

Riverine subsidies for inshore filter-feeder communities: potential influences on trophic patterns among bioregions

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ABSTRACT: In the Natal Bioregion of eastern South Africa, biomass of marine subtidal filter feeders is particularly high and makes a central contribution to distinguishing this bioregion from adjacent ones. We analysed the trophic role of riverine suspended particulate organic matter (POM) and the extent to which subsidies from rivers may explain this high filter-feeder biomass. Using carbon, nitrogen and sulphur isotopes, and a 3-end-member Bayesian-mixing model, we determined (1) the proportions of various primary producers contributing to the inshore POM pool and (2) the relative amounts of marine seaweed, pelagic POM and riverine POM assimilated by filter-feeder communities at various distances from 4 river mouths during austral summer and winter. Of the inshore POM pool available to filter feeders, riverine POM contributed 17 to 62%, pelagic POM 18 to 77% and seaweed 6 to 53%. The contributions of riverine POM to inshore POM declined significantly with distance from river mouth, but were unaffected by season or river size. Most material assimilated by filter feeders was of marine origin, notably seaweed detritus (39–62%), but with a noteworthy uptake of riverine POM (9–33%). Only small seasonal differences (<10%) and no biologically meaningful spatial trends were detected in the proportional assimilation of the 3 food sources by filter feeders. Although important, the trophic contribution of riverine POM may be subordinate to other factors such as turbidity and productivity in explaining the high biomass of filter feeders. Collectively, however, these river-associated factors are likely to explain the contrasts in trophic organisation among marine bioregions.

KEY WORDS: Rivers · Isotope · Sulphur · Seaweed · *Perna perna* · *Pyura stolonifera*

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INTRODUCTION

Several sources of organic matter are potentially important in the assimilated diets of coastal filter feeders. In intertidal and shallow subtidal systems, suspended particulate organic matter (POM) derived from macroalgae has been identified as a significant source of carbon and nitrogen for consumers (Seiderer & Newell 1985, Mann 1988, Bustamante & Branch 1996, Hill et al. 2008), as has

POM from phytoplankton (Seiderer & Newell 1985, Newell et al. 1995, Yokoyama et al. 2005) and, to a lesser degree, POM from terrestrial macrophytes (Darnaude et al. 2004a, Wai et al. 2008, Tallis 2009). In addition, selective dietary preferences for POM of marine versus terrestrial origin have been recorded, particularly in estuaries (Peterson & Howarth 1987, Riera & Richard 1996, Deegan & Garritt 1997, Hsieh et al. 2002, Darnaude et al. 2004b, Yokoyama et al. 2005).

By virtue of their position, inshore reefs are exposed to both autochthonous sources of primary production and allochthonous sources from the marine and terrestrial environments. Autochthonous sources primarily constitute macroalgae (Schleyer 1984, Branch 2008, Hill et al. 2008), whereas allochthonous sources include pelagic phytoplankton (Dunton & Schell 1987, Branch 2008) and terrestrial and aquatic POM introduced by rivers (Berry et al. 1979, Schleyer 1981, Wai et al. 2008, Tallis 2009). In the Natal Bioregion on the east coast of South Africa, the 2 dominant sources of detritus are thought to be seaweed-derived POM and terrestrial plant material introduced into the sea by numerous rivers (Berry et al. 1979, Schleyer 1981). However, the seaweed flora of the Natal Bioregion is dominated by unpalatable coralline species, with the biomass of palatable red and green foliose species being comparatively low; kelp beds that are major contributors to POM on the west coast (Bustamante & Branch 1996) are absent (Evans 2005, Lawrence 2005, Sink et al. 2005, Porter et al. 2013).

The ash-free dry biomass of filter feeders in the Natal Bioregion is high, averaging 1270 g m^{-2} , whereas in the adjacent Delagoa Bioregion to the north, it averages only 373 g m^{-2} (Porter et al. 2013). On intertidal rocky shores, Sink et al. (2005) have shown a comparable decline of filter feeders from the Natal Bioregion to the Delagoa Bioregion, with the relative abundance of the brown mussel *Perna perna* being chiefly responsible for the divergence between these 2 bioregions. These patterns may be attributable to the relative amounts of terrestrial detritus entering the sea via rivers: in the Natal Bioregion, more than 70 rivers and estuaries collectively introduce approximately 10^{10} m^3 of water into the inshore zone annually, whereas input into the Delagoa Bioregion is small—only 2 rivers enter the region, and their annual flow amounts to approximately $3 \times 10^7 \text{ m}^3$ (Sink 2001). As autochthonous coastal production is low in the Natal Bioregion (Bustamante et al. 1995), riverine subsidies may constitute an important addition to nearshore foodwebs.

Additional potential explanations for elevated levels of filter-feeder biomass in the Natal Bioregion include the fact that significantly higher levels of turbidity and suspended sediment from rivers may reduce light penetration (Riegl & Branch 1995, Porter et al. 2013) and increase nutrients, although Hutchings et al. (2010) reported that rivers contribute less than 1% of the nitrogen budget for the northern Agulhas system. Moreover, non-trophic factors such as larval retention and delivery by particular oceanographic

conditions (Roughan et al. 2005) may influence filter-feeder biomass in the region, but this has been the subject of separate research (Porri et al. 2006a,b, Reaugh 2006). These influences may collectively alter trophic structure with high levels of POM favouring filter feeders and turbidity disfavoured by macrophytes.

Our study focussed on determining both the relative contributions of different sources comprising POM suspended in the water column (POM composition), and the proportional assimilation of these sources by filter feeders (POM assimilation). We explored the possibility that inputs from rivers provide supplementary support for filter-feeder communities. Specifically, we addressed the role river input plays in providing potential energy subsidies to inshore filter feeders in the form of riverine POM, as distinct from its potential influence on dissolved organic inputs, turbidity and light penetration. To achieve this, we used stable isotopes to quantify the relative importance of riverine POM over small spatial scales at various distances from river mouths and during different seasons spanning times of high and low river flow.

The following hypotheses were investigated: (1) Inshore POM composition is influenced by riverine inputs, and the extent of this influence will be dependent on distance from river mouth, season, mean annual runoff and the amount of river runoff experienced in preceding months, with the influences of river input being greater during the summer rainy season and close to river mouths. (2) Inshore filter feeders assimilate suspended riverine POM in addition to pelagic POM and seaweed detritus, and the proportion of riverine POM assimilated will be higher during the rainy season and at sites close to river mouths.

