

# Processes controlling the benthic food web of a mesotrophic bight (KwaZulu-Natal, South Africa) revealed by stable isotope analysis

A. M. De Lecea<sup>1,\*</sup>, S. T. Fennessy<sup>2</sup>, A. J. Smit<sup>3</sup>

<sup>1</sup>Geological Sciences, and <sup>3</sup>Biological Sciences, School of Agricultural, Earth and Environmental Sciences, Westville Campus, University of KwaZulu-Natal, Durban 4001, South Africa

<sup>2</sup>Oceanographic Research Institute, PO Box 10712, Marine Parade, Durban 4056, South Africa

**ABSTRACT:** The KwaZulu-Natal Bight is considered oligotrophic/mesotrophic with distinct sources of nutrients entering the system by a series of oceanographic processes, including an upwelling cell and several estuaries, of which the Thukela River is the most important; the upwelling cell is suggested to be the main factor controlling the biology of the Bight. Our aim is to describe the main nutrient/organic matter (OM) source driving the benthic system of the Bight and to produce a food web to aid in understanding the trophic interactions occurring in the demersal ecosystem. For this, marine and riverine sediment samples, total suspended solids and marine demersal organisms were collected across the Bight, and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition was analysed during 2 seasons. Our results, based on  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , percent organic carbon, percent nitrogen and carbon:nitrogen ratios, suggest that the OM in the sediments is mainly dominated by riverine input and the benthic food web is controlled mainly by riverine total suspended solids input. Future studies should look at the role played by bacteria in the degradation of terrestrial OM and the overall effect in the food web of the Bight. Omnivory appears to be a widespread strategy for demersal organisms throughout the Bight, a finding supported by the lack of clear  $\delta^{15}\text{N}$  enrichment between prey and predators and the low variability of trophic positions across a wide array of organisms.

**KEY WORDS:** Demersal · Food web · Stable isotope · Marine · Riverine · Organic matter · Sediment

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

The KwaZulu-Natal Bight (the Bight) on the oligotrophic/mesotrophic east coast of South Africa (Bus-tamante et al. 1995, Barlow et al. 2008) is recognised as an oceanographically important area highly influenced by the Agulhas Current (Lutjeharms 2006). The biology of the Bight has not been well studied (Ayers & Scharler 2011), but the shallow Thukela Bank, off the Thukela River mouth (Fig. 1), is suggested to be dominated by riverine input and, hence, is important to a limited number of fisheries (Lamberth et al. 2009). However, overall, little work has been done on the biology of the (demersal) system

and how it is driven by the nutrient inputs associated with the complex hydrography of the Bight.

Nutrients are introduced into the Bight by a series of fluvial and oceanographic processes that have been relatively well described (Fig. 1) (Lutjeharms et al. 2000b, Meyer et al. 2002). Topographically induced upwelling close to the Richards Bay area in the north of the Bight is regarded by oceanographers as the most important source of nutrients into the Bight (Lutjeharms et al. 2000a, Meyer et al. 2002). A cyclonic lee eddy off the coast of Durban in the south of the Bight is also thought to be another source of oceanic nutrients to the system (Lutjeharms et al. 2000b).

\*Email: a\_lezea@yahoo.co.uk

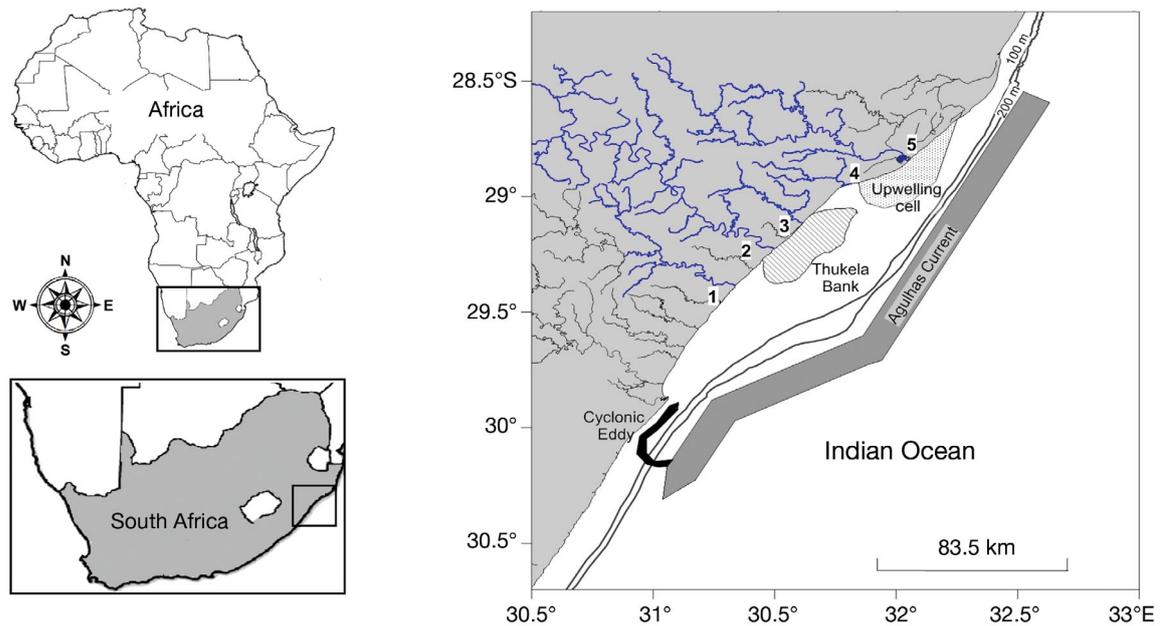


Fig. 1. Oceanographic and riverine phenomena affecting water masses in the area of the KwaZulu-Natal Bight. Rivers and their catchment areas that were sampled for this study are in blue, and other rivers entering the Bight but not sampled for this study are in black. (1) Mvoti River, (2) Thukela River, (3) Matikululu River, (4) Mlalazi River, (5) Mhlathuze River

In addition to the oceanic sources, the KwaZulu-Natal province also has a total of 73 fluvial sources (rivers), with 6 major estuaries and several smaller estuaries providing fluvial materials to the Bight (Begg 1978). Of these, the Thukela River generates more than 35% of the freshwater entering the KwaZulu-Natal nearshore environment, with an annual runoff of  $3865 \times 10^6 \text{ m}^3$  and a total sediment input of  $6.79 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$  (Birch 1996, Hutchings et al. 2010). Nevertheless, there seems to be some contradiction on the importance of rivers as a nutrient source. Some researchers suggest that the role of river runoff in shaping the biological aspects of the Bight is relatively small (Meyer et al. 2002), while others suggest that, at least for the central area known as the Thukela Bank, riverine input plays a very important role (Lamberth et al. 2009). Overall, little is known about the biology of the system and how it is driven by the oceanic and fluvial dissolved and particulate material inputs associated with the complex hydrography of the Bight.

The mesotrophic nature of the Bight means that it does not support large fisheries, as in other regions of the country, but it does host South Africa's only prawn trawl fishery (Fennessy & Groeneveld 1997) and a hook and line fishery, which is the most important fishery on the east coast in terms of participation and catch (Lamberth et al. 2009). Limited commercial fisheries' interest in the region, compared to the

much larger west coast fisheries, has led to little ecosystem-type research in the Bight that has mainly addressed the economically important prawn species and associated by-catch (Fennessy et al. 1994, Fennessy & Groeneveld 1997, Olbers & Fennessy 2007). These studies mainly focused on the Thukela Bank, a shallow trawl ground in the northern Bight (Fig. 1), and there are no studies for greater depths or areas which are not trawled. One study looked at the effect of riverine flux on fisheries catches (Lamberth et al. 2009) and suggested that any flow reduction in freshwater, mainly from the Thukela River, into the Bight will negatively affect fisheries catches, highlighting the important role that riverine input can have on the Bight.

The broad aim of this study is to present an understanding of the ecosystem and food web for benthic (demersal) organisms within a framework of the underlying hydrography and sedimentary material distributions using stable isotopes, from which inferences about food web structure and function will be derived. The focus here is on demersal ecosystem functioning, as the pelagic system will be dealt with in other publications. First, we aim to identify the main source of carbon (C) and nitrogen (N) to the Bight benthic ecosystem, i.e. the origin of the sediment organic matter (OM). We hypothesise that OM in riverine total suspended solids (TSS), which is delivered to the Bight throughout the year and pre-

dominantly during the wet austral summer (December to March) (Day 1981), plays a more important role as a determinant of benthic food webs than previously thought. Our second hypothesis is that sediment OM stable isotope signatures vary spatially and that these variations are consistent with the variations in the biological drivers in the Bight (i.e. fluvial, upwelling and/or cyclonic eddy). This hypothesis stems from the work of Iken et al. (2010), who found that the isotopic signatures of macrobenthic organisms resembled those of the OM in the overlying water masses. As macrobenthos will mainly feed on the OM in the sediments, the surface sediments should also resemble the stable isotope signature of the OM in the overlying water masses. Our third hypothesis is that the isotopic signatures of demersal organisms vary spatially with the signatures of the associated sediments (Hobson et al. 1995, Iken et al. 2010).

The premise of this research is that the oceanographic processes in the Bight, particularly the upwelling cell, provide nutrients/OM with unique isotopic characteristics (specifically  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), which allows us to use this ecological tool to test these hypotheses. Stable isotopes have successfully been used to describe the origin of OM in aquatic systems and the food webs associated with them (Schell et al. 1998, Lara et al. 2010). Ultimately, the intention of this research is to produce an understanding of what processes are driving the Bight and likely trophic pathways involving demersal organisms and their dependence on the benthos, pelagos

or riverine effluvium through the generation of a demersal food web of the Bight.

## MATERIALS AND METHODS

### Study site

The Bight (Fig. 1) extends for 160 km from St. Lucia to an area just south of Durban on the east coast of South Africa. It is about 50 km wide at its broadest point, offshore of the Thukela River (Bosman et al. 2007). Three major processes have been suggested as possible drivers for primary productivity in the Bight: (1) topographically induced upwelling off Richards Bay (Lutjeharms et al. 1989), (2) a cyclonic lee eddy off the coast of Durban (Schumann 1982) and (3) a series of fluvially induced processes dominated mainly by the Thukela River (Bosman et al. 2007).

