and Wada 1984), isotopic fractionation (Vanderklift and Ponsard 2003) or owing to nitrogen-specific physiological or metabolic processes (Olive et al. 2003). In these instances, δ15N isotopic equilibrium in the tissue may not manifest, and rather than the signature showing either the current or the past diet, it may reflect a mixture of both (Gannes et al. 1997; Sweeting et al. 2005). Omnivory might also complicate the interpretation of the data, because organisms might reach an equilibrium that reflects a mixture of prey items at different trophic levels. Thompson et al. (2007) found that omnivory is common in marine systems, and that the higher the trophic level of an organism, the more common omnivory becomes. In our study, the majority of organisms are from higher trophic levels and are omnivorous (see Appendix 2). Five of the species sampled in this study had seasonal differences in C/N ratios (*C. lida*, *P. olivaceum*, *P. indicus*, *P. sanguinolentus* and *S. undosquamis*). It has been shown that high C/N ratios (>3) indicate a poor-quality diet, with a nitrogen-poor diet having a similar effect on tissues to that of fasting (Vanderklift and Ponsard 2003). Four of the five species, *C. lida* being the exception, had higher C/N ratios in the wet than in the dry season, perhaps an indication that during the wet season there is a more varied and higher abundance of food. This study concurs with similar findings from other recent studies in the region (Ayers and Scharler 2011; de Lecea et al. 2013; de Lecea et al. 2015; Scharler et al. 2016) in highlighting the importance of riverine input in the ecology of the bight, which is contrary to previous understanding. Summary This study set out to understand the dependence of Thukela Bank organisms on organic input originating from the nearby estuaries. It was found that most of the OM accumulated in the sediments of the bank in the wet and dry seasons of 2010 was of riverine origin. Furthermore, it appears that, within a season, the food web supporting the majority of organisms under study was supported by the OM accumulated in the sediments. There were some exceptions that had higher dependency on marine POM, and the dependency of two species (*A. nibe* and *P. olivaceus*) differed between seasons. Considering seasonal stable isotope values for 2008, 2009 and 2010 combined, we found that the isotopic differences observed for OM (13C-enriched in the wet season compared with the dry season), were the converse of those seen for organisms (13C-enriched in the dry season). This discrepancy was attributed to a lag in the time taken for tissue to acquire the isotopic signature of the diet. C/N ratios and mixing models provided supporting evidence for the view that OM from estuaries was the main driver of the studied food webs on the Thukela Bank. In conclusion, given the important role of the Thukela River, in particular, in providing input to demersal food webs (de Lecea et al. 2013; this study), and to fisheries (Lamberth et al. 2009; Turpie and Lamberth 2010), further consideration should be given to the impacts of freshwater impoundments planned for the Thukela catchment area (DWAF 2004), including their potential effects on the ecosystem of the KZN Bight and on two important fisheries in the region. *Acknowledgements* — We thank the African Coelacanth Ecosystem Programme, and the KZN Bight Thukela Bank Functioning Project (funded by the National Research Foundation of the South African Department of Science and Technology), for their financial contribution towards this study. We are grateful to the following: the late Dr Sven

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Appendix 1: Number of samples (total suspended solids [TSS for POM analysis] and sediments) and number of organisms collected from trawls conducted in different years and seasons. Note that marine TSS and sediments were only collected in the wet and dry seasons of 2010; n/a = no data

Sample type/species	2008		2009		2010	
	Wet	Dry	Wet	Dry	Wet	Dry
Marine TSS	n/a	n/a	n/a	n/a	3	3
Marine sediment	n/a	n/a	n/a	n/a	9	11
Thukela TSS	6	6	3	3	3	3
Thukela sediment	3	3	3	3	3	3
Matigulu TSS	6	6	3	3	3	3
Matigulu sediment	3	3	3	3	3	3
Metapenaeus monoceros	n/a	18	12	n/a	n/a	6
Panaeus indicus	n/a	19	9	n/a	n/a	3
Portunus hastatoides	n/a	19	9	n/a	n/a	n/a
Portunus sanguinolentus	n/a	10	14	n/a	6	8
Atrobucca nibe	n/a	1	6	n/a	3	3
Cynoglossus attenuatus	n/a	12	8	n/a	9	6
Cynoglossus lida	n/a	6	3	n/a	n/a	6
Johnius dorsalis	n/a	18	12	n/a	6	3
Otolithes ruber	n/a	18	18	n/a	6	9
Pomadasys olivaceus	n/a	14	8	n/a	n/a	6
Saurida undosquamis	n/a	14	6	n/a	2	6

Appendix 2: General prey items, determined from the literature, for species collected on the Thukela Bank in the wet and dry seasons of 2010; n/a = no data

Species	Description	General prey items	Reference
Atrobucca nibe	Teleost	Crustacea: Mysidacea, Natantia, Anomura; Cephalopoda; Osteichthyes	Fennessy (2000)
Cynoglossus attenuatus	Teleost	Benthic invertebrates	Fischer et al. (1990)
Cynoglossus lida	Teleost	Bivalvia; Cnidaria; Crustacea: prawns (*Lucifer* spp.), Amphipoda, diverse Brachyura, Isopoda, Copepoda; Asteroidea; Gastropoda; Osteichthyes; Polychaeta. Other prey items include diverse zoobenthos, diatoms, benthic algae and fish eggs	Rajaguru (1992)
Johnius dorsalis	Teleost	Polychaeta; Crustacea: Copepoda, Ostracoda, Mysidacea, Stomatopoda, Natantia, Anomura, Brachyura; Cephalopoda; Pelecypoda; Osteichthyes	Fennessy (2000)
Metapenaeus monoceros	Decapod	Crustacea: Copepoda, Mysidacea, Tanaidacea, Amphipoda, decapod larvae; vegetable matter; diatoms; Polychaeta; detritus	George (1974)
Otolithes ruber	Teleost	Crustacea: Natantia, Brachyura, Mysidacea, Stomatopda, Anomura; Osteichthyes; Cephalopoda; Polychaeta; Pelecypoda; vegetation; prawns; *Acetes*; *Squilla*; apogonid fishes and juvenile sciaenids	Fennessy (2000)
Penaeus indicus	Decapod	n/a	
Pomadasys olivaceus	Teleost	Benthic Crustacea, and a variety of other invertebrates, but not Annelida	van der Elst and Adkin (1991)
Portunus sanguinolentus	Decapod	Predator of slow-moving benthic macroinvertebrates. Preference for crustaceans and molluscs. Females prefer Osteichthyes in addition to Crustacea. Although fish remains are important, it is unlikely that this species can actively hunt healthy fish	Sukumaran and Neelakantan (1997)
Saurida undosquamis	Teleost	Osteichthyes; Crustacea: shrimp/prawn, *Penaeus* spp., *Stolephorus* sp., crabs; Cephalopoda: octopus, squid/ cuttlefish; other molluscs; fish eggs and larvae	Bingel and Avsar (1988)