MATERIALS AND METHODS

Study areas

Four independent study areas (A, B, C, D), each incorporating a river mouth, were chosen along the east coast of South Africa in the Natal Bioregion (Fig. 1). The river mouths encompassed in each of the 4 study areas were isolated from each other and from other rivers, with no evidence of plume overlap, and they covered a range of simulated mean annual runoffs (MARs) calculated from catchment sizes and rainfall: $\sim 400 \times 10^6 \text{ m}^3$ for the Mvoti, $\sim 1000 \times 10^6 \text{ m}^3$ for the Mfolozi, $\sim 1100 \times 10^6 \text{ m}^3$ for the Mkomasi, $\sim 4000 \times 10^6 \text{ m}^3$ for the Thukela (Sink 2001; see Table 1) rivers.

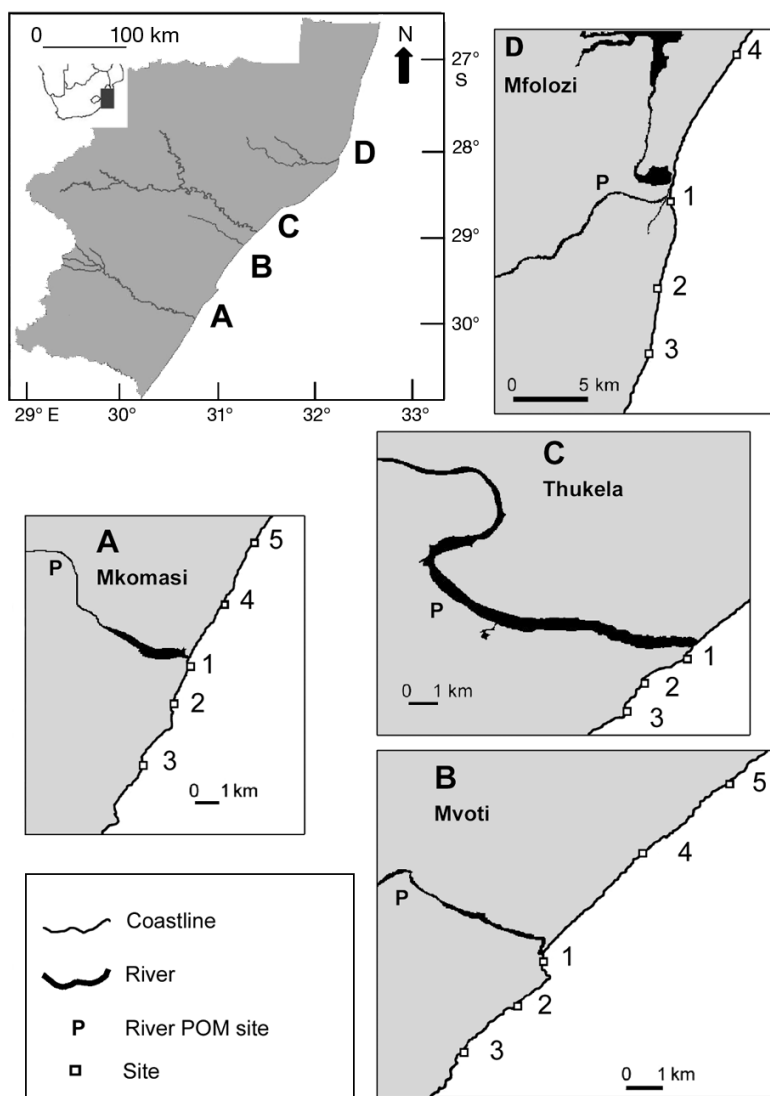


Fig. 1. Study areas A–D in the KwaZulu-Natal political province, South Africa, showing numbered sites at which filter feeders (1–5) and inshore particulate organic matter (POM) samples (1) were collected, and where riverine POM was sampled (P). Pelagic POM sites (not shown) were located 40 km offshore and due east of the Mkomasi and Mvoti River mouths

Collection and preparation of samples

Three potential POM food sources were subjected to stable isotope analysis: suspended river POM, suspended seaweed detritus, and suspended pelagic POM (assumed to be essentially phytoplankton). Water samples (5 l each, $n = 3$ replicates) containing suspended river POM were collected 2 to 5 km upstream of each river mouth during low or outgoing tide to reduce the possibility of marine contamination, an assumption supported by refractometer readings of 0 salinity. Particulate seaweed detritus samples ($n = 3$) were acquired immediately adjacent to

the rocky intertidal site closest to each river mouth by dragging a 200 μm mesh plankton net through the water and then picking out identifiable seaweed fragments from the samples in the laboratory. Pelagic POM samples (20 l each, $n = 3$) of Agulhas Current surface water containing phytoplankton were collected at a depth of <50 cm, 40 km offshore to ensure there was no terrestrial contamination. Due to logistic constraints, pelagic POM samples were collected only at 2 sites: one offshore of the Mkomasi River mouth and the other offshore of the Mvoti River mouth. Restriction of this sampling to 2 sites was justified on the grounds that (1) a single well-mixed current exists at this distance offshore of all 4 study areas (Lutjeharms 2006), and (2) the 2 sets of samples yielded very similar values (see 'Results'). In addition to these 3 end-member food sources, 20 l inshore water samples ($n = 3$), containing an assumed mix of POM from these 3 food sources, were collected within 3 h of low tide at the intertidal site closest to each river mouth in all 4 study areas. This entire sampling protocol was conducted within 3 wk periods, on 2 separate occasions in the austral summer rainy season (December 2006 to March 2007) when river input peaks, and on 2 separate occasions in the austral winter dry season (May to August 2007) when river input is relatively low (Schulze 1997). All water samples were collected in plastic containers pre-rinsed with deionised water and then with sample water, and stored in a dark refrigerator and processed within 24 h.

Three replicate samples per site of each of 4 species of filter feeders (the solitary ascidian *Pyura stolonifera* and the bivalves *Perna perna*, *Striostrea margaritacea* and *Saccostrea cucullata*) were haphazardly collected for stable isotope analysis from each of 3 to 5 intertidal rocky reefs lying within 15 km of each river mouth (Fig. 1). All 4 are abundant intertidal to shallow-water species in the Natal Bioregion and extend north into the Delagoa Bioregion (Sink et al. 2005). Individuals of similar size were chosen to avoid possible ontogenetic variability that can influence isotope results (Jennings et al. 2008). Specimens were immediately

placed on ice in the field and stored frozen (-15°C) until processed.

Water samples containing suspended POM were filtered through pre-combusted (500°C , 8 h), 47 mm diameter, $0.7\ \mu\text{m}$ pore size Whatman® GF/F glass microfibre filters under moderate vacuum ($\leq 4\ \text{cm Hg}$) until clogged. Thereafter, filters were thoroughly rinsed in deionised water. Large particles ($>1\ \text{mm}$) and zooplankton were removed manually under a dissecting microscope (Hill et al. 2006). From each POM water sample, 2 filters were obtained. The filter intended for carbon and nitrogen isotope analysis was treated with dilute HCl (1%) to remove inorganic carbonates, then thoroughly rinsed with deionised water to remove acid and any residual salt (Darnaude et al. 2004b). The other filter, intended for sulphur isotope analysis, was left untreated. All filters were oven-dried at 60°C for 24 h.