### Sample collection and storage

During January/February (wet season, summer) 2010 and July/August (dry season, winter) 2010, physico-chemical variables, TSS, zooplankton and sediment were sampled on board the FRV 'Algoa'. A Sea-Bird 911 plus CTD and oxygen meter (Sea-Bird Electronics) with twelve 5 l PVC Niskin bottles attached to a rosette were used to measure temperature, salinity and oxygen across the Bight (Fig. 2a). For this study, only CTD data from the bottom, just

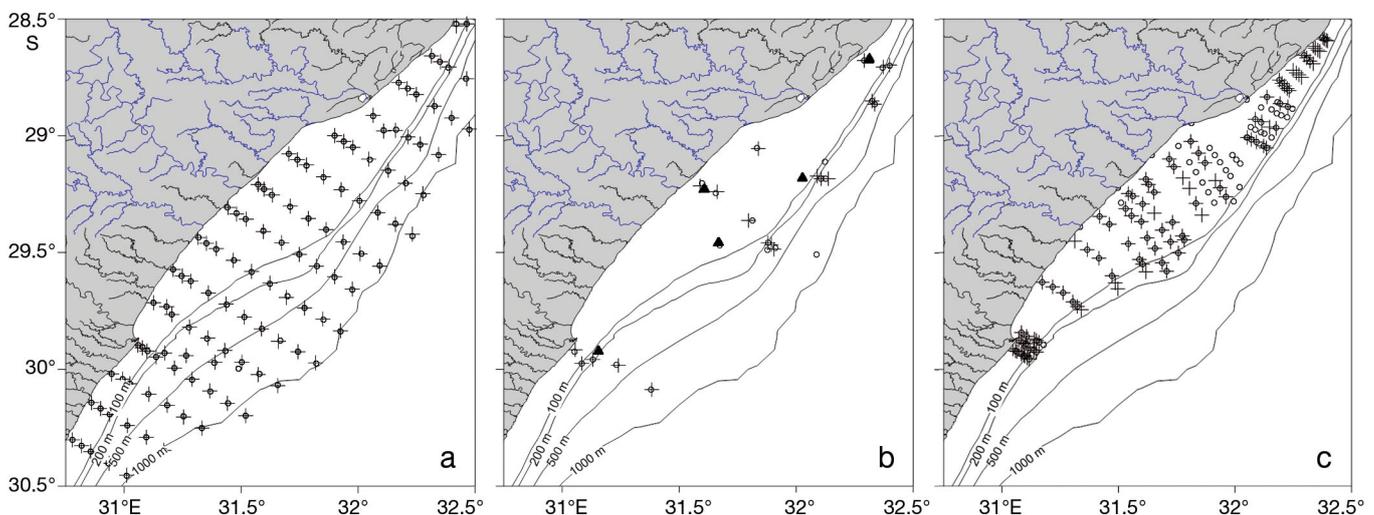


Fig. 2. Sampling stations throughout KwaZulu-Natal Bight for (a) CTD casts, (b) trawling and marine total suspended solids (TSS) and (c) surface sediments. Circles indicate summer stations, crosses indicate winter stations and triangles indicate marine TSS collection points for both winter and summer. Sampled river mouths are highlighted in blue and were sampled in both seasons (see Fig. 1 for names)

above the sediments, were considered. TSS sample preparation involved filtering 500 ml of water from the Niskin through pre-combusted (4 h at 450°C) 25 mm diameter Whatman GF/F filters to collect TSS from 5 different points in the Bight (Fig. 2b). The filters were frozen at  $-20^{\circ}\text{C}$  and stored for later isotopic analysis.  $\text{CaCO}_3$  was removed by acidification with a 2% HCl solution to prevent it from affecting  $\delta$ -values.

A modified Van Veen grab was used to collect sediment samples from across the Bight (Fig. 2c). A spoonful of sediment was immediately collected from the top layer of the grab, placed in a zip-sealed bag and frozen at  $-20^{\circ}\text{C}$  for later isotopic analysis. Great care was taken to ensure that no macrobenthos were placed in the zip-sealed bag along with the sediments. Because of the proximity and speed of the Agulhas Current (core speeds of up to  $2\text{ m s}^{-1}$ ; de Ruijter et al. 1999), the sediment grab could not be deployed deeper than  $\sim 180\text{ m}$ . Sediment and TSS samples for the Mhlatuze, Mlalazi, Matikulu, Thukela and Mvoti river mouths were obtained concurrently for both seasons (Fig. 2c, highlighted blue). For marine sediment, only 1 sample per station was collected, and for riverine sediment, 3 replicates were collected for each river. These samples were treated the same as those from the vessel. Surface TSS samples from the river mouths were collected during low tide to ensure that riverine and not marine TSS was collected.

Zooplankton sampling sites correspond to the locations where marine TSS was collected (Fig. 2b), which is where physical processes are thought to play a major role in driving the productivity of the Bight through the nutrient delivery mechanisms that operate there (Fig. 1). Samples were collected using a double oblique bongo net (200 and 300  $\mu\text{m}$  mesh) lowered to a few meters from the recorded bottom. Zooplankton collected in the 200  $\mu\text{m}$  mesh net were immediately preserved in 4% formalin and stored in plastic jars. All samples were size fractionated within 2 mo of collection through 1000, 500 and 250  $\mu\text{m}$  Nitex mesh, with the largest size fraction being separated to species level under a dissecting microscope. Only species for which sufficient numbers or biomass for isotope analysis could be collected were chosen for the study. The entire contents of size fractions of 500 and 250  $\mu\text{m}$  were each analysed as a sample.

Demersal samples were collected on board the industrial crustacean trawler 'Ocean Spray' for both the wet and dry seasons simultaneously with the other samples collected (Fig. 2b). A total of 22 trawls (over 5 d) in the wet season and 20 trawls (over 7 d) in the dry season were successfully deployed, with depths ranging from 29 to 569 m and 27 to 563 m,

respectively. Within each trawl, only species for which at least 3 individuals could be collected were included in the analysis, with the exception of species of 'interest' (those species common in commercial trawl catches but that were not collected commonly in our trawls), for which at least 2 individuals were required per trawl. For each trawl, species were individually bagged, with a maximum of 5 individuals from each species per bag, and immediately frozen at  $-20^{\circ}\text{C}$ . Samples were processed in the laboratory within 2 wk of collection.

### Sample preparation and stable isotope analysis

Demersal organisms were partially defrosted prior to tissue sampling to minimize leaching of tissue liquids. Muscle tissue was taken from the back of the head of cephalopods, from the caudal peduncle on the same side of the fish at all times for the elasmobranchs and teleosts and from the muscular foot of the gastropods and one bivalve. For decapods, muscle tissue collection was more varied; for the Nantia, the shell was removed from the abdomen prior to tissue collection, while for the brachyurans, leg muscle tissue from inside the carapace was collected. Echinoderms were also collected but were lost due to a freezer power failure. Great care was taken to ensure that non-muscle tissue (skin, bone, exoskeleton, intestine) was excluded from the samples.

Following the suggestions of Boecklen et al. (2011), we decided not to perform any chemical lipid removal on the muscle tissue to avoid increasing uncertainties in  $\delta^{15}\text{N}$  values, since an increasing number of authors are questioning the need for lipid removal (Mintebek et al. 2008). This decision was further supported by the findings of a concurrent study on the effect of different chemical lipid removal techniques on some of the demersal species used in this study, which showed that such removal had no significant effect on isotope ratios (A. M. de Lecea unpubl. data). Lipid removal models were consequently deemed unnecessary.

Muscle tissue samples were immediately transferred to an air circulation oven for drying ( $60^{\circ}\text{C}$  for 48 h). Dried samples were homogenised and weighed into tin capsules (Santis Analytical);  $\sim 1.00\text{ mg}$  dry mass was required to yield sufficient N and C for isotope analysis.

Filter samples (TSS) were dried, weighed, acidified using 2% HCl solution (to obtain the isotopic signature of the OM) and dried and weighed once again prior to placing the filters into tin capsules for isotope analysis.

Both sets of 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 was 0.09‰ for  $^{15}\text{N}/^{14}\text{N}$  and 0.08‰ for  $^{13}\text{C}/^{12}\text{C}$ .

To avoid uncertainty in isotopic ratios caused by preservation and/or acidification, as suggested by De Lecea et al. (2011), zooplankton samples were sorted within 2 wk of collection and were not acidified. Lipid extraction may enrich  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and increase variability of results (Post 2002, Sotiropoulos et al. 2004). Because of this and to keep these samples standard with the muscle tissues, lipid removal was not performed. Zooplankton samples were dried for 24 h at 50°C, homogenised and weighed into tin capsules (Säntis Analytical); 0.5 to 0.6 mg dry mass was encapsulated. Samples were analysed in the Archaeometry Laboratory, University of Cape Town, as explained below.

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 obtain the isotopic signature of the OM within the sediments, rinsed with Milli-Q water and returned to the oven for desiccation. Samples were processed at the Archaeometry Laboratory, 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, calculated from solid standards, had a standard deviation of 0.06‰ for  $^{15}\text{N}/^{14}\text{N}$  and 0.06‰ for  $^{13}\text{C}/^{12}\text{C}$ .

The isotope ratios of  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$  are expressed in terms of their value relative to atmospheric  $\text{N}_2$  and to Pee-Dee Belemnite, respectively.  $\delta$  notation is used to express the differences:

$$\delta \text{ value (‰)} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where  $R$  is the ratio of  $^{15}\text{N}:^{14}\text{N}$  or  $^{13}\text{C}:^{12}\text{C}$  in the sample ( $R_{\text{sample}}$ ) and in the standard ( $R_{\text{standard}}$ ), expressed relative to the international standard.

At both laboratories, the IRMS is attached to an elemental analyser (see IRMS explanation for make and model), which separates and subsamples the gases prior to IRMS analysis, producing the percent carbon (%C) and percent nitrogen (%N) results as a by-product of the stable isotope analysis. Precision values at the IsoEnvironmental isotope facility for the elemental analysis of the samples in this study were 0.37 for %N and 1.31 for %C. Precision values at the Archaeometry Laboratory, University of Cape Town, for the elemental analysis of samples in this study were 0.11 for %N and 0.59 for %C.

### Statistical analysis, trophic positions and mixing models

Benthic contour maps were produced for salinity, oxygen, temperature, sediment isotope values ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ), percent organic carbon (%C<sub>org</sub>), %N and C:N ratios using Surfer 9. Data were analysed for normality and homoscedasticity and transformed where appropriate, and ANOVA and Tukey's post hoc tests were run in R version 2.12.0 (R Development Core Team 2010). Because of the lack of replication for the sediment stations, ANOSIM analyses on the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  sediment data were run in Primer 6 (Plymouth Marine Laboratory) (Clarke 1993). TSS  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotope values were used to represent 'riverine' sources (those collected at the mouth of the rivers during low tide; these values were entered into the model as a mean value  $\pm$  SD) and 'marine' sources (those collected from the marine focus stations) in a MixSIR (Moore & Semmens 2008) analysis of the sediments, which allowed determination of the relative proportions of marine and riverine sediments in the sites that had mixed sediments.

