

Biogeographic and nearshore–offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa

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ABSTRACT: There are broad differences in oceanography and primary production around the southern African coast that are likely to give rise to major differences in trophic pathways. Stable isotope ratios provide integrated information on trophic relationships, yet there has been limited research on geographic variation in isotopic composition of marine consumers and their food. In this study, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of suspended particulate matter (SPM), intertidal mussels and common macroalgae along the southern African coastline were explored. Nearshore–offshore isotope trends as well as biogeographic and temporal patterns in isotopic ratios of mussel tissue, macroalgae and SPM were investigated at 12 sites along the coast from Namibia to the Mozambique border. SPM exhibited overall trends of nearshore ^{13}C depletion from south-west to north-east along the coastline and from nearshore (0 km) to offshore (10 km) waters, in both cases suggesting a shift from a nearshore signature strongly influenced by macroalgal detritus to one more representative of oceanic phytoplankton. With one exception it was possible, using discriminant analysis, to categorize mussel populations into 4 geographic groups, on the basis of both carbon and nitrogen signatures: the east coast, the south-east coast, the south-west coast and the west coast. Macroalgae showed no consistent biogeographic trends and need to be examined in greater detail to relate nearshore SPM values to living macroalgal signatures. A linear mixing model indicated that mussels along the entire coastline generally demonstrated more than 50% dependence on nearshore carbon and nitrogen, emphasizing the importance of nearshore primary production to intertidal consumers.

KEY WORDS: $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Stable isotope analysis · Biogeographic trends · Mussels · Diet

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INTRODUCTION

Variation in coastal hydrography plays an important role in intertidal community ecology. Nearshore conditions of coastal waters have significant effects on intertidal benthic organisms (Blanchette et al. 2005), and several studies have shown strong correlations between coastal oceanography and nearshore benthic community structure (e.g. Menge et al. 1999, Nielsen & Navarrete 2004). Because of biogeographic variation of nearshore hydrography, the influence of coastal water extends beyond the effects on recruitment rates that are a present focus of attention (Alexander & Roughgarden 1996, McQuaid & Lawrie 2005), and

includes effects on the nature of the food available to primary consumers, especially suspension feeders. This coupling of oceanographic conditions and nearshore community structure has significant implications for the southern African shoreline, which is influenced by both the Benguela and the Agulhas current systems (McQuaid & Payne 1998), implying biogeographic differences in the food resources available to intertidal communities. The Agulhas current, along the east and south coasts, brings warm, oligotrophic water from the Mozambique channel (Lutjeharms et al. 2000), while the Benguela current flows northwards along the west coast bringing cold eutrophic water of Antarctic origins (Andrews & Hutchings 1980).

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Broad geographic and possibly temporal differences therefore exist in the oceanography, pelagic primary production (Andrews & Hutchings 1980, Brown 1992) and macroalgal species that generate detritus (Bolton et al. 2004) along the southern African coastline, implying that intertidal filter feeders in particular may experience differences not only in the quantity, but also the quality of food available to them. It has long been suggested that both estuarine and marine bivalves assimilate most of their dietary carbon through the uptake of phytoplankton (Widdows et al. 1979, Asmus & Asmus 1991, Dame & Prins 1998). Recently, however, with the introduction of stable isotope analysis, it has been possible to trace the flow of organic matter directly from source to consumer (Kaehler et al. 2000). The application of this technique has led to the suggestion that uptake of macroalgal carbon by filter feeders, through detrital food webs in benthic and pelagic communities has been underestimated (e.g. Dunton & Schell 1987, Duggins et al. 1989, Bustamante & Branch 1996). As a result, the importance of phytoplankton versus macroalgal detritus as food sources for intertidal communities is increasingly being called into question (Stuart et al. 1982, Bustamante & Branch 1996, Vizzini et al. 2002).

Stable isotope analysis has proven to be a powerful tool for resolving trophic relationships and several studies have shown the importance of biogeography in relation to isotope signatures. Rau et al. (1982) reported changes in plankton $\delta^{13}\text{C}$ values with latitude and Burton & Koch (1999) presented evidence that pinnipeds demonstrate latitudinal differences in collagen carbon values, indicating variation in lower trophic levels. Similarly, in other marine mammals, carbon isotope signatures vary with geographical position (Hobson et al. 2002), allowing the identification of movement over large latitudinal ranges, by identifying different sources of primary production (Burton et al. 2001). Despite these studies, there has been limited research on biogeographic variation in isotopic composition of marine consumers and their food, especially within intertidal benthic communities.

The aims of this study were to investigate the effects of biogeographic and temporal variation in coastal hydrography on food resources of intertidal mussels along the southern African coastline by means of stable isotope analysis, examining the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios from suspended particulate matter (SPM), mussels and macroalgae. These were analyzed to establish (1) if nearshore–offshore isotopic gradients exist, and whether they can be linked to isotopi-

cally distinct sources of production, (2) if existing nearshore–offshore gradients and isotopic signatures of intertidal consumers and producers vary biogeographically and/or temporally, and (3) the relative importance of pelagic primary production (i.e. phytoplankton) versus coastal detritus in the diet of intertidal mussels.

MATERIALS AND METHODS

Sample collection. SPM samples were obtained from 5-liter surface water samples taken at 12 rocky shore sites along the southern African coastline, from Walvis Bay in Namibia to Sodwana Bay, near the Mozambique border (Fig. 1), in austral summers January to February 2002 and November to December 2003, and austral winter June to July 2004. At each site, duplicate water samples were collected along a transect running perpendicular to the coast at distances of 0, 0.25, 0.5, 1, 2, 4 and 10 km. In 2002, samples were collected at only 5 sites, the Port Nolloth transect was collected once in the June to July 2004 period and the Walvis Bay transect was collected once in the November to December 2003 period. Due to logistic constraints, only 2 of the samples collected were between 0 and 10 km at Walvis Bay. Five mussels (either *Perna perna* or *Mytilus galloprovincialis* depending on the site) and samples of the most abundant macroalgae species ($n = 2$ to 8 depending on availability) were collected at each of the SPM transect sites and at 2 additional sites: Zinkwaze Beach and St. Helena Bay (Fig. 1).