Seaweed particulate material was acquired by randomly picking out discernible pieces of macroalgae from the plankton net hauls. Samples were rinsed in distilled water and visible epibionts removed. To standardize the pre-processing of food sources, half of each seaweed sample was used for carbon and nitrogen isotope analysis, and the other for sulphur isotope analysis, employing the same procedures as for POM, and both halves were oven-dried at 60°C for 48 h.

Adductor muscles of the bivalves *Perna perna*, *Saccostrea cucullata* and *Striostrea margaritacea*, and muscular atrial siphons of *Pyura stolonifera* were extracted from each specimen and thoroughly rinsed with deionised water, then dried at 60°C for 48 h.

Isotopic analyses

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of all samples were simultaneously determined using a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron) after sample combustion in a Flash EA 1112 series elemental analyser (Thermo Finnigan) yielded CO_2 and N_2 that were passed via a ConFlo III gas control unit (Thermo Finnigan). $\delta^{34}\text{S}$ was determined on a ThermoFinnigan MAT Delta Plus Advantage isotope ratio mass spectrometer in continuous flow mode after the addition of 5 mg vanadium pentoxide to each sample before combustion. Carbon and nitrogen isotope analyses were conducted at the University of Cape Town Goldfields Stable Light Isotope Laboratory, and sulphur analyses at the University of California, Santa Barbara, Marine Science Institute Analytical Laboratory. Internal reference materials were compared

against International Atomic Energy Agency reference materials based on the original Vienna Pee Dee Belemnite, atmospheric N_2 and triolite (FeS) from the Vienna Canyon Diablo meteorite for carbon, nitrogen and sulphur, respectively. Results are expressed in standard delta notation (Peterson & Fry 1987): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ where X is the element in question and R is the ratio of heavy to light isotope. Precision of replicate determinations based on their standard deviations was $\pm 0.1\%$ for both carbon and nitrogen and $\pm 0.4\%$ for sulphur.

Data analysis

Before input into the mixing models, isotope signatures of the 3 primary producer end-member food sources (river POM, inshore seaweed detritus and pelagic POM) were subjected to a canonical analysis of principal coordinates (CAP) with PERMANOVA+ for PRIMER (Anderson et al. 2008) to determine whether the *a priori* end-member food sources were isotopically distinguishable. A separate CAP analysis of inshore POM and end-members was then undertaken to determine what resemblance inshore POM showed to these food sources.

To determine the composition of the inshore POM mixture, Stable Isotope Analysis in R (SIAR; Jackson et al. 2009) was computed with R v. 2.7.2, using all 3 isotope ratios simultaneously. SIAR uses a Bayesian-model based upon a Gaussian likelihood function to calculate source contributions and has advantages over IsoError (Phillips & Gregg 2001) and IsoSource (Phillips & Gregg 2003) because it accounts for uncertainty associated with multiple food sources, fractionation and isotope signatures (Jackson et al. 2009). Ten model runs were undertaken using sulphur alone, to test whether that would improve resolution of source contributions. The outcomes differed by less than 3% from those based on all 3 isotopes; as each of the 3 isotopes yielded significant differences among food sources, we elected to employ all 3 to increase robustness of the analyses.

The SIAR mixing model was applied to each replicate inshore POM signature, using average \pm SD values from each of the 3 primary producer end-member sources collected at the same sampling area and time, and each time the model was run for 200 000 iterations. Fractionation values were not incorporated because no known processes cause differential uptake of heavy and light isotopes in the POM pool (Bode et al. 2006). The median value from each of the 3 end-member feasible-contribution outputs

from SIAR was then extracted and used in the following ANOVA models and descriptive figures.

To investigate differences in seaweed detritus and pelagic POM contributions to inshore POM (both as dependent variables), 2-factor crossed permutational ANOVAs (PERMANOVA; unbalanced, untransformed data, Euclidian distance measure, 9999 permutations of residuals under a reduced model, type III partial sums of squares) were run with PERMANOVA+ for PRIMER (Anderson et al. 2008). Study area was fixed with 4 levels and season was fixed with 2 levels, and both held as independent variables. Variation in river POM contribution to inshore POM was investigated as a dependent variable using a permutational multivariate analysis of covariance (PERMANCOVA) so that the variability in river POM contribution could be partitioned among the following covariates (independent variables): (1) distance from river mouth to inshore POM collection site, (2) mean annual river runoff, and (3) 3-monthly runoff for the month of POM collection plus the 2 preceding months (Table 1). The same model was run on river POM, although type I sequential sums of squares had to be used because the sums of squares for individual terms in a PERMANCOVA model are

Table 1. Values of the 3 covariates used in the permutational multivariate analysis of covariance (PERMANCOVA) of inshore POM for each study area (A–D) per sampling period (1 = early summer, 2 = late summer, 3 = early winter, 4 = late winter). Distance: distance between river mouth and inshore POM sampling site, MAR: mean annual runoff (from Sink 2001), 3-monthly runoff: the total runoff during the month sampled plus 2 mo previous, derived from *in situ* gauges (DWAf, www.dwaf.gov.za/hydrology, accessed 12 Feb 2009) and modelled data (R. Lawrie unpubl. data)

Study area	Sampling period	Covariates		
		Distance (m)	MAR ($\times 10^6 \text{ m}^3$)	3-monthly runoff ($\times 10^6 \text{ m}^3$)
A (Mkomasi)	1			291
	2	400	1100	255
	3			136
	4			58
B (Mvoti)	1			129
	2	280	400	198
	3			112
	4			41
C (Thukela)	1			818
	2	1370	4000	810
	3			363
	4			79
D (Mfolozi)	1			250
	2	1390	1000	115
	3			46
	4			31

not independent from one another (see Anderson et al. 2008). The analysis was run twice, with different orders of the 2 factors study area and season as independent variables, because type I sums of squares can influence conclusions in multi-factorial designs depending on the order these factors are run (Anderson et al. 2008). Only the most conservative results are shown, and re-ordering of factors did not alter conclusions.