Based on the assumption that as C and N are transferred along the food web, enrichment of  $^{13}\text{C}$  is small ( $\sim 1\%$ ) and enrichment of  $^{15}\text{N}$  is larger ( $\sim 3.4\%$ ) (Post 2002), the trophic position was calculated following the method of (Hobson & Welch 1992):

$$\text{TP} = 1 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{source}}) / \Delta^{15}\text{N} \quad (2)$$

where  $\delta^{15}\text{N}_{\text{consumer}}$  is the  $\delta^{15}\text{N}$  of the individual consumer,  $\delta^{15}\text{N}_{\text{source}}$  is the  $\delta^{15}\text{N}$  of the main nutrient source in the consumer diet and  $\Delta^{15}\text{N}$  is the enrichment factor of 3.4‰ (Post 2002). Primary C sources were assigned a trophic position of 1.

To calculate the proportional contribution, we used the Bayesian mixing model MixSIR (Moore & Semmens 2008) version 1.0.4 with uninformative priors.

Fractionation values of  $0.4 \pm 1.3\%$  for  $^{13}\text{C}$  and  $3.4 \pm 1\%$  for  $^{15}\text{N}$  were used for this study (Post 2002). The maximum importance ratio was below 0.001, suggesting that the models were effective in estimating the true posterior density (Moore & Semmens 2008). Results for MixSIR are presented as the median and the 5th and 95th credibility intervals.

Using mixing models, a possible food web of the demersal organisms of the Bight was constructed. A literature review of the possible diet of these organisms was undertaken (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m484p097\\_supp.pdf](http://www.int-res.com/articles/suppl/m484p097_supp.pdf)) and used as a guide to the likely local prey items for each. Due to limited biological research in the Bight, no stomach content or diet studies existed for the majority of organisms in our study. Where possible, local diets for the species were obtained; alternatively, diets of the same species or related species were obtained from other parts of the world. Possible prey species listed in the literature were offered as potential dietary items for the relevant predator in the mixing models only if either (1) the predator and prey occurred in the same trawl or (2) the possible prey item was found in another trawl from the same area and in the known (from literature) depth range of the predator (see Supplement), making it possible for the predator and suspected prey item to interact. Some animals occurred at more than one site in the Bight. In these cases, mixing models were run for each site independently. From the results of these analyses, prey species that comprised 10% or more of the diet at any one site were included as potential prey items in a further dietary site-combined mixing model analysis. For these widely occurring animals,

Table 1. Zooplankton isotopic data ( $\pm$ SD) used in the mixing models. Mixture 250 and Mixture 500 indicate the size fractionation in  $\mu\text{m}$

Name	n	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$
Cephalopoda larva	3	$7.00 \pm 1.65$	$-20.45 \pm 0.51$
<i>Diacavolinia longirostris</i>	2	$5.68 \pm 0.71$	$-19.51 \pm 0.30$
<i>Euphausia</i> sp.	30	$6.76 \pm 0.53$	$-19.97 \pm 0.42$
<i>Euphausia frigida</i>	16	$6.18 \pm 1.03$	$-20.01 \pm 0.40$
<i>Ferosagitta</i> sp.	7	$7.98 \pm 0.50$	$-19.77 \pm 0.31$
<i>Flaccisagitta enflata</i>	52	$8.31 \pm 0.78$	$-19.53 \pm 0.75$
Jellyfish mixture	3	$7.99 \pm 0.84$	$-19.65 \pm 0.39$
Larvacea	2	$5.87 \pm 0.64$	$-21.25 \pm 0.36$
<i>Liriope tetraphylla</i>	3	$8.54 \pm 0.14$	$-19.41 \pm 0.07$
<i>Lucifer typus</i>	8	$6.94 \pm 0.74$	$-19.87 \pm 0.57$
Mixture 250	51	$6.24 \pm 0.82$	$-20.20 \pm 0.65$
Mixture 500	56	$6.86 \pm 0.72$	$-20.05 \pm 0.64$
<i>Subeucalanus monachus</i>	34	$7.04 \pm 0.59$	$-19.91 \pm 0.53$
<i>Thalia democratica</i>	13	$5.44 \pm 0.61$	$-20.40 \pm 0.54$
<i>Undinula vulgaris</i>	34	$7.09 \pm 0.80$	$-19.66 \pm 0.80$

the final site-combined diet was used in generating the general food web of the Bight. For known zooplanktivores (from the literature, see Supplement), zooplankton isotopic data were used (Table 1).

Using the results of the mixing model analyses, 2 possible food webs were produced, a 'shallow' food web containing animals found from 20 to 200 m and a 'deep' food web containing animals from 201 to 600 m, with certain ubiquitous organisms occurring in both.

## RESULTS

### Environmental variables

As expected, bottom temperatures dropped with depth in both seasons (1st order polynomial relationship,  $R^2 = 0.95$ ) (Fig. 3a,d). The only visible difference between the 2 seasons was that in the summer, there was a warm water mass close inshore (<100 m depth) in the northern part of the Bight reaching temperatures greater than  $27^\circ\text{C}$ . Bottom salinity clearly decreased below the 200 m isobath in both seasons (2nd order polynomial relationship,  $R^2 = 0.97$ ); however, this decrease was not greater than 1.4 psu (Fig. 3b,e). Bottom oxygen levels for summer and winter increased below the 200 m isobath but decreased again between the 500 and 1000 m isobaths (3rd order polynomial relationship,  $R^2 = 0.55$ ) (Fig. 3c,f). During the winter, higher bottom oxygen levels were observed in the shallower areas, around the Thukela Bank. Overall, the major physical differences were between shelf waters shallower than 200 m and those deeper than the 200 m isobath.

### Sediment and TSS isotope values and sediment sources

The sediment  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  composition of the Bight was found to be similar among Locations and Origin (marine vs. riverine) (1-way ANOSIM; Locations  $R = 0.607$ ,  $p = 0.01$ ; Origin  $R = 0.507$ ,  $p = 0.01$ ). The sediment isotope maps of the Bight (Fig. 4) suggest that, overall, there are localised differences close inshore to the estuaries and near the 100 m isobath, where signatures are stronger, while the remainder of the Bight appears to be more homogeneous.

Marine TSS and sediments formed isotopically distinct groups when C:N ratios were considered (Fig. 5), while estuarine TSS overlapped mainly with

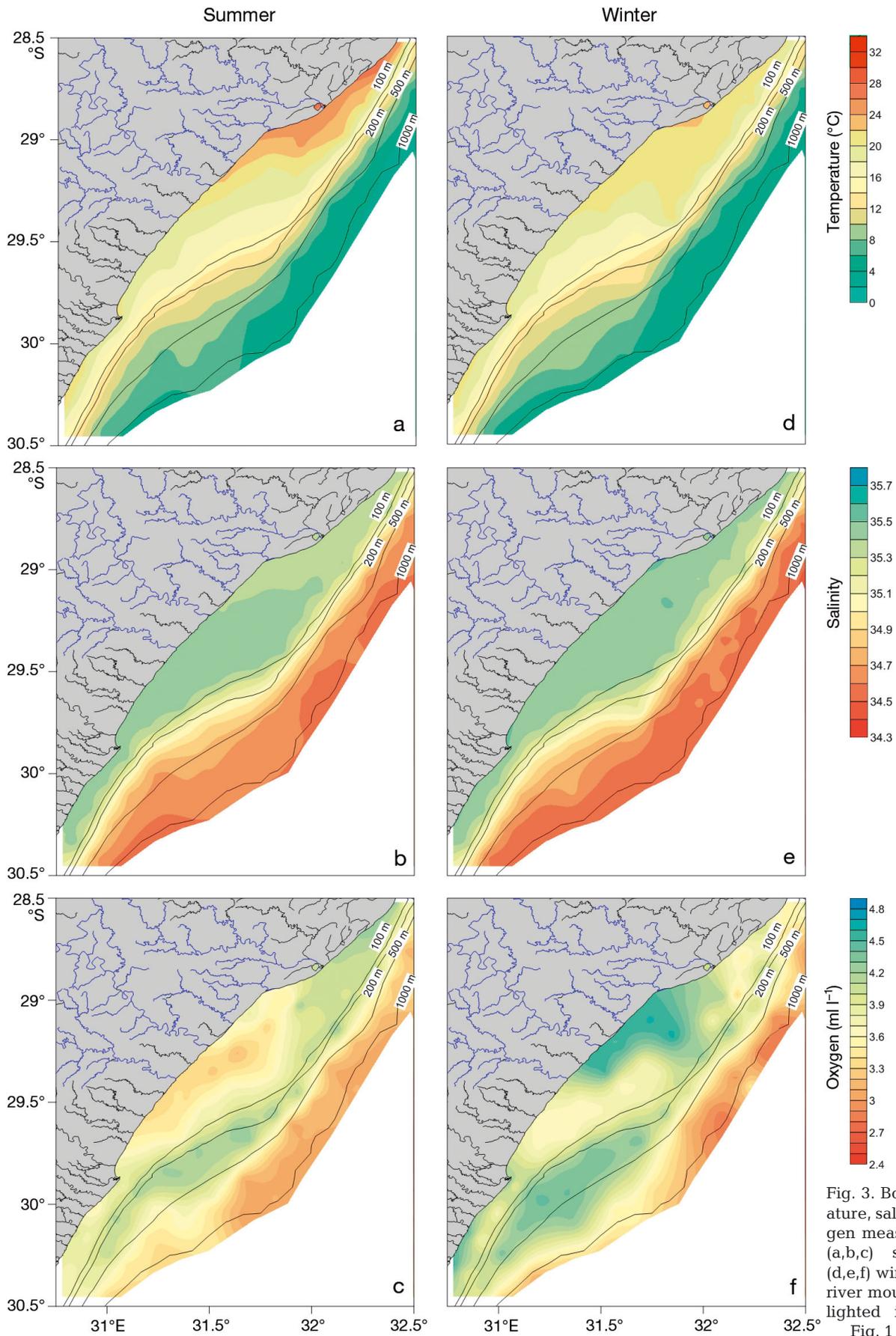


Fig. 3. Bottom temperature, salinity and oxygen measurements for (a,b,c) summer and (d,e,f) winter. Sampled river mouths are highlighted in blue (see Fig. 1 for names)