Because different mussel species occur around the coast (*Mytilus galloprovincialis* is found on the west coast and *Perna perna* on the east coast), 15 indi-

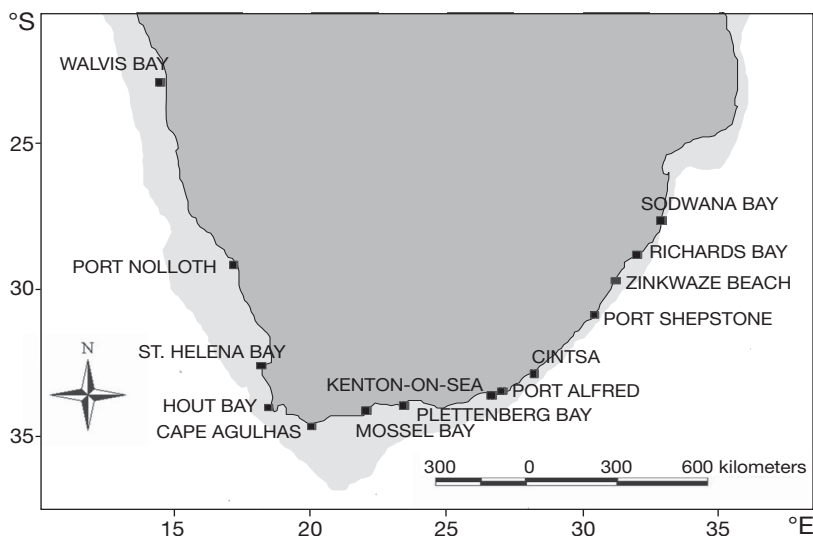


Fig. 1. Map of southern Africa, showing sample sites along the coastline. Light grey shaded area: continental shelf (≤ 500 m depth)

viduals of each species were collected from the same shore and intertidal zone, near Port Alfred, where the 2 co-occur. These animals were analyzed to test for interspecific differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. *t*-tests showed no significant difference between mean isotopic carbon ($p > 0.05$) or nitrogen ($p > 0.05$) values between species (power of test was 0.99).

Sample preparation. Water samples were filtered through pre-combusted (500°C, 6 h) GF/F (Whatman®) filters (0.45 μm pore size), using a vacuum pump (≤ 4 cm Hg) and then oven dried at 60°C for 24 h. Zooplankton and other large particles were manually removed under a dissecting microscope (16 \times). Mussel adductor muscle tissue was removed, rinsed in distilled water (dH₂O) and oven dried (60°C, 48 h). Adductor muscle tissue was used in this study, as muscle tissue has low turnover rates (Gorokhova & Hansson 1999) and is therefore more representative of a time-integrated diet. All macroalgae were rinsed in dH₂O, visible epiphytes were removed and algae were also oven dried (60°C, 48 h). Two replicates of each macroalgal sample were prepared for analysis.

Isotopic analysis. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of all samples were determined using a continuous flow Isotope Ratio Mass Spectrometer (IRMS), after sample combustion in on-line Carlo-Erba preparation units calibrated relative to the standards of air and the International Atomic Energy reference material of PDB (PeeDee Belemnite). Beet sugar, air and gelatine (Merck) were used as standards, calibrated against multiple International Atomic Energy reference materials. Results are expressed in standard delta notation, $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where X is the element in question and R is the ratio of heavy to light isotope. Precision of replicate determinations was $\pm 0.05\text{‰}$ for both carbon and nitrogen.

Data analysis. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mussel signatures were analyzed using a k-means cluster analysis based on Euclidian distances, validated using a discriminant function analysis (DFA). All analyses were performed using Statistica v7 (StatSoft 2004). Carbon and nitrogen contour graphs were created using Ocean Data View 3 (Schlitzer; available at www.awi-bremerhaven.de/GEO/ODV). A linear 2-source mixing model (Bustamante & Branch 1996) was used to determine the percentage of organic carbon and nitrogen contributed to mussel diet by nearshore SPM:

$$\% \text{ Isotope} = [(d_{\text{mussel}} - d_{\text{offshore}} - I) / (d_{\text{nearshore}} - d_{\text{offshore}})] \times 100$$

where *I* is the average fractionation of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ per trophic level and *d* is the isotopic ratio of the sample. In this study the average fractionation values of 1‰ for $\delta^{13}\text{C}$ (DeNiro & Epstein 1978, Fry & Sherr 1984) and 3 to 4‰ for $\delta^{15}\text{N}$ (Fry & Sherr 1984, Minagawa & Wada 1984) were used.

RESULTS

Suspended particulate matter

SPM showed highly enriched $\delta^{15}\text{N}$ ratios ($>10.0\text{‰}$) between 0 and 4 km at Port Alfred and Mossel Bay in 2003, but otherwise lacked clear geographic, spatial or