For analyses of filter feeders, SIAR was used to model the contributions of the 3 end-member food sources to their assimilated diets. Study area and season-specific average \pm SD isotope values of river POM, seaweed and pelagic POM were used for each individual filter feeder. Species-specific fractionation rates were not known for the species we sampled, so we followed the practice of other authors (Choy et al. 2008, Yokoyama et al. 2009) in using average (\pm SD) values from a pool of comparable species, and adopted $0.47 \pm 1.23\%$ for carbon, $2.52 \pm 2.5\%$ for nitrogen (Vander Zanden & Rasmussen 2001) and $0.5 \pm 1.9\%$ for sulphur (McCutchan et al. 2003). Concentration dependence was also incorporated into the model because the proportional contribution of the 3 elements (carbon, nitrogen and sulphur) among the end-member food sources was not equal (see Phillips & Koch 2002). Average \pm SD percentage values of carbon, nitrogen and sulphur concentration in seaweed were obtained from seaweed-sample isotopic analyses while those for river POM were obtained from the isotopic analyses of small (<10 mm) decaying identifiable terrestrial plant pieces collected from the shore near river mouths ($n = 3$ for each of the 2 seasons and 4 rivers). Values for pelagic POM, assumed to be largely phytoplankton, were obtained from Hedges et al. (2002). Average \pm SD values for carbon, nitrogen and sulphur respectively of 32.61 ± 5.88 , 3.03 ± 0.70 and $2.43 \pm 0.99\%$ were used for seaweed; 41.87 ± 3.50 , 0.86 ± 0.36 and $0.62 \pm 0.31\%$ for river POM; and 16.20 ± 3.02 , 3.16 ± 0.62 and $0.86 \pm 0.42\%$ for pelagic POM. Median values were then extracted from the feasible contribution outputs produced by SIAR for each end-member food source, graphed and used in subsequent PERMANOVA models. Site, season and species were fixed with orthogonal contrasts. PERMANOVA post hoc tests on the median values of the food source contributions produced by SIAR were run only for site and the interaction term Site \times Season, as the other factors were irrelevant to the primary hypothesis. Post hoc analyses were not run on species, as signatures differed among them by $<1\%$ and were therefore regarded as being biologically insignificant.

RESULTS

Defining food-source isotopic signatures

The CAP analyses confirmed that the *a priori* end-member food sources (i.e. seaweed, river POM and pelagic POM) for all study areas and for each season were statistically distinguishable ($p_{\text{perm}} < 0.005$) and thus employable in mixing models (Table 2). Leave-one-out allocation successes for end-member food sources (i.e. excluding inshore POM mixture) were high (84.7–87.0%). End-member food sources were seldom misclassified with other end-member sources but when this did occur, it was most often pelagic POM and seaweed that were confused. When inshore POM was included with the end-members it had a lower average classification success (67.4%) than end-member sources, which is to be expected, as it comprised a mixture of the other sources.

Isotopic signatures for the 3 end-members and for inshore POM are compared in Fig. 2. In terms of average signatures, river POM carbon spanned -15.5 to -25.8‰ and nitrogen $+1.2$ to $+6.4$. Sulphur had a greater range from -3.2 to $+16.3\text{‰}$, but most values were $< +5\text{‰}$. Seaweed detritus had carbon signatures (-17.4 to -27.6‰) similar to river POM, but nitrogen ($+4.8$ to $+6.4\text{‰}$) was enriched relative to river POM, and sulphur ($+19.5$ to $+21.6\text{‰}$) even more enriched than river POM. Pelagic POM had carbon signatures (-19.5 to -22.7‰) similar to both seaweed and river POM, and nitrogen signatures ($+4.6$ to $+7.5\text{‰}$) similar to seaweed, but its sulphur signatures ($+13.7$ to $+16.7\text{‰}$) were enriched relative to river POM and depleted relative to seaweed. Inshore POM, being a mixture of the 3 end-

members, had carbon signatures overlapping all 3 end-members (-19.1 to -21.8‰); its nitrogen ($+2.9$ to $+7.7\text{‰}$) was similar to seaweed and pelagic POM but enriched relative to river POM, and its sulphur ($+6.3$ to $+18.0\text{‰}$) was generally more enriched than river POM but more depleted than both seaweed and pelagic POM.

Table 2. Canonical analysis of principal coordinates (CAP) on raw isotope signatures using Euclidian distance, for the 3 end-member food sources and for inshore POM (mixture)

Food source	Classified as				Total	% Correct	Trace statistic	p
	River POM	Sea-weed	Pelagic POM	Inshore POM mix				
River POM	40	1	5	–	46	87.0	0.989	0.0050
Seaweed	0	41	7	–	48	85.4		
Pelagic POM	2	9	61	–	72	84.7		
Inshore POM mix	4	2	8	29	43	67.4	1.172	0.0002

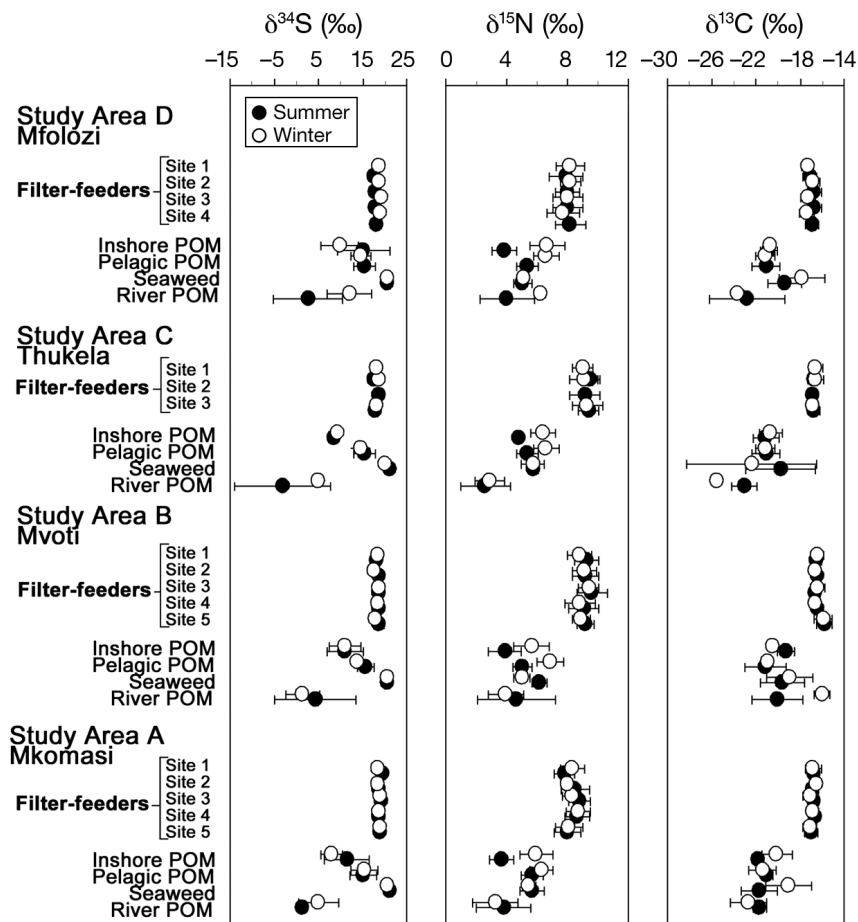


Fig. 2. Mean \pm SD $\delta^{34}\text{S}$, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope values (‰) for the 3 end-member food sources, inshore POM mixture and filter feeders, averaged across each site, in summer and in winter, for study areas A–D