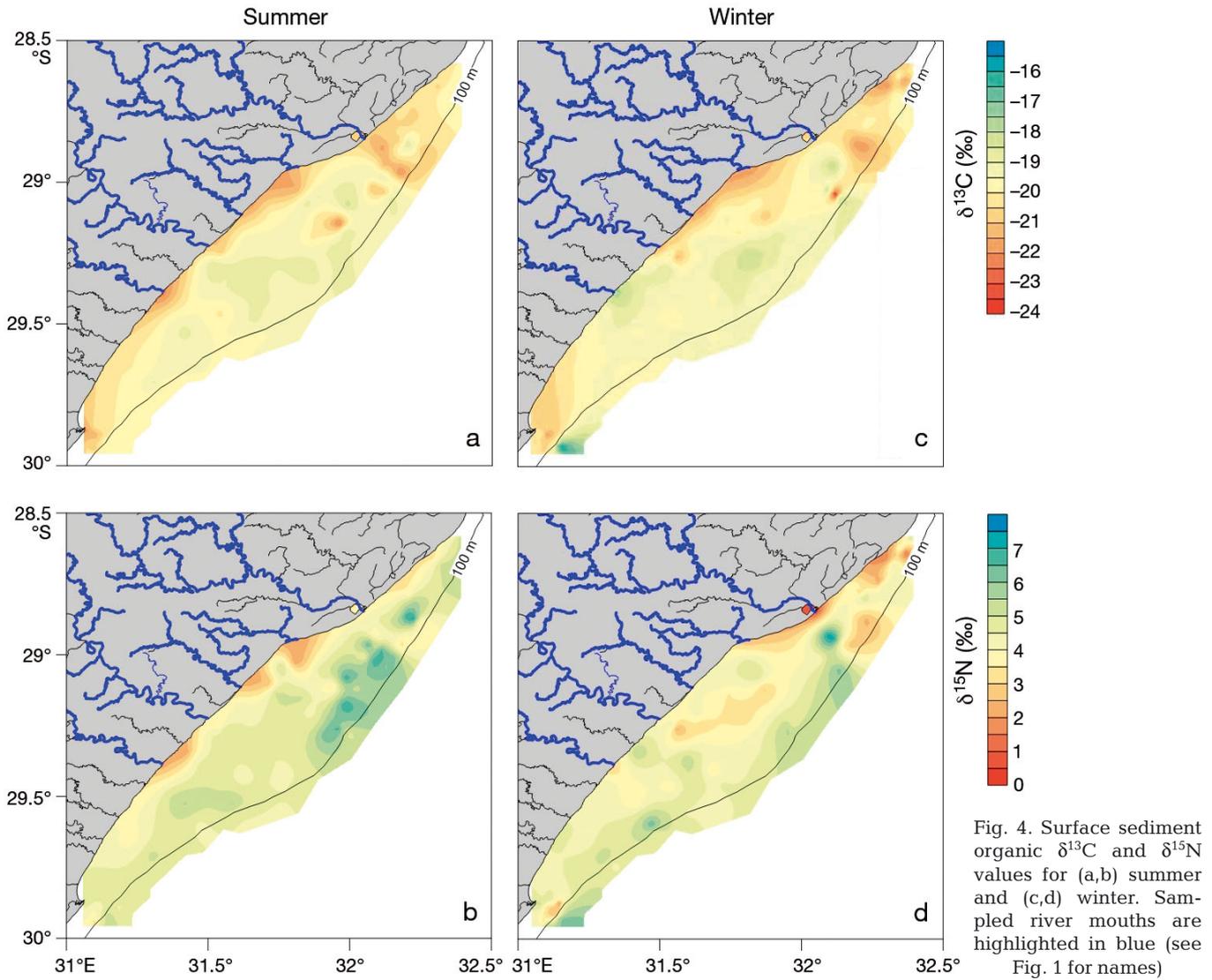


Fig. 4. Surface sediment organic  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for (a,b) summer and (c,d) winter. Sampled river mouths are highlighted in blue (see Fig. 1 for names)

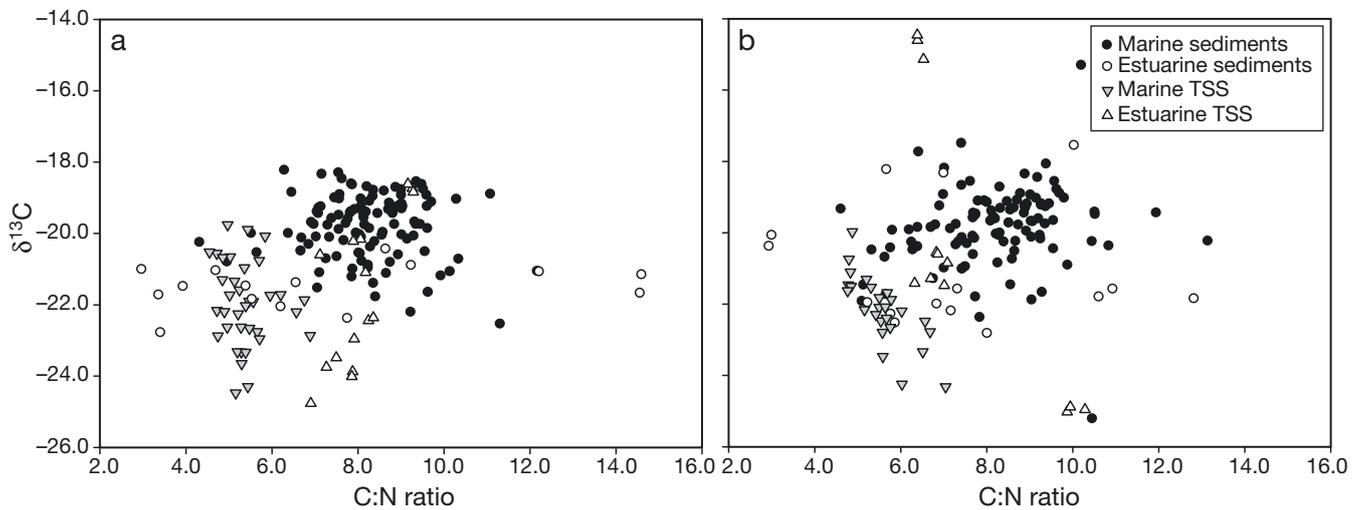


Fig. 5. Carbon:nitrogen ratios and  $\delta^{13}\text{C}$  values for marine and estuarine total suspended solids (TSS) and sediment stations for (a) summer and (b) winter

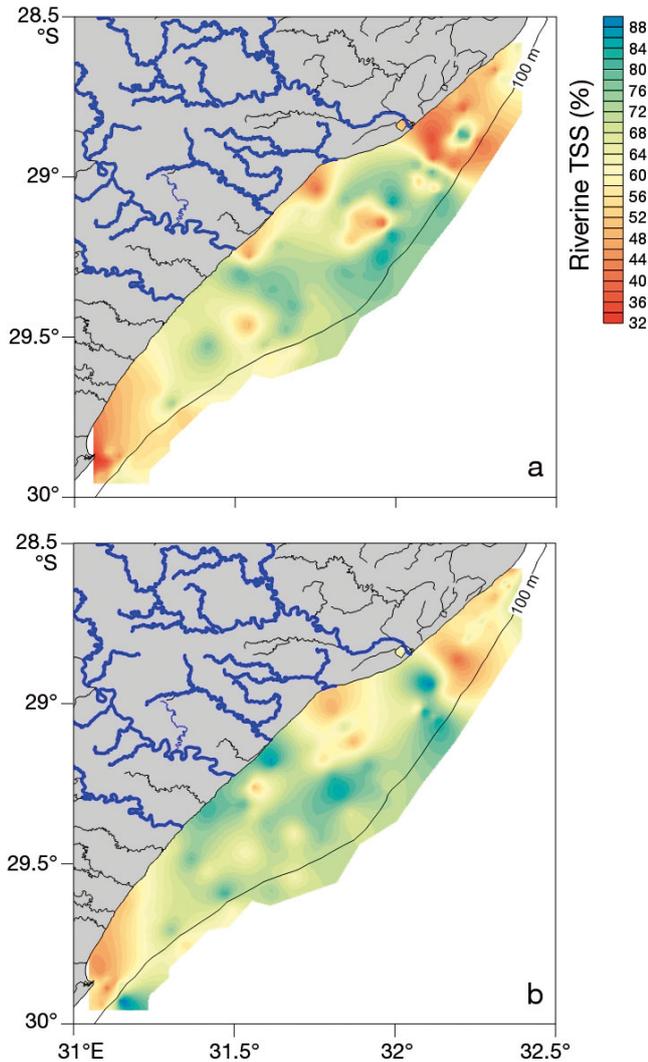


Fig. 6. Percentage source of riverine total suspended solids (TSS) in the sedimentary organic matter for (a) summer and (b) winter as calculated with the mixing models. Sampled river mouths are highlighted in blue (see Fig. 1 for names)

marine sediments (Fig. 5). There were significant similarities between some of the groups (ANOSIM; marine TSS vs. marine sediment  $R = 0.791$ ,  $p = 0.01$ ; riverine TSS vs. marine sediment  $R = 0.438$ ,  $p = 0.01$ ). Differences between marine TSS and estuarine TSS (ANOSIM;  $R = 0.183$ ,  $p = 0.04$ ) were indicated by the low  $R$  value. To determine the importance of each TSS source to the sediment OM, a mixing model (MixSIR) analysis was completed. The MixSIR analysis indicated that both marine and riverine TSS made contributions to the sediment OM at most sites throughout the Bight (Fig. 6). Riverine TSS appears to have dominated the surface sediment composition throughout the centre of the Bight in both seasons, with riverine TSS accounting for more than 60% of

the OM origin in the central region of the Bight. The riverine TSS lost importance at the north and south edges of the Bight to marine TSS but still played a major role, comprising more than 40% of OM. The central riverine TSS influence appears to have continued to the deepest sampling stations (~180 m).

Maps of the %C<sub>org</sub> and %N of the sediment in the Bight indicated a plume of high levels of OM in the sediment protruding outwards from the Thukela River, with levels greater in the wet season than in the dry season (Fig. 7a,b,d,e). C:N indicated that the Bight could contain OM from 2 origins; the northern end of the Bight had lower C:N ratios (~4), while the centre-southern region of the Bight had values >8 for both seasons (Fig. 7c,f). Overall, the results appeared to indicate that the C and N in the central Bight were more labile, possibly hinting that younger OM originating from the estuaries was being deposited in this region and consumed during the dry months.