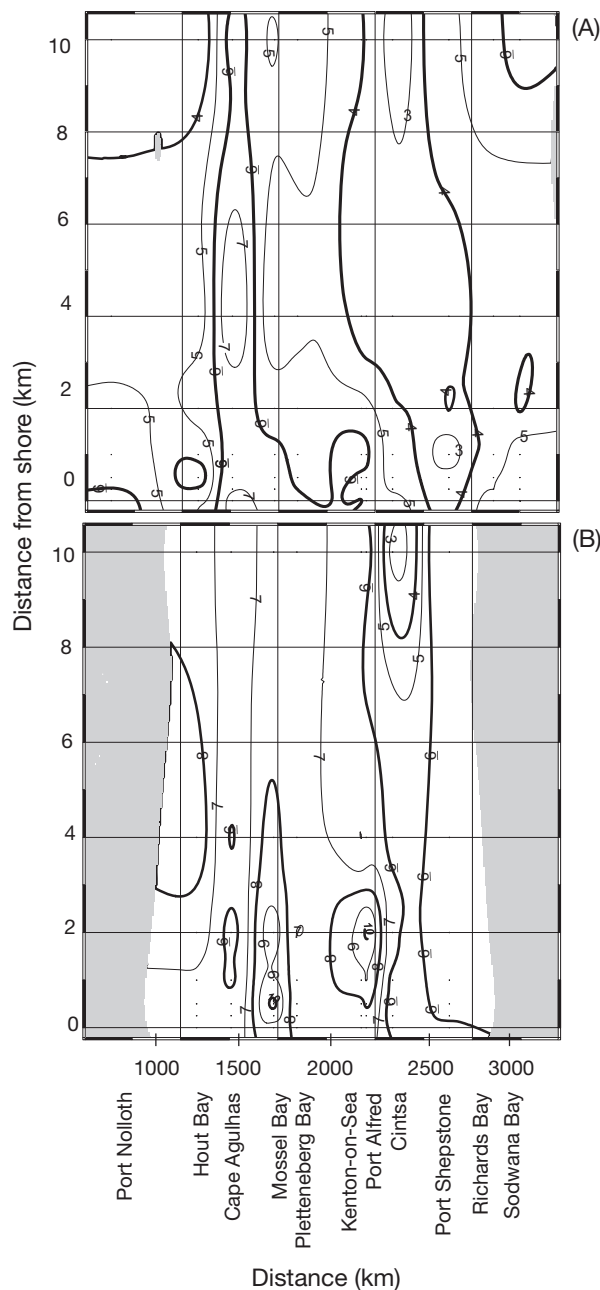


Fig. 2. Contour graphs of $\delta^{15}\text{N}$ signatures from suspended particulate matter (SPM) transects in (A) winter 2004 and (B) summer 2003 (graph excludes Walvis Bay as only 2 points in the transect fell between 0 and 10 km). Distance is in km along the coastline from Walvis Bay, Namibia. Shaded areas: no data available

temporal trends (Fig. 2A,B). In contrast, $\delta^{13}\text{C}$ signatures exhibited spatial trends of depletion from nearshore to offshore water along the entire coastline (Walvis Bay is excluded as only 2 samples fell between the 0 and 10 km range). Clear depletion patterns were displayed at 5 sites in all years (Port Shepstone, Kenton-on-Sea, Mossel Bay, Cape Agulhas and Port Nolloth; Fig. 3A [not all sites included]), 3 sites showed patterns that were less clear but conformed to the general depletion trend in at least 1 of 3 yr (Richards Bay, Plettenberg Bay and Hout Bay; Fig. 3B [not all sites included]) and 3 sites demonstrated enrichments on some occasions between 4 and 10 km offshore (Sodwana Bay, Cintsa and Port Alfred; Fig. 4). Values for nearshore (intertidal, 0 km) water ranged from highly enriched carbon values of $-6.99 \pm 0.81\text{‰}$ (Cape Agulhas) to much more depleted values of $-19.4 \pm 0.01\text{‰}$ (Sodwana Bay), with an average of $-15.4 \pm 3.06\text{‰}$, while offshore (10 km) waters displayed less variation, ranging between $-16.98 \pm 0.25\text{‰}$ (Hout Bay) and $-23.58 \pm 0.09\text{‰}$ (Port Nolloth), with an average of $-20.36 \pm 1.84\text{‰}$. $\delta^{13}\text{C}$ depletion curves were more enriched at 5 sites (Richards Bay, Cintsa, Port Alfred, Plettenberg Bay and Hout Bay) in 2003 than in other years, ranging from a 2 to 4‰ increase depending on site and sample, suggesting overall enrichment in austral summer but with no obvious geographic trends.