Food-source contributions to inshore POM composition

Considering the signatures from carbon, nitrogen and sulphur together, the composition of the inshore POM at study areas A and B most closely resembled the isotope signatures of pelagic POM and river POM, whereas the inshore POM at study areas C and D most closely resembled that of pelagic POM (Fig. 2). At all study areas, inshore POM isotope signatures least resembled those of seaweed. Mixing models indicated that inshore POM comprised a mixture of all 3 end-member food sources to varying degrees (Fig. 3). Average \pm SD river POM contribution to inshore POM per study area per season ranged from 17.1 ± 15.9 to $61.9 \pm 38.1\%$. Seaweed material contributed 6.0 ± 4.5 to $52.8 \pm 20.4\%$, while pelagic POM added 17.9 ± 22.7 to $76.6 \pm 19.4\%$.

Significant seasonal differences ($p_{(\text{perm})} < 0.05$) existed in the contributions to inshore POM by seaweed material (higher in summer) and pelagic POM (higher in winter), but no significant seasonal differ-

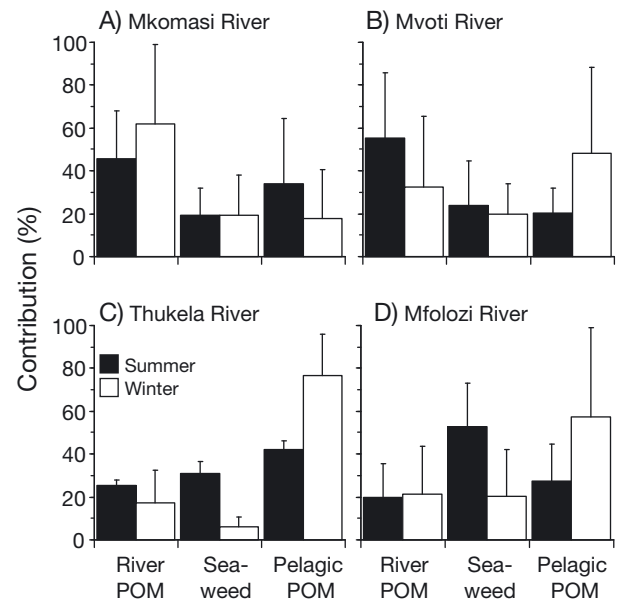


Fig. 3. Mean \pm SD percentage contributions of the 3 end-member food sources to the inshore POM mixture adjacent to river mouths from study areas A–D, for summer and winter periods

Table 3. Two-factor PERMANOVA and a PERMANCOVA to investigate variation in the contributions of the 3 end-member food sources to the inshore POM mixture, between study areas and seasons, based on SIAR mixing models. Long-shore distance from river mouth to where the inshore POM sample was collected, mean annual runoff (MAR) and 3-monthly runoff were added as covariates in the analysis of river POM contributions. Asterisks indicate significant differences ($p < 0.05$)

Source of variation	df	Pelagic POM			Seaweed		
		MS	F	$P_{(\text{perm})}$	MS	F	$P_{(\text{perm})}$
Study area	3	0.179	2.268	0.0972	0.079	2.746	0.0588
Season	1	0.371	4.702	0.0381*	0.247	8.541	0.0041*
Study area \times Season	3	0.149	1.886	0.1520	0.069	2.378	0.0883
Residual	35	0.079			0.029		
Total	42						
River POM							
Source of variation	df	MS	F	$P_{(\text{perm})}$			
Study area	1	0.108	4.128	0.0471*			
Season	1	0.046	1.768	0.1986			
Long-shore distance	1	0.828	31.616	0.0001*			
MAR	1	0.002	0.084	0.7749			
3-monthly runoff	1	0.004	0.152	0.6887			
Study area \times Season	1	0.071	2.708	0.1064			
Long-shore distance \times 3-monthly runoff	1	0.607	23.184	0.0001*			
Long-shore distance \times Season	1	0.741	28.279	0.0001*			
MAR \times 3-monthly runoff	1	0.041	1.549	0.2185			
MAR \times Season	1	0.038	1.438	0.2317			
3-monthly runoff \times Study area	1	0.024	0.906	0.3414			
3-monthly runoff \times Season	1	0.058	2.197	0.1458			
Long-shore distance \times 3-monthly runoff \times Season	1	0.086	6.929	0.0148*			
MAR \times 3-monthly runoff \times Season	1	0.086	3.283	0.0774			
Residual	28	0.026					
Total	42						

ences in riverine POM contributions were exhibited (Table 3). Although inshore POM at 2 of the study areas (B and C) comprised respectively 23.1 and 8.4% more river POM in summer than in winter, the reverse was true at study area A where river POM contributed 16% more in winter than in summer, and at study area D, river POM contributions were approximately equal in summer and winter (Fig. 3).

An inshore–offshore gradient of enrichment in $\delta^{34}\text{S}$ of POM existed from river to pelagic systems best described by a non-linear regression between $\delta^{34}\text{S}$ and distance from coast (d) in km: $\delta^{34}\text{S}_{\text{POM}} = 10.41 + 4.58(1 - 0.83^d)$, $r^2 = 1$ (Fig. 4).

PERMANCOVA on river POM contribution did reveal significant differences among samples taken at different distances along the shore from river mouths (covariate), for study area, and for all interaction terms involving long-shore distance from river mouth (Table 3). River POM contributions to inshore POM showed a significant decreasing linear trend with distance from river mouths in km (river POM% contribution = $-0.0265[\text{distance}] + 57.548$; $r^2 = 0.23$, $p = 0.001$). Other covariates (mean annual runoff and 3-monthly runoff) did not explain any significant amounts of variation in river POM contribution.