#### Isotope values and C:N ratios of demersal organisms

A total of 71 species were collected in both seasons, of which 25 and 12 species were exclusive to the wet and dry seasons, respectively (for species and mean isotope values, see Fig. 8). Organisms had significantly different  $\delta^{13}\text{C}$  values among locations (ANOVA  $df = 4$ ,  $SS = 40.20$ ,  $MS = 10.05$ ,  $F = 17.1$ ,  $p < 0.0001$ ). Further investigation revealed that the  $\delta^{13}\text{C}$  values of organisms collected on the Thukela Bank were significantly different from those collected from all other locations (Tukey's post hoc  $p < 0.01$ ). No significant differences in the  $\delta^{15}\text{N}$  values of demersal organisms were found.

If the isotope values for organisms in the Thukela Bank area were separated from those of the stations in the Bight and the analysis repeated, the emerging pattern changed completely. The  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values of demersal organisms of the same species were spatially homogeneous for the entire Bight (ANOVA,  $p > 0.05$ ), with the exception of the Thukela Bank, which was isotopically distinct. Within the Thukela Bank area, however, neither  $\delta^{13}\text{C}$  nor  $\delta^{15}\text{N}$  values of the demersal organisms were significantly different among the suite of species.

Similarly, C:N ratios, an indicator of food quality, did not differ for the same species collected at different locations or between different species collected at the same location, with the exception of 4 organisms, all of them teleosts, which had a much larger standard deviation (Fig. 8).

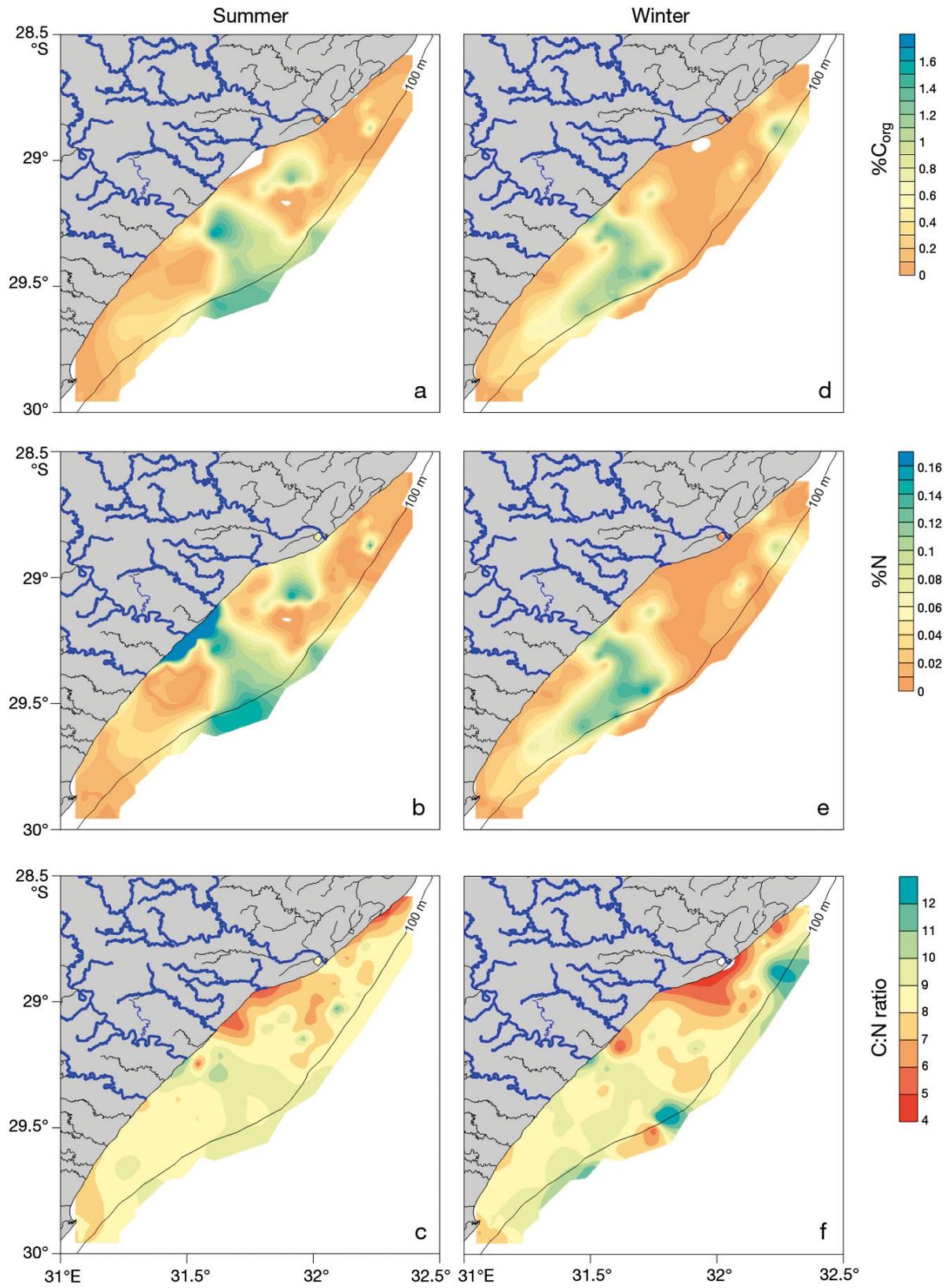


Fig. 7. Percent organic carbon (%C<sub>org</sub>), percent nitrogen (%N) and carbon:nitrogen (C:N) ratios for (a,b,c) summer and (d,e,f) winter. Sampled river mouths are highlighted in blue (see Fig. 1 for names)

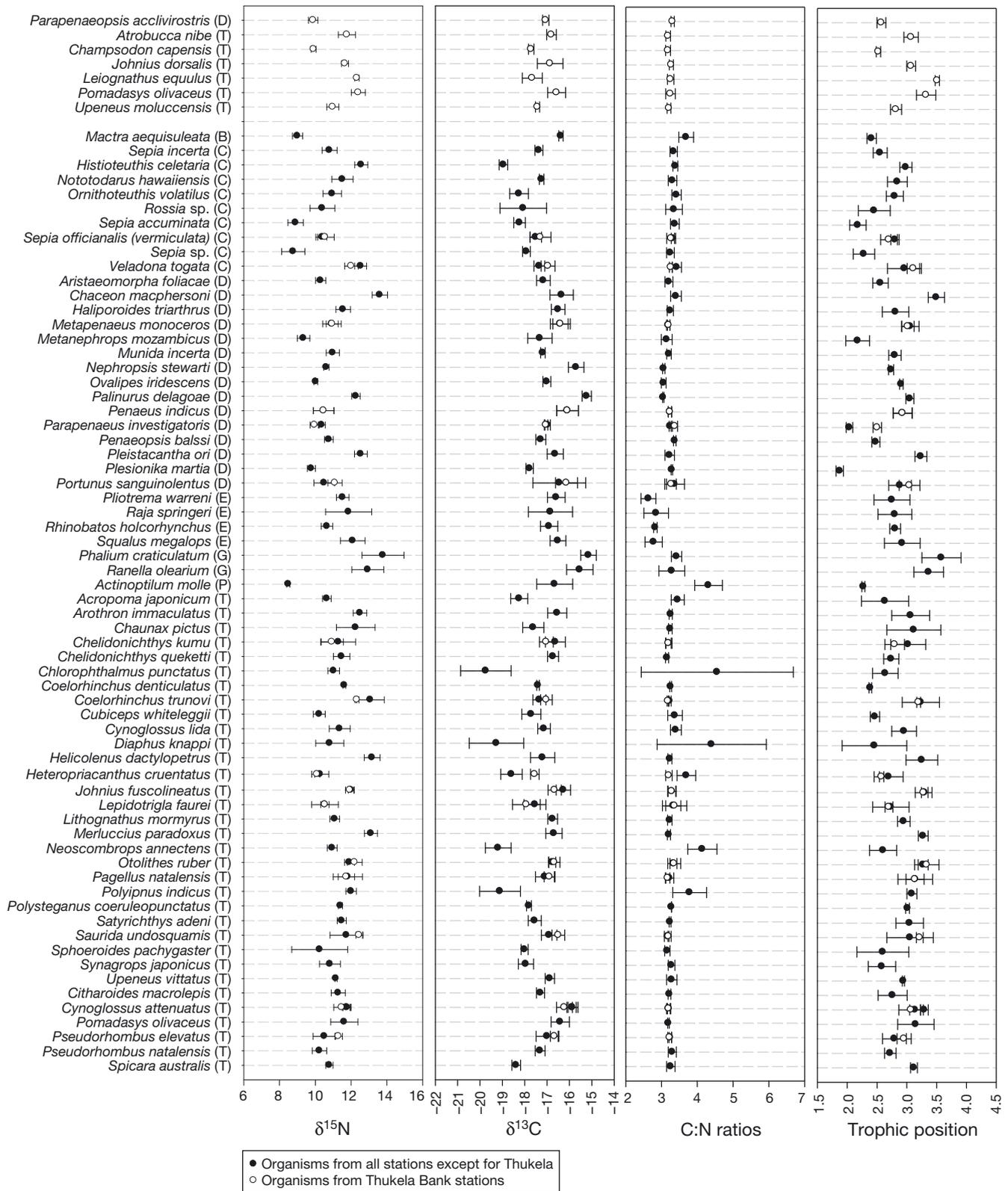


Fig. 8. Mean ( $\pm$ SD)  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  and trophic position for Thukela Bank stations and all other stations from the KwaZulu-Natal Bight. Letters in brackets indicate animal group (B: Bivalvia; C: Cephalopoda; D: Decapoda; E: Elasmobranchii; G: Gastropoda; P: Pennatulacea; T: teleost). Upper 7 rows show organisms that were collected only in the Thukela Banks

### Trophic position and trophic linkages

A range of trophic positions were represented during both seasons, but the majority of organisms were between trophic positions 2 and 3 (Fig. 8). The organisms with the highest trophic positions were the gastropod *Phalium craticulatum* ( $3.58 \pm 0.33$ ), while the lowest trophic positions were occupied by the decapod *Plesionika martia* ( $1.87 \pm 0.06$ ). Cephalopods ranged in TP from  $2.18 \pm 0.14$  (*Sepia acuminata*) to  $2.98 \pm 0.26$  (*Veladona togata*); decapods ranged from  $3.50 \pm 0.14$  (*Chaceon macphersoni*) to  $1.9 \pm 0.06$ , the lowest TP recorded in this study (*Plesionika martia*); teleosts ranged from  $3.51 \pm 0.04$  (*Leiognathus equulus*) to  $2.39 \pm 0.02$  (*Coelorinchus denticulatus*); and elasmobranch TPs were generally low, ranging from  $2.75 \pm 0.30$  (*Pliotrema warreni*) to  $2.92 \pm 0.30$  (*Squalus megalops*). Other organisms collected included a bivalve species (*Macra aequisuleata*) with a TP of  $2.41 \pm 0.08$ , and a pennatulacean (*Actinoptilum molle*) with a TP of  $2.29 \pm 0.03$ .