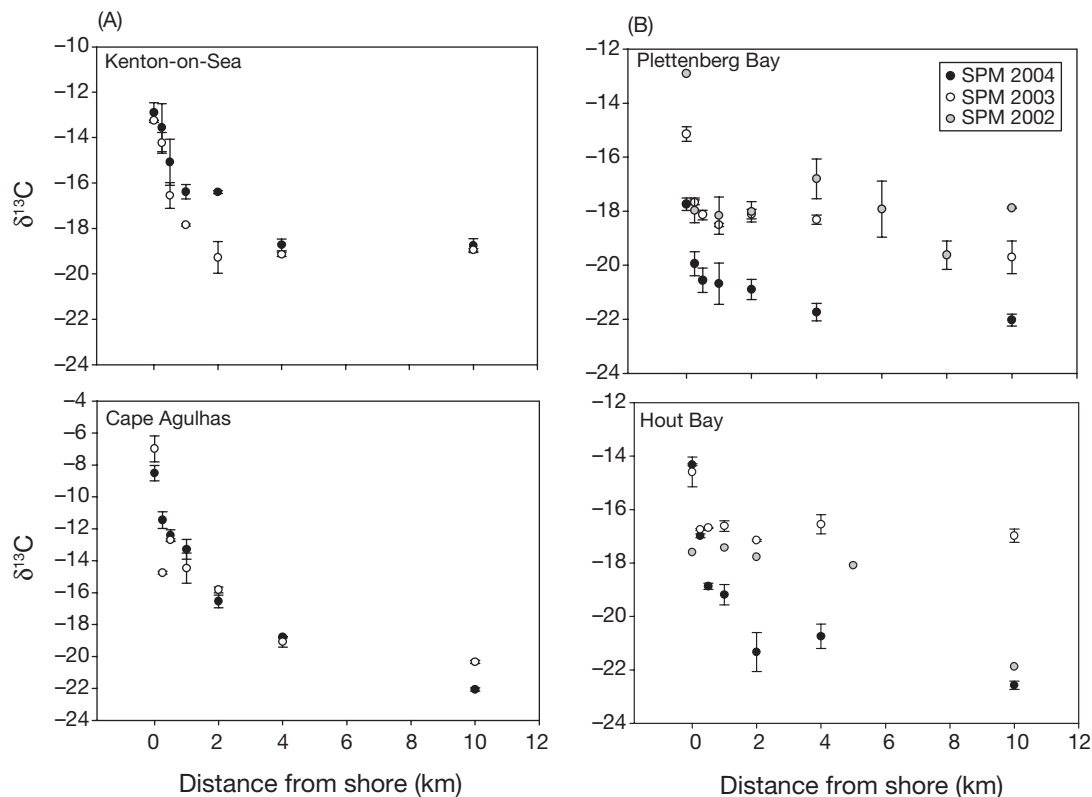


Fig. 3. (A) Examples of nearshore–offshore $\delta^{13}\text{C}$ gradients from sample sites along the coastline showing clear depletion trends; (B) as (A) but showing weaker depletion trends. Values are mean \pm SD

Nearshore SPM demonstrated an overall geographic enrichment in $\delta^{13}\text{C}$ from the east coast (Sodwana Bay) with a mean $\delta^{13}\text{C}$ of $-18.7 \pm 0.67\text{‰}$, to the south coast (Cape Agulhas) with a mean $\delta^{13}\text{C}$ of $-7.8 \pm 1.08\text{‰}$, while offshore water remained relatively constant at an average of $-20.36 \pm 1.84\text{‰}$ (Fig. 5).

Along the coastline, 6 sites (Sodwana Bay, Richards Bay, Cintsa, Plettenberg Bay, Mossel Bay, Port Nolloth) showed nearshore SPM $\delta^{13}\text{C}$ values lower than the midpoint between nearshore and offshore signatures ($< -17.88\text{‰}$). The remaining 5 sites showed nearshore SPM values higher than the midpoint ($> -17.88\text{‰}$) and these pockets of enriched nearshore SPM extended out to a maximum of 2 km from the shoreline (Fig. 6A,B).

Macroalgae

Macroalgal signatures showed no consistent geographic or temporal trends in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, with erratic enrichments and depletions in consecutive years, and most macroalgae showed large ranges in both carbon and nitrogen. Both *Ulva* sp. and *Gelidium pristoides*, for example, demonstrated large scale differences along the coastline ranging between $\delta^{13}\text{C}$ values of -10.89 to -17.83‰ and -11.49 to -15.66‰ and $\delta^{15}\text{N}$ values of 4.39 to 7.20‰ and 5.85 to 7.69‰ , respec-

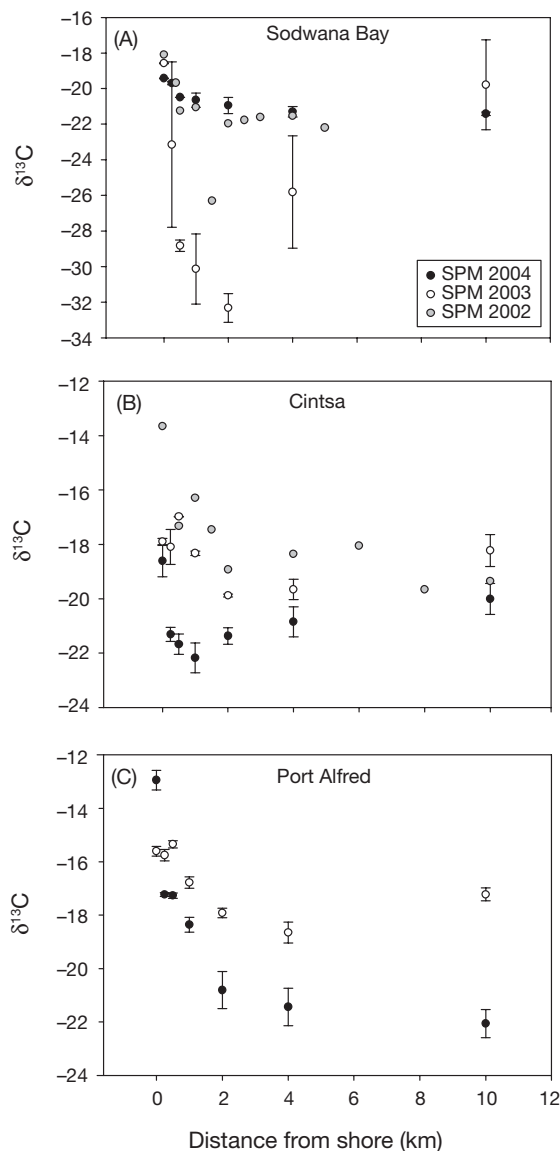


Fig. 4. Deviations from the overall nearshore to offshore $\delta^{13}\text{C}$ trends of suspended particulate matter (SPM). Values are means \pm SD

tively. Consequently, macroalgal isotopic ratios could not be related to either mussel diet or nearshore SPM and the data are therefore not presented.