Isotope signatures of filter feeders

All 4 species had tightly clustered isotopic signatures, and the variance among replicates was extremely small (Fig. 2). Differences among study areas, sites, and seasons were slight and ranged from -18.1 to -15.1% for carbon, $+6.2$ to $+10.6\%$ for nitrogen

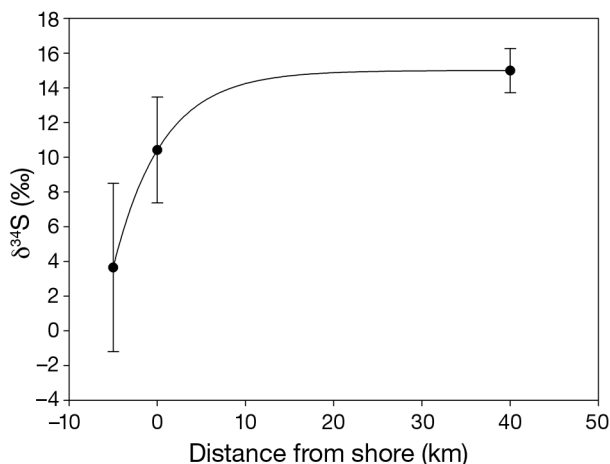


Fig. 4. Mean \pm SD $\delta^{34}\text{S}$ isotope signatures of POM versus distance from shore (d). Negative distance equals distance inland upriver. Regression: $\delta^{34}\text{S}_{\text{POM}} = 10.41 + 4.58(1 - 0.83^d)$, $r^2 = 1$, $n = 3$

and $+17.0$ to $+19.9\%$ for sulphur isotope signatures. The isotope signatures of the 4 species of filter feeders more closely resembled those of seaweed than any of the other end-member food sources or the inshore POM mixture (Fig. 2).

Spatial and seasonal patterns in food source assimilation were assessed by pooling across species because of their close isotopic similarity, and because the mixing models predicted maximum interspecific assimilation differences of only 6.08% for river POM assimilation, 5.94% for seaweed detritus and 2.97% for pelagic POM. Mixing models indicated that seaweed detritus was the dominant food source for all filter feeders at all 4 study areas, with average \pm SD values ranging from 38.7 ± 1.7 to $62.1 \pm 3.0\%$ (Fig. 5). The proportion of seaweed detritus assimilated varied little among sites lying at different distances from river mouths (1.5–5.0%). Nevertheless, significant differences among sites were found within all 4 study areas ($p_{(\text{perm})} < 0.01$), although this was not usually the case in the interaction term Site \times Season. Only during summer at study area A and winter at study area B were slight but consistent trends of increasing seaweed assimilation found with increasing distance from river mouth. Generally, about 2 to 10% more seaweed was assimilated in summer than in winter, with the differences being significant ($p_{(\text{perm})} \leq 0.0002$) in all areas except area B ($F_{(1,76)} = 3.9$, $p_{(\text{perm})} = 0.0521$), and area D reversed the trend as 7% more seaweed was assimilated in winter than in summer ($F_{(1,54)} = 562.5$, $p_{(\text{perm})} = 0.0001$).

Pelagic POM, assumed to be largely phytoplankton, was the next-most assimilated food source after seaweed at 3 of the 4 study areas, with average \pm SD dietary contributions ranging from 23.7 ± 5.6 to $36.2 \pm 1.4\%$ (Fig. 5). Spatial variation among sites was small (0.4–4.1%) although significant differences ($p_{(\text{perm})} < 0.01$) were found at all study areas bar one, namely area A, which was also the only place where no significant interaction was found between site crossed with season ($F_{(4,61)} = 1.6$, $p_{(\text{perm})} = 0.1770$). Very gradual decreasing trends in pelagic POM assimilation with respect to distance from river mouth were evident at study areas A and C during winter, and negligible increasing trends were observed at area B during both summer and winter. Significant seasonal differences were found within all study areas ($p_{(\text{perm})} = 0.0001$) except at area D ($F_{(1,54)} = 0.006$, $p_{(\text{perm})} = 0.9439$), with marginally more pelagic POM (10.4% on average) being assimilated in winter than in summer.

River POM was assimilated at all study areas and sites in proportions ranging from 8.6 ± 1.3 to $33.3 \pm$

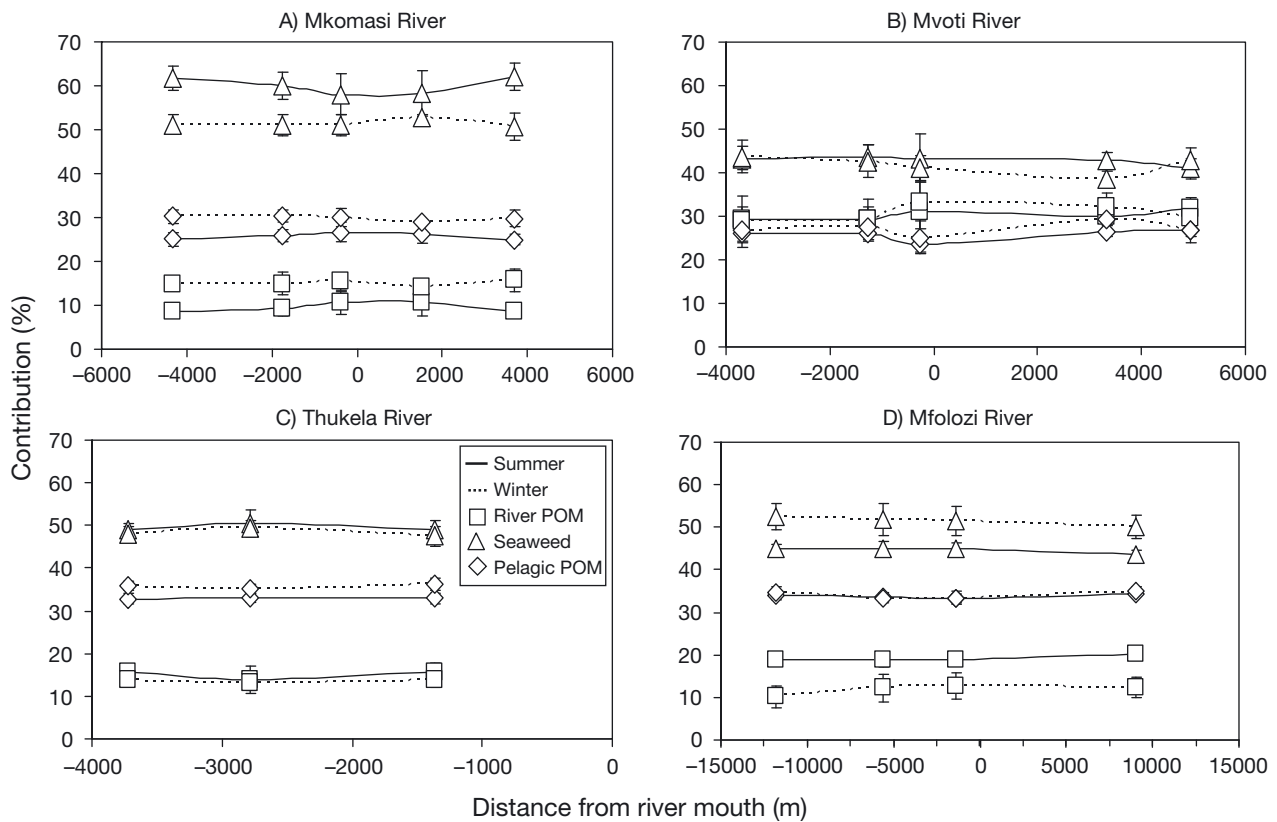


Fig. 5. Mean \pm SD percentage contributions of river POM, seaweed detritus and pelagic POM assimilated by filter feeders, according to the median value derived from mixing model outputs per season, expressed relative to distances south (negative values) or north of river mouths (positive values), for study areas A–D

6.2% (Fig. 5). Little spatial variation in assimilation (0.9–4.5%) was evident among sites, but these small differences were statistically significant ($p_{\text{perm}} < 0.005$). The interaction term Site \times Season was significant at areas B and D ($P_{\text{perm}} < 0.005$).