A plausible food web of all organisms collected for both seasons combined was constructed from the results of the mixing model analyses; the food web matrix for 'shallow' (up to 200 m) and 'deep' (201 to 568 m) can be viewed in Figs. S1 & S2, respectively, in the Supplement. Mixing models indicated that food webs were strongly driven by the OM on the sediments at both shallow and deep sites. Sediment OM isotope data were used as a proxy for macrobenthic infauna, which are highly dependent on this OM (Iken et al. 2010). Of the 45 species in the shallow food web, 39 were offered the sediment OM as a possible food source in replacement of the macrobenthos, which were not sampled in this study. Of these organisms, 20.5% had more than 40% of their diet derived from the OM in the sediments, and a further 64.1% of organisms derived 20 to 40% of their requirements from the OM in the sediments. For the deep food web, OM in the sediments was given as one of the potential food sources for 26 of the 45 species, of which 36.2% of species obtained more than 40% of their diet from this source, while 29.9% obtained 20 to 40% of their diet from organisms that were directly dependent on the OM in the sediments. For the shallow food web, the decapods *Penaeus indicus*, *Parapenaeopsis acclivirostris* and *Parapenaeus investigatoris* as well as the bivalve *Macra aequisulcata* and the pennatulacean *Actinoptilum molle* appeared to be of great importance as a food source, as did some of the cephalopods. Decapods such as *Metanephrops mozambicus*, *Munida incerta* and *Haliporoides triarthrus* as well as some of the

cephalopods also appeared to be of great importance for organisms in the deep food web.

### DISCUSSION

Our research constitutes one of the most comprehensive stable isotope studies in the world on demersal organisms both on and off the continental shelf. Furthermore, this study thoroughly sampled and mapped sediment organic isotopes of a large marine system, covering ~160 km along the coast from depths of ~20 to ~180 m, and included the nearby estuaries.

#### Environmental variables, TSS and sediment stable isotopes

The decreasing salinities and temperature with depth is in accord with previous work that found low salinities for the deeper waters close to the Bight (Pearce 1977). Oxygen levels were higher in the dry season close to the Thukela River mouth, probably due to a decreased OM load from the nearby estuaries. Overall, the bottom environmental variables did not appear to greatly change between these 2 seasons, which suggests a reasonably stable benthic environment.

Riverine TSS was found to be the dominant input of OM to the central Bight sediments according to the mixing model results. It is therefore likely to have been an important source of food for the demersal organisms in this low-productivity environment. Although its role was less marked in the north and south of the Bight, its relative importance remains high (~40%). This finding is further supported by the high %C<sub>org</sub> and %N plume off the Thukela River and the small isotopic signature variability across the Bight for both seasons. Furthermore, it has been confirmed elsewhere that organic detrital material in the sediments can have a residence time of years in the deep sea (Rowe et al. 1991). The lack of seasonal differences in sedimentary OM was likely due to the low productivity of the Bight and long residence time of the OM in the sediments, further suggesting that riverine OM input into the benthos was of great importance spatially and temporally. Finally, recent research on the primary productivity in the Bight from an upwelling event in 2010 indicated that increased algal biomass and nutrient levels at the edge of the continental shelf were flushed out of the Bight within days of its occurrence (Lammont and

Barlow unpubl.). This suggests that there would have been very little opportunity for any OM from these upwelling events to settle on the sediments of the Bight and may explain our findings of riverine dominance in the demersal environment.

The range of riverine TSS  $\delta^{13}\text{C}$  values ( $-14.73 \pm 0.48\%$  to  $-24.01 \pm 1.42\%$ ) corresponds to that expected from terrestrial runoff. The isotopic signature of OM contained in terrestrial runoff is influenced by the type of vegetation present in the region (Knies & Martinez 2009). The vegetation in the province of KwaZulu-Natal is comprised of a range of woodlands, coastal forest, montane forest, thicket and grasslands (Fairbanks & Benn 2000).  $\text{C}_3$  plant  $\delta^{13}\text{C}$  values range from  $-21$  to  $-33\%$ , while  $\text{C}_4$  plant  $\delta^{13}\text{C}$  values range from  $-9$  to  $-16\%$  (O'Leary 1988, Lamb et al. 2006). The values obtained in this study for riverine TSS were within a range that could be explained by a mixing of the isotopic signatures of runoff from the 2 vegetation types. In addition, isotopic values for riverine phytoplankton, which range from  $-25$  to  $-35\%$  for  $\delta^{13}\text{C}$  and around  $5\%$  for  $\delta^{15}\text{N}$  (Boutton 1991), fall outside the isotopic range found for riverine TSS isotopic values, indicating that they probably had a negligible or minor influence. Also, their smaller size makes them less refractory, reducing the chances of their accumulating on the sediments, as demonstrated by a study of sedimentation of algae in lakes (Larocque et al. 1996). In addition, Kibirige et al. (2002) found that the Mpenjati Estuary (south of Durban) microphytobenthos had  $\delta^{13}\text{C}$  values of  $-19.53 \pm 0.92$  and  $-21.19 \pm 0.82\%$  and OM had values of  $-18.53 \pm 1.53$  and  $-23.08 \pm 0.95\%$  for summer and winter, respectively. These values closely resembled the values obtained in this study for the estuarine and marine sediments. This highlights the importance of the terrestrial organic input from river outflow into a system like the Bight and appears to indicate that rivers play a more fundamental role than previously thought (Meyer et al. 2002), at least as far as the demersal system is concerned.

In addition to the influence of riverine TSS on marine sediments, marine TSS in the sediments play a limited role, probably resulting from marine phytoplankton particles, which have isotopic signatures that range from  $-8.8$  to  $-22\%$  for  $\delta^{13}\text{C}$  and  $3$  to  $12\%$  for  $\delta^{15}\text{N}$ , sinking to the seafloor (Maberly et al. 1992). Because the marine sediment isotope values were not consistent with studies where  $\text{C}_3$  plants are the dominant vegetation on the coast (Knies & Martinez 2009), we suggest that a combination of terrestrial  $\text{C}_3$  aided by small marine phytoplankton deposition explains the  $\delta^{13}\text{C}$  values seen in the marine sedi-

ments of the Bight, similar to results elsewhere (Goñi et al. 1998). In addition, results obtained by T. Lamont and R. Barlow (unpubl.) suggest that the window of opportunity for phytoplankton to settle within the Bight is small, highlighting once again the importance of other OM sources, such as terrestrial input, in supporting the biology of the benthos.

The C:N ratios further support the view of a central Bight dominated by riverine TSS input and a north Bight dominated by phytoplankton outfall. The marine TSS mirrored the typical C:N ratios for phytoplankton of 5 to 7 throughout the Bight, as phytoplankton tends to be rich in N (Meyers 1994). In the central area of the Bight, this marine TSS clearly did not settle in the marine sediment, which had C:N ratios of between 9 and 10, values which are just slightly lower than values for terrestrial  $\text{C}_3$  plants (Andrews et al. 1998, Lamb et al. 2006), suggesting that they originated in terrestrial runoff and riverine outflow. This is particularly evident in the winter season, where C:N values were  $>9$  for most of the central Bight, even below 100 m. Because winter is the dry season on the east coast of South Africa, this accumulation of terrestrial material must have occurred during the wet season. Ogrinc et al. (2005) found C:N ratios in sediment cores elsewhere with values similar to those found in this study and described them as a mixture of marine and terrestrial OM. Similarly, Bristow et al. (2012) described the C:N values of 8.5 to 18.3 found for the OM of the Humber and Thames estuaries as having an origin other than phytoplankton. Furthermore, although terrestrial plant material C:N ratios are traditionally regarded as being  $>11$  and geographically variable, they tend to be significantly decreased during bacterial degradation in the sediments and produce values similar to the values of 9 and 10 found in this study (Thornton & McManus 1994). Conversely, in the north of the Bight, sediment C:N ratios of 4 to 7 were similar to the marine TSS values, indicating that this area was dominated by marine input in both seasons. C:N ratios, therefore, support the evidence that terrestrial input plays an important role within the majority of the Bight. It also raises further questions for future research on the importance of bacteria in degrading the terrestrial material as a food source for the benthic and demersal ecosystems of the Bight.

In addition, due to the greater levels of sedimentary  $\%C_{\text{org}}$  and  $\%N$  extending eastwards off the Thukela River along the sea floor, we suggest that most OM available in the benthos of the Bight to at least a depth of 200 m originates from the Thukela River and other estuaries in the vicinity, particularly

during the wet season. The increase in the levels of %N and %C appears to correspond with the position of the Thukela Cone, which leads to the Thukela canyon (Flemming & Hay 1988), as well as with a series of inner and outer shelf mud facies described by Bosman et al. (2007). Underwater canyons are considered a mechanism for exporting sediments and OM into the adjacent abyssal areas (Ramsay 1994). They are also an important means for terrestrial organic material such as plant detritus to reach the deep sea (Gage & Tyler 1991, Lawson et al. 1993).

Terrestrial input plays a diminished role at the north and south ends of the Bight, where marine TSS appears to be more dominant. These 2 areas closely match the locales where (1) the cyclonic eddy occurs in the south of the Bight (Meyer et al. 2002) and (2) the upwelling occurs in the north of the Bight (Lutjeharms et al. 1989). As such, it is likely that these 2 upwelling phenomena are making a contribution to the OM in sediments in these 2 areas.

#### Isotope values and C:N ratios of demersal organisms

Initially, we anticipated finding more variability in the isotope values for such a wide variety of organisms occurring over a range of depths and locations and in 2 seasons. However, considering that the sediment OM environment showed limited variability in space and time in terms of isotope signatures, the limited variation in the isotopic signatures of the demersal organisms between seasons and sites obtained here seems appropriate. There were, however, 5 teleost species, *Chlorophthalmus punctatus*, *Diaphus knappi*, *Neoscombrops annectens*, *Polyipnus indicus* and *Heteropriacanthus cruentatus* (except for Thukela Bank individuals of the latter species), which had a distinct  $\delta^{13}\text{C}$  value compared to the rest (Fig. 8). A detailed inspection revealed these to have a much larger C:N standard deviation than the other species, indicating that they fed on a wider range of food sources of variable quality.  $\delta^{13}\text{C}$  values and the low C:N ratios for other species indicated that the food sources were all originally from a similar source and of relatively good quality (Vanderklift & Ponsard 2003), with a value close to 3.