Mussels

Although many sites showed considerable variation in $\delta^{13}\text{C}$ values of mussel tissue between sampling occasions, there were no consistent seasonal or interannual trends among sites. There were, however, distinct geographic patterns, allowing the k-means cluster analysis to classify the mussels into 4 isotopic groups

that represent animals collected from the east, south-east, south-west and west coasts (Fig. 7). Subsequent DFA showed that these clusters could be identified by their signatures alone with 97 to 98% accuracy. The east coast group (group A) was characterized by low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$: -17.63 to -16.56‰ ; $\delta^{15}\text{N}$: 6.31 to 7.78‰), the south-east coast group (group B) by intermediate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$: -16.19 to -15.37‰ ; $\delta^{15}\text{N}$: 6.73 to 8.17‰) and the south-west (group C) and west coasts (group D) ($\delta^{13}\text{C}$: -15.85 to -14.45‰ ; $\delta^{15}\text{N}$: 8.35 to 9.033 and $\delta^{13}\text{C}$: -17.50 to -16.78‰ ; $\delta^{15}\text{N}$: 8.85 to 9.6‰ , respectively) by their high $\delta^{15}\text{N}$ values (Fig. 7). Two exceptions were Site 11 (S11: Hout Bay), which fell into the south-east grouping in all 3 years, and Site 5 (S5: Cintsa) which was grouped with group A in 2002 and 2003, but with group B during 2004. From the east to the south coast, both mussel carbon ($r^2 = 0.71$, $p < 0.01$) and nitrogen ($r^2 = 0.69$, $p < 0.01$) ratios demonstrated enrichment (excluding all sites west of Cape Agulhas) (Fig. 8). Although it was not possible to associate near-offshore carbon values with distinct sources of production, links were found between isotopic values of nearshore water and macroalgae, and offshore water and phytoplankton. The linear mixing model revealed that mussels demonstrated more than a 50% dependence on nearshore water for their organic carbon and nitrogen, at 8 and 7 out of 11 sites respectively. In both cases, 2 locations (Cintsa and Hout Bay) showed strong temporal variation (Fig. 9).

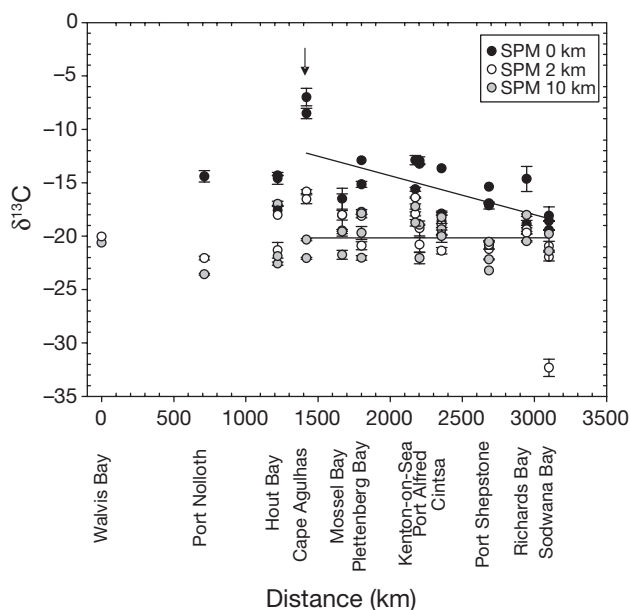


Fig. 5. $\delta^{13}\text{C}$ of suspended particulate matter (SPM) along the coastline. Regression excludes values to the west of Cape Agulhas, i.e. to the left of the arrow. Distance is in km along the coastline from Walvis Bay, Namibia. Values are means \pm SD and are presented separately for each yr

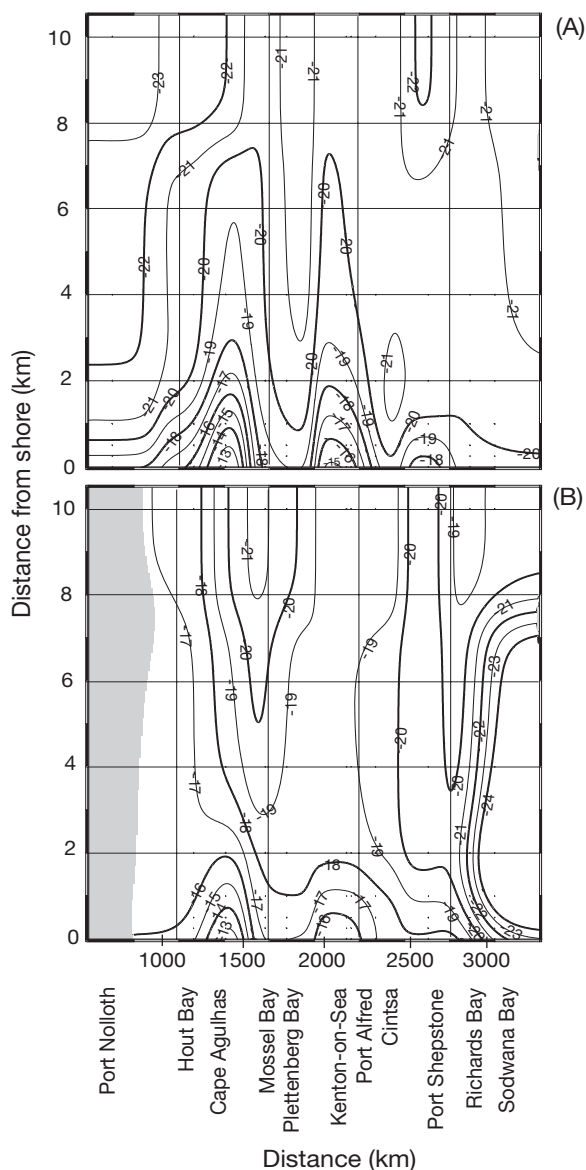


Fig. 6. Contour graphs of $\delta^{13}\text{C}$ signatures from suspended particulate matter (SPM) transects in (A) winter 2004 and (B) summer 2003 (graph excludes Walvis Bay as only 2 points in the transect fell between 0 and 10 km). Distance is in km along the coastline from Walvis Bay, Namibia. Shaded areas: no data available

DISCUSSION

Spatial and biogeographic gradients

Spatial patterns in carbon signatures reflect patterns in the distribution or signatures of primary producers, which in turn are likely to reflect environmental gradients, and recent investigations have also shown variation in carbon isotopes on several physical scales. These include spatial patterns within estuarine ecosys-