Small spatial trends of decreasing assimilation of river POM with distance from river mouth were evident at study area A in summer but not in winter, during both seasons at area B and in winter only at area D. There were no trends at area C in either season. As was the case with seaweed and pelagic POM, there was a small seasonal shift in the amount of river POM assimilated, which was significant in areas A, C and D ($p_{\text{perm}} = 0.0001$) but was inconsistent across study areas, with 0 to 3% more being assimilated during winter in areas A and B, and 1 to 8% more in summer in areas C and D.

When post hoc tests were run, 2 trends were revealed. Firstly, in terms of river POM assimilation, sites were most often significantly different ($p < 0.05$) if comparisons were being made between sites situated at the mouth versus those at some distance from the mouth, or between sites that lay far apart. Sec-

ondly, when Site \times Season interactions were compared for pelagic POM assimilation, significant differences were always more frequent in winter, when pelagic POM proportions were highest, than in summer.

DISCUSSION

Food sources and their contribution to inshore POM

The 3 sources of primary production were sufficiently distinct isotopically to discriminate their proportional contributions to the inshore POM mixture and to the assimilated diets of the filter feeders examined. Carbon, nitrogen and sulphur isotope signatures of seaweeds lay within the ranges found by other studies (Stephenson et al. 1984, Peterson & Fry 1987, Smit 2001, Yamanaka et al. 2003), and carbon and nitrogen values were similar to those reported specifically for the South African east coast where we worked (Hill et al. 2006). River POM carbon isotopic signatures averaged -20‰ , implying more or less

equal proportions of C_3 and C_4 plants (Pate 2001), which reflects the mix of savanna and grassland biomes in the region (Rutherford et al. 2006). Carbon and nitrogen isotopic values of seaweed closely resembled those of river POM, but sulphur isotope signatures clearly differentiated between them: river POM was far more depleted than seaweed, which derives its sulphur from oceanic sulphate with a $\delta^{34}\text{S}$ of +20 to +21‰ (Rees et al. 1978). Terrestrial and aquatic plants, thought to comprise the bulk of river POM, derive most of their sulphur from precipitation with a $\delta^{34}\text{S}$ of +2 to +6‰ (Michener & Schell 1994). The assimilation of different pools of inorganic sulphur (terrestrial versus marine) into organic matter and the mixing of these in the inshore zone was illustrated by the inshore–offshore trend in $\delta^{34}\text{S}$, which rose with distance offshore, reflecting differential inputs of riverine, inshore and pelagic sources. Carbon and nitrogen isotope signatures of pelagic POM, assumed to be largely phytoplankton, closely approximated those found offshore on the east coast of South Africa (Hill et al. 2006, 2008). Sulphur isotope signatures of pelagic POM, on the other hand, were slightly more depleted than in the literature (Peterson & Fry 1987).

To test whether any artefactual depletion of sulphur could have biased our results, we re-ran mixing models using values of $+21 \pm 0.5\%$, spanning the accepted norms for organisms deriving their sulphur exclusively from marine sulphate (Michener & Schell 1994). The resultant estimations of POM assimilated by filter feeders were consistently scarcely influenced by these re-runs. River POM could have been underestimated by $5.6 \pm 4.2\%$, and seaweed and pelagic POM overestimated by $2.1 \pm 4.3\%$ and $3.0 \pm 4.5\%$, respectively. Thus, our results would not have been materially influenced by any artefact effect, and our conclusions remain robust.

The inshore POM mix was isotopically different from all of the 3 food sources contributing to it, demonstrating that no single source dominated its composition at all sites and times. Relative to other end-member sources, river POM contributed most to the inshore POM pool when samples were taken within hundreds of meters of a river mouth but contributed less to inshore POM at distances exceeding 1000 m.

Hill et al. (2008) found that macroalgae usually contributed more than 50% of the material in the inshore POM pool when they sampled approximately 700 km south of our study. However, the area they studied is much less influenced by river input, as the 2 main rivers within 25 km of their sampling site—the Kariega and Kowie—are heavily impounded and

exude a combined mean annual runoff of only $38 \times 10^6 \text{ m}^3$ (Noble & Hemens 1978). Our study is therefore more likely to show a proportionally higher input of riverine POM because it focused on rocky shores within kilometres of relatively larger rivers (with runoffs of 400 to $4000 \times 10^6 \text{ m}^3$).

Unexpectedly, riverine contributions to inshore POM were not consistently greater in summer (the rainy season) than in winter, with such a pattern being evident at only 2 of the 4 sites. It was also not significantly related to mean annual river runoff. This indicates that the amount of river POM injected into the inshore zone is not necessarily a function of seasonal or annual runoff. In the Danube River, which flows into the Black Sea, the amount of river POM is similarly unrelated to runoff (Bănarau et al. 2007), and the same is true where the Mattaponi River in Virginia (USA) flows into the sea (Hoffman & Bronk 2006). Factors that could explain the absence of river-size and seasonal effects include the nature and quantity of terrestrial vegetation (with greater litter-fall increasing POM input), the time between plant growth and litter-fall (which could decouple rainfall from litter input), the intensity of agricultural abstraction (reducing runoff) and relative rainfall runoff (influenced by catchment area and climate).

River POM contributions to inshore POM did, however, decline linearly with distance from river mouths. Satellite images indicate that river plumes are concentrated near the coast (Porter 2009), where the strong wave action will result in well-mixed water and supply these riverine materials to the benthos. River plume processes are influenced by a range of factors, but river POM can be expected to be diluted by marine POM sources with an increase in distance from the mouth. In both the Changjiang River, which enters the East China Sea, and the Vistula River, which drains into the Baltic Sea, river POM contributions decreased with distance from the river mouth (Wu et al. 2003, Voss et al. 2005) in a pattern similar to that recorded here. Coastal wind direction and ambient coastal flow are likely to be the dominant agents determining plume direction (García Berdeal et al. 2002). Prevailing wind velocity and its temporal variability, inshore vertical stratification and the degree of mixing due to turbulence (Gibbs & Konwar 1986) will influence the concentration of riverine POM in the inshore POM pool (Naudin et al. 1997) and whether or not its dilution proceeds linearly.