The findings for the Bight demersal system appear to disagree with the scenario of well-mixed riverine and marine food sources put forward elsewhere by Schmidt et al. (2010). Instead, they suggest a system

with a well-defined source of food being introduced into it, as has been found by others elsewhere (Carrier et al. 2007). This food source appeared to be riverine OM throughout the Bight, even in the north and south of the Bight where marine OM was the more dominant OM source in the sediments, since no differences were found in the isotopic signatures of demersal organisms from the different locations throughout the Bight.

The Bight has been described as an oligotrophic system (Bustamante et al. 1995) and more recently as a mesotrophic system (Barlow et al. 2008). Benthic communities are reliant on organic particles, mainly phytoplankton, reaching the seafloor (Beaulieu 2002). However, low-productivity systems are dominated by small planktonic organisms, and any production from these cells is unlikely to reach the benthos in biologically significant amounts due to the complex pelagic microbial food web recycling it (Calbet & Landry 2004). This further supports the evidence gathered from the sediment OM of a stable benthic system dependent on riverine input.

We did, however, find what could potentially be a localised effect of riverine inputs on demersal organisms collected from 2 stations close to the Thukela River mouth. If this localised effect is due to the Thukela River, the possibility exists of studying whether the isotopic signatures of these organisms on the Thukela Bank respond to isotopic changes in the OM provided by the river over time. If isotopic seasonality occurs, it is probably explained by the marked wet and dry seasons in KwaZulu-Natal, leading to changes in the quantity and type of OM washed from the river.

As mentioned in the Introduction, the TSS isotopic signature ranged within that of  $\text{C}_3$  and  $\text{C}_4$  plants; along with the TSS, whole plant material along with OM detritus or TSS are also washed into the sea. Some deep-sea invertebrates depend on terrestrial plant detritus being transported to the deep (Lawson et al. 1993, Young et al. 1993). Furthermore, deep-sea fish are frequently opportunistic, feeding and scavenging on a wide range of OM and organisms (Kaehler et al. 2000, Drazen et al. 2001, Stowasser et al. 2009) including terrestrial plant material and phytodetritus (Jeffreys et al. 2010, 2011). In a low-productivity scenario, plant detritus derived from the nearby estuaries might be one of the dominant factors controlling the food web. The importance of this terrestrial detritus as a food source could extend as far as the nearby deep-sea food web in the area adjacent to the continental shelf. This is supported by observations of terrestrial plant material in commer-

cial trawls made at depths of ~400 m (S. T. Fennessy pers. obs.). The occurrence of a plume of C and N recorded off the Thukela River and reaching to a depth of ~180 m (Fig. 6) provides further support for this suggestion.

### Trophic position and linkages

The majority of organisms from the Bight exhibited similar trophic positions and  $\delta^{15}\text{N}$  levels. Trophic position is not always related to the size of the demersal organism, i.e. larger organisms do not always feed on and have a higher trophic position than smaller organisms (Jennings et al. 2001, Layman et al. 2005). An explanation for this is that predators feed in a wide variety of niches (Layman et al. 2005) and omnivory may be a common strategy (Link 2002, Al-Habsi et al. 2008). Because the Bight is a low-productivity system, omnivory could be the second most important factor determining the food web structure, after terrestrial detritus input. Thompson et al. (2007) found that moving up the food web from primary consumers, the existence of a tangled web of omnivores becomes apparent in the marine environment. As shown in Table S1 in the Supplement, the majority of organisms collected in this study appear to be omnivorous, supporting the findings of Thompson et al. (2007). This further substantiates omnivory as an important strategy in the Bight and provides an additional explanation for the low  $\delta^{15}\text{N}$  variability of demersal organisms. Furthermore, demersal fish and invertebrates could scavenge on nekton carcasses and fisheries discards (Witte 1999), i.e. on organisms theoretically higher up the food chain, which would probably further reduce TP variability owing to animals of different trophic levels scavenging on the same source of food. To complicate matters, tissue isotopic values can take a period of time to reach equilibrium with that of the diet (Martínez del Rio et al. 2009, Wolf et al. 2009), and consumers can change their diets repeatedly. As such, isotopic equilibrium in the tissue may not manifest, and instead of displaying either the current or the past diet, isotopic signatures become a mixture of both diets (Sweeting et al. 2005).

The food web created in this study attempts to produce a visualisation (Figs. S1 & S2 in the Supplement) of a possible predator–prey interaction. It should be viewed as a preliminary guideline only, and its function is to aid the general understanding of the type of trophic interactions that seem likely in the Bight and for which there is presently little informa-

tion. The food web demonstrates that there is a very complex system of trophic interactions even though diets were trimmed to a suitable set of prey candidates for each predator. It supports the omnivory hypothesis, with a high level of interactions within and between each trophic level. It also suggests the possible importance of the macrobenthic organisms, underlying most higher trophic positions, which is in agreement with the findings of studies elsewhere (Snelgrove 1997).

This latter conclusion, however, was based on the assumption that the OM in the sediments was a lower trophic level proxy for the macrobenthos (macrobenthic samples were not available in time for our study). Mixing models indicated that several demersal species favoured the OM proxy, which suggests that they are indirectly dependent on the OM. The previous subsection demonstrated that OM in the Bight was predominantly of terrestrial origin. Because terrestrial OM is difficult for organisms to digest without the aid of bacterial degradation (McLeod & Wing 2009), it follows that some degradation and possibly incorporation through macrobenthos must occur prior to ingestion by the demersal animals. There is a need for further research to investigate the importance of the macrobenthic link from OM to demersal organisms and the role played by bacteria in the sediments of the Bight.

For the specific case of the Bight, the lack of clear distinctions in isotope values in either the sediments or the demersal organisms provides the insight that the benthic infauna, not analysed here, are likely to show a similar lack of clear isotopic distinction.

### CONCLUSION

Our study sought to find the dominant OM source driving the system of the nutrient-poor KwaZulu-Natal Bight. We found that riverine TSS dominated as a source of OM in the marine sediments across most of the Bight, especially the central region, with oceanographic processes playing only a small role in shaping the demersal ecosystem. This was supported by  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\%C_{\text{org}}$ ,  $\%N$  and C:N ratio spatial patterns and the mixing model results, which all independently suggested that riverine/estuarine TSS was a very important source of OM for the demersal ecosystem. However, this dominance was not absolute, and marine OM did play a role, albeit small, in the northern end of the Bight. As recent studies have suggested (T. Lamont and R. Barlow unpubl.), this may be because phytoplankton only have a small

window of opportunity to settle within the Bight before being washed away. Therefore, bacteria likely play a very important role throughout the Bight in making the terrestrial OM available as a food source for the demersal ecosystem. We suggest that future studies should examine the role of bacteria in the sediments and their role in shaping the isotopic and C:N values of demersal ecosystems, as well as their role in the biology of the Bight as a whole.

Of great interest was the proposed likely dominance of the riverine OM role controlling the production and food web structure of the benthic communities, from the shallow Thukela Bank to the deep sea of the nearby ecosystem. Omnivory appeared to be a widespread strategy for demersal animals throughout the Bight. This was supported by the lack of clear  $\delta^{15}\text{N}$  enrichment between possible prey and predator and the low variability of trophic positions across a wide array of organisms. However, to fully understand the food web and ecosystem processes of the benthic and demersal ecosystems of the Bight, or similar ecosystems elsewhere, it would be highly beneficial to understand (1) the interactions occurring within and between macrobenthic communities, (2) the interactions between the demersal and macrobenthic communities and (3) how these benthic and demersal communities interact with the pelagos. As Kaiser et al. (1999) pointed out, there is strong support for macrobenthic communities influencing assemblages of demersal organisms. Therefore, there is a need for future research to include bacterial degradation of OM and benthic infaunal organisms in studies of demersal organisms to deepen our understanding of the processes occurring within the Bight and elsewhere, including the links between these assemblages.

*Acknowledgements.* We acknowledge the African Coelacanth Ecosystem Programme (ACEP), the Thukela Bank Ecosystem Functioning Project and the National Research Foundation (NRF) of the South Africa Department of Science and Technology for their financial contributions towards this study. We also acknowledge Dr. S. Kaehler from the IsoEnvironmental laboratory at Rhodes University for the running of and useful comments on the samples, D. Hayes and C. Wilkinson of the Oceanographic Research Institute (ORI) for their assistance in the collection and processing of samples, and F. McKay (ORI) and Dr. M. Ovechkina (UKZN) for providing sediment samples. We also thank K. Sorenson, owner and crew of the 'Ocean Spray', for kindly making his trawler available and the FRV 'Algoa' crew for their help while at sea. A.M.D.L. acknowledges Dr. J. Huggett for allowing us to work with the samples in her lab. Last, but not least, we acknowledge R. Cooper from the University of Cape Town for her editorial comments and the reviewers, whose comments greatly strengthened the general points of the paper.

#### LITERATURE CITED

- Al-Habsi SH, Sweeting CJ, Polunin NVC, Graham NAJ (2008)  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  elucidation of size-structured food webs in a Western Arabian Sea demersal trawl assemblage. *Mar Ecol Prog Ser* 353:55–63
- Andrews JE, Greenaway AM, Dennis PF (1998) Combined carbon isotope and C/N ratios as indicators of source and fate of organic matter in a poorly flushed, tropical estuary: Hunts Bay, Kingston Harbour, Jamaica. *Estuar Coast Shelf Sci* 46:743–756
- Ayers MJ, Scharler UM (2011) Use of sensitivity and comparative analyses in constructing plausible trophic mass-balance models of a data-limited marine ecosystem in the KwaZulu-Natal Bight, South Africa. *J Mar Syst* 88: 298–311
- Barlow R, Kyewalyanga M, Sessions H, van den Berg M, Morris T (2008) Phytoplankton pigments, functional types, and absorption properties in the Delagoa and Natal Bights of the Agulhas ecosystem. *Estuar Coast Shelf Sci* 80:201–211
- Beaulieu S (2002) Accumulation and fate of phytodetritus on the sea floor. *Oceanogr Mar Biol Annu Rev* 40:171–232
- Begg GW (1978) Estuaries of Natal. Natal town and regional planning report, No. 41. National Provincial Administration, Pietermaritzburg
- Birch GF (1996) Quaternary sedimentation off the East Coast of Southern Africa (Cape Padrone to Cape Vidal), Bull 118. Council for Geoscience, Pretoria
- Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. *Annu Rev Ecol Evol Syst* 42:411–440
- Bosman C, Uken R, Leuci R, Smith AM, Sinclair D (2007) Shelf sediments off the Thukela River mouth: complex interaction between fluvial and oceanographic processes. *S Afr J Sci* 103:490–492
- Boutton TW (1991) Stable carbon isotope ratios of natural materials. II. Atmospheric, terrestrial, marine, and freshwater environments. In: Coleman DC, Fry B (eds) Carbon isotopes techniques. Academic Press, San Diego, CA, p 173–185
- Bristow LA, Jickells TD, Weston K, Marca-Bell A, Parker R, Andrews JE (2012) Tracing estuarine organic matter sources into the southern North Sea using C and N isotopic signatures. *Biogeochemistry* 113:9–22
- Bustamante RH, Branch GM, Eekhout S, Robertson B and others (1995) Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102:189–201
- Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol Oceanogr* 49:51–57
- Carlier A, Riera P, Amouroux JM, Bodiou JY, Gremare A (2007) Benthic trophic network in the Bay of Banyuls-sur-Mer (northwest Mediterranean, France): an assessment based on stable carbon and nitrogen isotopes analysis. *Estuar Coast Shelf Sci* 72:1–15
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Day JH (1981) Estuarine ecology with particular reference to southern Africa. AA Balkema, Cape Town
- De Leece AM, Cooper R, Omarjee A, Smit AJ (2011) The effects of preservation methods, dyes and acidification on the isotopic values ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of two zooplankton species from the KwaZulu-Natal Bight, South Africa.