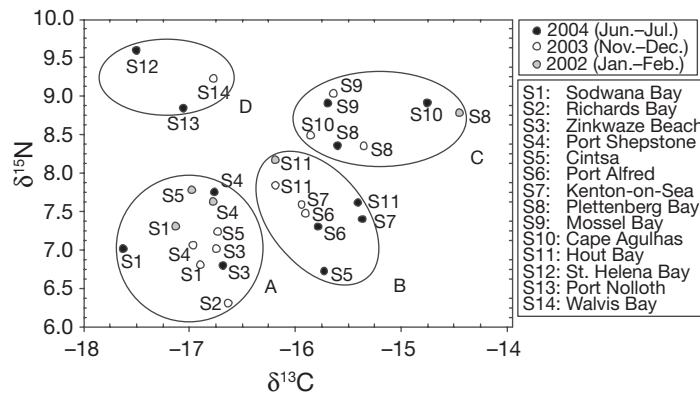


Fig. 7. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of intertidal mussels. Groupings according to k-means cluster analysis: (A) east coast, (B) south-east coast, (C) south-west coast, (D) west coast

tems (Deegan & Garritt 1997), which exhibit very strong environmental gradients, and global latitudinal trends in pinnipeds (Burton & Koch 1999, Hobson et al. 2002) and squid (Takai et al. 2000). In the present study we explored trends in carbon signature along 2 gradients. The first was a nearshore–offshore gradient likely to reflect a gradient of decreasing macrophyte influence; the second was a biogeographic gradient that reflects the influence of 2 very different oceanographic regimes, rather than a latitudinal effect.

Nearshore–offshore gradients

With few exceptions, $\delta^{13}\text{C}$ signatures of SPM became depleted with distance from shore. This trend of depletion suggests a shift from a nearshore carbon supply to one more representative of a pelagic carbon source. Although it was not possible to link these $\delta^{13}\text{C}$ values directly to distinct sources of production, the nearshore (0 km) signatures, with an average of 15.4‰, fell into the range of carbon values previously reported for macroalgae (Smith & Epstein 1971, Bustamante & Branch 1996), and are presumably representative of a nearshore primary production signature. Nearshore water consists of a mixture of phytoplankton, organic and inorganic debris (Stuart 1982, Bustamante & Branch 1996) and is likely dominated by macroalgal detritus (Mann 1988, Duggins et al. 1989, Bustamante & Branch 1996, Vizzini et al. 2002). Although nearshore carbon values fell within the range of algal signatures found along the coast in this study, the two could not be directly related to one another. In retrospect, this is not surprising, as SPM samples are unlikely to have had the same algal composition as the seaweeds subsampled from the intertidal zone. Offshore (10 km) signatures (average: -20.36‰) fell into the $\delta^{13}\text{C}$ range previously reported for oceanic phyto-

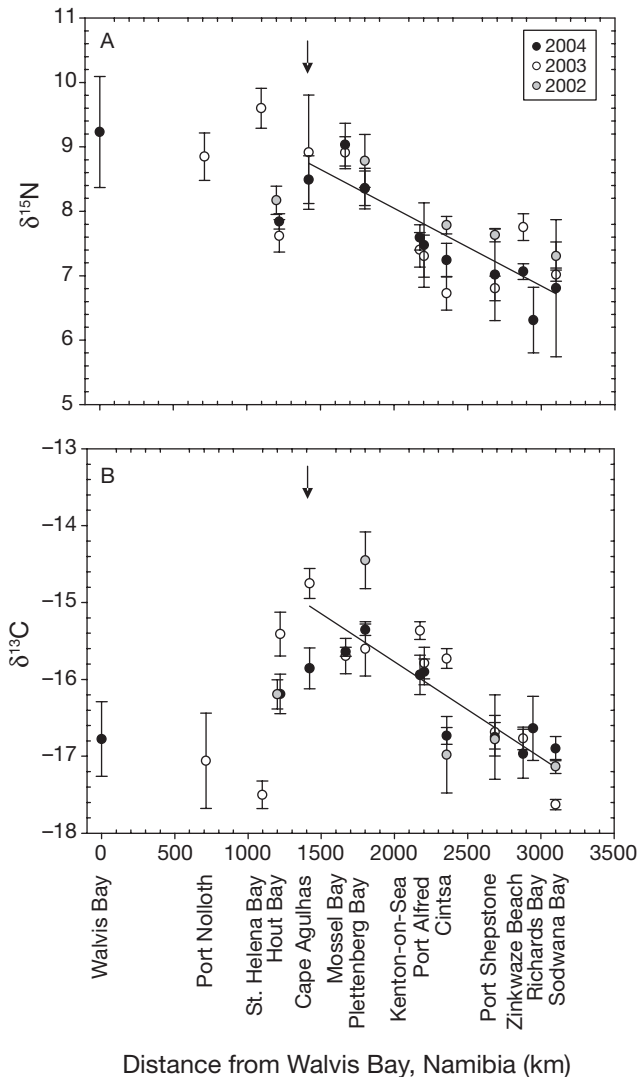


Fig. 8. (A) $\delta^{15}\text{N}$ geographic enrichment of intertidal mussels, $r^2 = 0.69$, $p < 0.01$, $y = 10.4594 - 0.0012x$; (B) $\delta^{13}\text{C}$ geographic enrichment of intertidal mussels, $r^2 = 0.71$, $p < 0.01$, $y = -13.2726 - 0.0012x$. Regression excludes values to the west of Cape Agulhas, i.e. to the left of the arrows. Values are means \pm SD

plankton (Rau et al. 1982, Fry & Sherr 1984) and appear to be typical of pelagic production, as carbon signatures at Kenton-on-Sea remain in the range of -20.00 to -21.5% as far as 50 km offshore (Kaehler unpubl.).