Thus, while riverine material contributed significantly to the inshore POM pool and was diluted with distance from the source, increasing river size

and a seasonal increase in runoff did not elevate the contribution of riverine contributions to the inshore POM.

Assimilation of different sources of POM by filter feeders

Many studies have found pelagic phytoplankton to be of major trophic importance to filter feeders (Leslie et al. 2005 and references therein). However, on the South African west coast where kelps contribute substantial amounts of detritus, filter feeders rely mostly on nearshore production in the form of seaweed detritus (Stuart et al. 1982, Fielding & Davis 1989, Bustamante & Branch 1996), as does *Perna perna* on the southern part of the east coast, where its reliance on nearshore algal production exceeds 50% (Hill & McQuaid 2008, Hill et al. 2008).

Our study showed a similarly high reliance on nearshore production, with seaweeds contributing 40 to 60% of the diets of inshore filter feeders. In addition, pelagic POM, assumed to be largely phytoplankton, comprised 25 to 35% of their diets. The overall trophic contribution of river POM to filter feeders spanned 8.6 to 33.3%, providing evidence for moderate terrestrial subsidies to their diets.

A feature of our analyses of the filter feeders was that all 4 species yielded strikingly similar isotopic signatures—a pattern that was evident at all sites and in both seasons. This indicates that while the different consumer species may preferentially assimilate some food sources over others, they appear to do so uniformly.

Throughout the study, the contributions of riverine inputs to the consumers' diets were significantly less than those to the inshore POM pool. Conversely, seaweed contributions to the diets were proportionally greater than those to the mixed inshore POM pool. Pelagic POM was assimilated in proportions approximately equal to availability. This suggests unequal digestion or assimilation of different types of organic matter (Zimmer et al. 2002). Seaweed and phytoplankton tend to be more easily assimilated in particulate form than terrestrial plant material because the latter is structurally harder and comprises relatively indigestible cellulose (Mann 1988). This could explain why a greater proportion of marine-derived POM is assimilated relative to its availability in the inshore POM pool.

The high amount of riverine POM in the inshore POM pool is most likely characteristic of inshore waters close to river mouths, and it is unlikely to con-

tribute significantly far away from river mouths. In addition, the composition of the inshore POM pool is likely to be highly dynamic temporally and spatially, whereas consumers have isotopic signatures that integrate over months what has been assimilated from the organic matter pool, further complicating assessment of assimilation versus availability (see Hill et al. 2008). Hill & McQuaid (2008) showed that turnover of the adductor muscle of the mussel *Perna perna* is <10% after 3 mo, which means that in the 5 to 6 mo seasonal periods used in our study, there would have been only about 20% tissue turnover. In particular, this would hamper detection of seasonal trends in assimilation of different sources of POM.

Another source of variability complicating interpretation could come from plant material that is broken up by wave action and abrasion (Wotton 2004); microorganisms utilising the dissolved organic matter can in turn be assimilated efficiently by filter feeders (Schleyer 1981, Mann 1988).

The assimilation of terrestrially derived organic matter introduced by rivers, either particulate or dissolved, is probably more important in coastal areas such as the Natal Bioregion where productivity is relatively low (Bustamante et al. 1995, Hutchings et al. 2010), rather than in productive areas such as the west coast where large subtidal kelp beds contribute substantially to intertidal foodwebs (Stuart et al. 1982, Bustamante & Branch 1996) and shallow subtidal foodwebs (Velimirov et al. 1977, Newell et al. 1982, Fielding & Davis 1989).

Although statistically significant spatial differences in the proportions of various food sources assimilated by filter feeders were detected among sites (and in many cases the interaction term Site \times Season), they have little biological importance as the differences were small, typically less than 5% for all food sources, and in no cases were there prominent decreasing trends in the amount of riverine POM assimilated relative to distance from river mouths. Several scenarios could explain this.

First, inshore POM could be well mixed over the range of distances sampled, such that any variations in the proportions of various types of POM comprising the inshore POM pool were imperceptible at the scales studied. This seems unlikely, however, considering that there was a decreasing trend in the amount of riverine POM with distance from river mouths, as has also been recorded elsewhere (Wu et al. 2003, Voss et al. 2005). In contrast, an onshore/offshore gradient was clearly defined in the $\delta^{34}\text{S}$ isotope signal. The regression describing this relationship is weak because of the small number of data

points, and therefore subject to uncertainty; but the fact that there was a progressive decline offshore can robustly be construed as reflecting progressive dilution of riverine POM by oceanic water.

Second, river POM concentration may exceed levels beyond which assimilation can take place because it is difficult to digest, and may be rejected as pseudofaeces (Bayne et al. 1993). The absence of any strong, consistent, spatial trends in assimilated riverine POM, despite a demonstrable gradient in availability, is possibly because the filter feeders are at the upper limits of their ability to assimilate river POM.

CONCLUSIONS

The primary goal of this work was to determine whether riverine POM is being assimilated by filter feeders, and to what extent this may enhance filter-feeder biomass in regions where riverine inputs are substantial. In all 4 study areas, riverine POM was assimilated in similar amounts by all 4 species of filter feeders examined. Relative assimilation of riverine POM, however, was secondary to that of marine origin. It is therefore unlikely that the dietary subsidies of POM from rivers can alone account for the high biomass of filter feeders in this particular bioregion.

In short, river POM contributed notably to inshore POM and its concentration was related to distance from the source river, supporting the first part of Hypothesis 1 outlined in the Introduction; but contrary to expectations, it did not contribute significantly more in summer than winter, nor did large rivers contribute more than smaller rivers. Filter feeders did assimilate riverine POM, but no biologically meaningful spatial or seasonal trends could be detected. Therefore Hypothesis 2—that inshore filter feeders will assimilate riverine POM in addition to pelagic POM and seaweed detritus—was upheld, although the proportion of river POM assimilated was never predominant, and was not higher during the rainy season or at sites close to river mouths, contradicting the second part of the hypothesis.

Our data do not support predominant direct consumption of riverine POM by filter feeders over other POM sources. However, rivers alter inshore environments in ways not explored by our analysis that are additional to trophic input. These include inputs of nutrients and alterations of turbidity. River inflow into the sea in the Natal Bioregion where we worked is >300 times greater than in the adjacent Delagoa Bioregion, coincident with the greater biomass of fil-

ter feeders in the Natal Bioregion (Sink et al. 2005, Porter et al. 2013). The collective effects of rivers may therefore contribute to the biogeographic break and the shift in trophic structure between these 2 bioregions. Future pursuit of the effects of riverine inputs on nutrients and turbidity and their consequences for trophic structure would help to resolve their effects on community composition.

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