- Rapid Commun Mass Spectrom 25:1853–1861
- de Ruijter WPM, van Leeuwen PJ, Lutjeharms JRE (1999) Generation and evolution of natal pulses: solitary meanders in the Agulhas Current. *J Phys Oceanogr* 29: 3043–3056
- Drazen J, Buckley T, Hoff G (2001) The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. *Deep-Sea Res I* 48:909–935
- Fairbanks DHK, Benn GA (2000) Identifying regional landscapes for conservation planning: a case study from KwaZulu-Natal, South Africa. *Landsc Urban Plan* 50: 237–257
- Fennessy ST, Groeneveld JC (1997) A review of the offshore trawl fishery for crustaceans on the east coast of South Africa. *Fish Manag Ecol* 4:135–147
- Fennessy ST, Villacastin C, Field JG (1994) Distribution and seasonality of ichthyofauna associated with commercial prawn trawl catches on the Tugela Bank of Natal, South Africa. *Fish Res* 20:263–282
- Flemming B, Hay R (1988) Sediment distribution and dynamics on the Natal continental shelf. In: Schumann EH (ed) *Coastal ocean studies off Natal, South Africa*. Springer-Verlag, Berlin, p 47–80
- Gage JD, Tyler PA (1991) *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge University Press, Cambridge
- Goñi MA, Ruttanberg KC, Eglinton TI (1998) A reassessment of the sources and importance of land-derived organic matter in surface sediments from the Gulf of Mexico. *Geochim Cosmochim Acta* 62:3055–3075
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Ambrose WG Jr, Renaud PE (1995) Sources of primary production, benthic–pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Mar Ecol Prog Ser* 128:1–10
- Hutchings L, Morris T, van der Lingen CD, Lamberth SJ, Connell AD, Taljaard S, van Niekerk L (2010) Ecosystem considerations of the KwaZulu-Natal sardine run. *Afr J Mar Sci* 32:413–421
- Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep-Sea Res II* 57:71–85
- Jeffreys RM, Lavaleye MSS, Bergman MJN, Duineveld GCA, Witbaard R, Linley T (2010) Deep-sea macrourid fishes scavenge on plant material: evidence from *in situ* observations. *Deep-Sea Res I* 57:621–627
- Jeffreys RM, Lavaleye MSS, Bergman MJN, Duineveld GCA, Witbaard R (2011) Do abyssal scavengers use phytodetritus as a food resource? Video and biochemical evidence from the Atlantic and Mediterranean. *Deep-Sea Res I* 58:415–428
- Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J Anim Ecol* 70:934–944
- Kaehler S, Pakhomov EA, McQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Mar Ecol Prog Ser* 208:13–20
- Kaiser MJ, Rogers SI, Ellis JR (1999) Importance of benthic habitat complexity for demersal fish assemblages. *Am Fish Soc Symp* 22:212–223
- Kibirige I, Perissinotto R, Nozais C (2002) Alternative food sources of zooplankton in a temporarily-open estuary: evidence from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . *J Plankton Res* 24: 1089–1095
- Knies J, Martinez P (2009) Organic matter sedimentation in the western Barents Sea region: terrestrial and marine contribution based on isotopic composition and organic nitrogen content. *Norwegian J Geol* 89:79–89
- Lamb AL, Wilson GP, Leng MJ (2006) A review of coastal palaeoclimate and relative sea-level reconstructions using  $\delta^{13}\text{C}$  and C/N ratios in organic material. *Earth Sci Rev* 75:29–57
- Lamberth SJ, Drapeau L, Branch GM (2009) The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore linefishery. *Estuar Coast Shelf Sci* 84:527–538
- Lara RJ, Alder V, Franzosi CA, Kattner G (2010) Characteristics of suspended particulate organic matter in the southwestern Atlantic: influence of temperature, nutrient and phytoplankton features on the stable isotope signature. *J Mar Syst* 79:199–209
- Larocque I, Mazumder A, Proulx M, Lean DRS, Pick FR (1996) Sedimentation of algae: relationships with biomass and size distribution. *Can J Fish Aquat Sci* 53:1133–1142
- Lawson GS, Tyler PA, Young CM (1993) Attraction of deep-sea amphipods to macrophyte food falls. *J Exp Mar Biol Ecol* 169:33–39
- Layman CA, Winemiller KO, Arrington D, Jepsen DB (2005) Body size and trophic position in a diverse tropical food web. *Ecology* 86:2530–2535
- Link J (2002) Does food web theory work for marine ecosystems? *Mar Ecol Prog Ser* 230:1–9
- Lutjeharms JRE (2006) Three decades of research on the greater Agulhas Current. *Ocean Sci Discuss* 3:939–995
- Lutjeharms JRE, Gründlingh ML, Carter RA (1989) Topographically induced upwelling in the Natal Bight. *S Afr J Sci* 85:310–316
- Lutjeharms JRE, Cooper J, Roberts M (2000a) Upwelling at the inshore edge of the Agulhas Current. *Cont Shelf Res* 20:737–761
- Lutjeharms JRE, Valentine HR, Van Ballegooyen RC (2000b) The hydrography and water masses of the Natal Bight, South Africa. *Cont Shelf Res* 20:1907–1939
- Maberly S, Raven J, Johnston A (1992) Discrimination between  $\delta^{12}\text{C}$  and  $\delta^{13}\text{C}$  by marine plants. *Oecologia* 91: 481–492
- Martínez del Río C, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. *Biol Rev Camb Philos Soc* 84:91–111
- McLeod RJ, Wing SR (2009) Strong pathways for incorporation of terrestrially derived organic matter into benthic communities. *Estuar Coast Shelf Sci* 82:645–653
- Meyers PA (1994) Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chem Geol* 114:289–302
- Meyer AA, Lutjeharms JRE, de Villiers S (2002) The nutrient characteristics of the Natal Bight, South Africa. *J Mar Syst* 35:11–37
- Mintenbeck K, Brey T, Jacob U, Knust R, Struck U (2008) How to account for the lipid effect on carbon stable isotope ratio ( $\delta^{13}\text{C}$ ): sample treatment effects and model bias. *J Fish Biol* 72:815–830
- Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol Lett* 11:470–480

- O'Leary MH (1988) Carbon isotopes in photosynthesis. *Bio-science* 38:328–336
- Ogrinc N, Fontolan G, Faganeli J, Covelli S (2005) Carbon and nitrogen isotope compositions of organic matter in coastal marine sediments (the Gulf of Trieste, N Adriatic Sea): indicators of sources and preservation. *Mar Chem* 95:163–181
- Olbers JM, Fennessy ST (2007) A retrospective assessment of the stock status of *Otolithes ruber* (Pisces: Sciaenidae) as bycatch on prawn trawlers from KwaZulu-Natal, South Africa. *Afr J Mar Sci* 29:247–252
- Pearce AF (1977) The shelf circulation off the east coast of South Africa. Stellenbosch Research Report No. 361. Stellenbosch Council for Scientific and Industrial Research, Stellenbosch
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718
- Ramsay PJ (1994) Marine geology of the Sodwana Bay shelf, southeast Africa. *Mar Geol* 120:225–247
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.R-project.org](http://www.R-project.org)
- Rowe G, Sibuet M, Deming J, Khripounoff A, Tietjen J, Macko S, Theroux R (1991) 'Total' sediment biomass and preliminary estimates of organic carbon residence time in deep-sea benthos. *Mar Ecol Prog Ser* 79:99–114
- Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. *Mar Ecol Prog Ser* 162:11–23
- Schmidt F, Hinrichs KU, Elvert M (2010) Sources, transport, and partitioning of organic matter at a highly dynamic continental margin. *Mar Chem* 118:37–55
- Schumann EH (1982) Inshore circulation of the Agulhas Current off Natal. *J Mar Res* 40:43–55
- Snelgrove PVR (1997) The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26:578–583
- Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecol Freshw Fish* 13:155–160
- Stowasser G, McAllen R, Pierce GJ, Collins MA, Moffat CF, Priede IG, Pond DW (2009) Trophic position of deep-sea fish—assessment through fatty acid and stable isotope analyses. *Deep-Sea Res I* 56:812–826
- Sweeting CJ, Jennings S, Polunin NVC (2005) Variance in isotopic signatures as a descriptor of tissue turnover and degree of omnivory. *Funct Ecol* 19:777–784
- Thompson RM, Hemberg M, Starzomski BM, Shurin JB (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* 88:612–617
- Thornton SF, McManus J (1994) Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems: evidence from the Tay Estuary, Scotland. *Estuar Coast Shelf Sci* 38:219–233
- Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet  $\delta^{15}\text{N}$  enrichment: a meta-analysis. *Oecologia* 136:169–182
- Witte UFM (1999) Consumption of large carcasses by scavenger assemblages in the deep Arabian Sea: observations by baited camera. *Mar Ecol Prog Ser* 183:139–147
- Wolf N, Carleton SA, Martínez del Río C (2009) Ten years of experimental animal isotopic ecology. *Funct Ecol* 23:17–26
- Young CM, Tyler PA, Emson RH, Gage JD (1993) Perception and selection of macrophyte detrital falls by the bathyal echinoid *Stylocidaris lineata*. *Deep-Sea Res I* 40:1475–1486

*Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany*

*Submitted: July 4, 2012; Accepted: February 18, 2013  
Proofs received from author(s): June 4, 2013*