Although nearshore–offshore depletion was ubiquitous around the coast, the slopes of the curves varied among sites and years, suggesting not only geographic but also temporal effects on offshore depletion. Previous studies on phytoplankton (a main component of offshore SPM) show that photoperiod, temperature, light intensity and nutrient supply all serve to increase growth rates (Rau et al. 1996, Burkhardt et al. 1999), and hence the $\delta^{13}\text{C}$ signature of SPM. Studies investi-

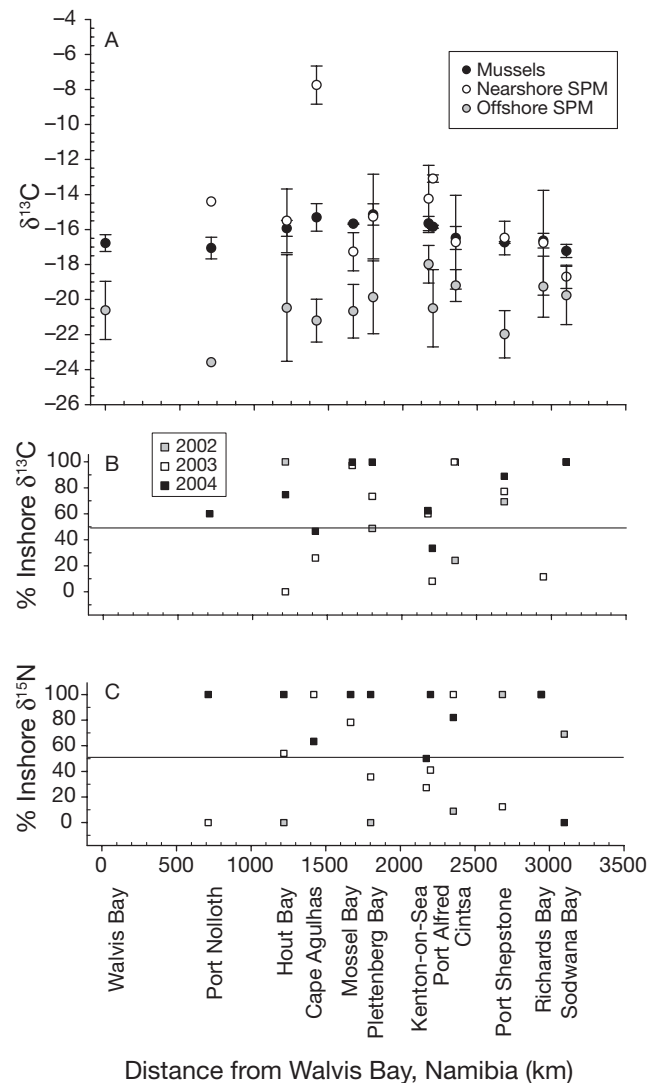


Fig. 9. (A) Isotopic relationships between mussels, nearshore and offshore suspended particulate matter (SPM) for 2002 to 2004; (B) percentage $\delta^{13}\text{C}$ contribution of nearshore SPM to mussel diet; (C) as (B) for $\delta^{15}\text{N}$

gating phytoplankton biomass in the southwest Indian Ocean using measurements of chlorophyll *a* have shown increased primary production and $\delta^{13}\text{C}$ of SPM in austral winter (Falkowski et al. 1998, Machu et al. 2005). Our transects started much farther inshore than these studies, overlapping marginally offshore, but showed austral summer (January to February 2002 and November to December 2003) depletion curves that were either more enriched, or in 4 cases, similar to carbon values found in winter (June to July 2004), suggesting a general tendency for SPM to be more enriched in austral summer than in winter. Unless seasonal differences exist in phytoplankton species composition of SPM, it is likely that the observed $\delta^{13}\text{C}$

enrichment during austral summer was due to local effects, rather than seasonal patterns in oceanic carbon. Variation in position and meandering of the Agulhas current (Goschen & Schumann 1990), extent of mixing between near and offshore waters and changes in local autochthonous or allochthonous inputs on a regional scale may have a large effect on SPM composition (Megens et al. 2001), changing $\delta^{13}\text{C}$ signatures on a daily basis.

$\delta^{13}\text{C}$ SPM inflection points, where nearshore signatures changed to more pelagic ones, generally occurred between 500 m and 1 km from the shore, but occurred further offshore at some sites (e.g. Hout Bay, Cape Agulhas, Kenton-on-Sea, Port Alfred and Port Shepstone; Fig. 6A,B). In both 2003 and 2004 Hout Bay/Cape Agulhas and Kenton-on-Sea/Port Alfred showed pockets of enriched nearshore SPM extending out to a maximum of 2 km from the shoreline and signatures only became typically pelagic (-20.0 to -21.5%) at 10 km. Port Shepstone showed a similar peak in $\delta^{13}\text{C}$, but on a much smaller scale. These data indicate that, while at 5 sites along the coastline, water with a pelagic signature may often come close inshore to introduce offshore organic carbon to the intertidal zone, the reverse may also occur, with nearshore water extending to fairly significant distances offshore. For example, Koop et al. (1982), working at Oudekraal Bay, showed that mannitol-fermenting bacteria derived from kelp beds within 100 to 200 m of the shore could be found as far as 10 km offshore. This site-specific offshore extension of enriched $\delta^{13}\text{C}$ values may represent local differences in coastal hydrography, dynamic upwelling (Lutjeharms et al. 2000), current position and limited forcing of nearshore water out to sea due to wind pressures and the circulation patterns of the Agulhas current (Goschen & Schumann 1990, Boyd & Shillington 1994).

Biogeographic gradients

$\delta^{13}\text{C}$ values for SPM of nearshore water showed an overall geographic enrichment from an average of $-18.7 \pm 0.67\%$ on the east coast to $-7.8 \pm 1.08\%$ on the south coast, while offshore water remained relatively constant at an average of $-20.36 \pm 1.84\%$. This trend of east-south enrichment of nearshore carbon applied only to sites within the Agulhas system and excluded all sites to the west of Cape Agulhas. The remaining sites showed lower carbon values both nearshore and offshore, most likely reflecting the influence of the Benguela current and the geographic shift to a colder water and more nutrient-rich ecosystem (Emanuel et al. 1992). Nearshore carbon enrichment from east to south reflects changes in coastal hydrography. Where the continental shelf is narrow (east coast), the Agul-

has current comes close inshore (Goschen & Schumann 1990, 1994), resulting in nearshore water being well mixed with offshore water. Further south, the shelf begins to widen and the Agulhas moves offshore (Roberts 2005), weakening the mixing effect and ensuring larger carbon differences between nearshore and offshore water. The biogeographic consistency in offshore $\delta^{13}\text{C}$ indicates well mixed pelagic waters 10 km from shore along the entire coast. Overall $\delta^{13}\text{C}$ signatures seem to reflect the existence of known hydrographic features along the coast (i.e. upwelling regions, current meanders, shelf width and shelf abnormalities such as canyons) and should therefore be considered for future use in studying water mixing and coastal hydrography. Nevertheless, instantaneous SPM samples give only a snapshot in time, and may not be the best measure for determining time-integrated carbon source availability and composition.

Mussels and diet

The lack of clear temporal variation in the adductor tissue, of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggests that either adductor tissue has a slow turnover rate or that at each site, the average mussel diet is relatively constant year round. We are not aware of any direct measurements of turnover rates in adductor muscle tissue, and recognize that individual tissues contribute differentially to whole body protein turnover rates. However, Hawkins (1985) found that laboratory-measured whole body protein turnover rates in *Mytilus edulis* varied with absorption rates, reaching maximum values of 0.29 to 0.4% d^{-1} . This suggests 100% turnover rates of the order of 244 to 350 d or approximately 8 mo to 1 yr and may explain the lack of temporal variation seen in the mussel tissue. Using carbon and nitrogen signatures, mussels around the southern African shoreline could be divided into 4 groups, with a clear geographic pattern. The east coast group (A) encompassed Sodwana Bay to Cintsa; the south-east coast group (B) encompassed Port Alfred and Kenton-on-Sea; the south-west coast group (C) encompassed Plettenberg Bay to Cape Agulhas; and the west coast group (D) encompassed St. Helena Bay to Walvis Bay, Namibia. Two sites did not conform to this biogeographic pattern, the first deviation was Site 11 (S11: Hout Bay), which lies on the west coast, near the Cape of Good Hope, but fell into the south-east coast group (group B) in all years, with its $\delta^{15}\text{N}$ values lying at the group boundary in 2 out of 3 years. The reason for the inclusion of Hout Bay in group B is unknown. The second exception was Site 5 (S5: Cintsa) which showed strong $\delta^{13}\text{C}$ enrichment during austral winter, indicating a change in diet in June–July 2004. Cintsa was grouped with its geo-

graphic neighbours in group B in the winter sample (2004), but with its other neighbour, the more depleted group A, in both summer samples (2002 and 2003). This suggests that either Cinsa lies close to the boundary between the east and south coast carbon sources, or that carbon sources available to mussels in group A are more thoroughly mixed than those from group B.

Among sites, $\delta^{15}\text{N}$ exhibited geographic enrichment with a clear gradient from east to south-west, excluding all sites to the west of Cape Agulhas. This reflects the isotopic gradient from oligotrophic to eutrophic conditions, described by Saino & Hattori (1980) and Minagawa & Wada (1984). These isotopic differences are likely due to a reliance on recycled nitrogen (especially ammonia) in oligotrophic waters, which is depleted in $\delta^{15}\text{N}$ relative to the upwelled nitrate used in eutrophic systems (Miyake & Wada 1967). Mussel tissue exhibited geographic $\delta^{13}\text{C}$ enrichment from the east to the south-west coast, again excluding all locations to the west of Cape Agulhas. The west coast sites showed significant carbon depletions, mirroring the trend seen in nearshore SPM. Although a consistent fractionation value of 1.0‰ (DeNiro & Epstein 1978, Fry & Sherr 1984) was not evident between offshore or nearshore SPM and mussel tissue, the latter two show similar patterns in $\delta^{13}\text{C}$ enrichment from east to south-west coast, indicating a close overall link between them. It is unrealistic to expect time-integrated mussel tissue to reflect the instantaneous nature of the SPM sample, which is subject to constant interplay between nearshore and offshore water, varying temporally on a local scale (Goschen & Schumann 1990), and this difference in time-scale integration may mask the relationship between the two.

Mussels are unlikely to depend on a single food source, relying instead on the changing sources of carbon available in the water column, and filtering selectively (Bougrier et al. 1997, Ward et al. 1998). We hypothesized that mussels eating macroalgal detritus would reflect $\delta^{13}\text{C}$ values of the nearshore SPM, while those eating phytoplankton would have similar carbon values to offshore SPM. At 7 out of 10 sites (Walvis Bay lacked nearshore SPM values) mussel tissue showed $\delta^{13}\text{C}$ values similar to, or just above those of nearshore SPM. This indicates that mussels at these sites either fed non-selectively, and so reflected available carbon in nearshore SPM, or selected for macroalgal detritus. At the remaining 3 sites, mussel tissue had intermediate $\delta^{13}\text{C}$ values, falling between those for nearshore and offshore SPM (Fig. 9), suggesting a possible preferential selection of phytoplankton (Bougrier et al. 1997, Rouillon & Navarro 2003) from the nearshore SPM, but more likely reflecting local differences in nearshore SPM composition and available organic carbon.

The application of a linear mixing model allowed us to determine the percentage contribution of nearshore and offshore SPM to the overall $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for each mussel sample, investigating the dietary importance of nearshore versus pelagic primary production. Surprisingly, nearshore SPM accounted for over 50% of both carbon and nitrogen incorporated by mussels at all but 3 sites (for carbon) and 4 sites (for nitrogen) along the coastline (2 sites demonstrated temporal variation; Fig. 9), although there was otherwise little congruence between the two. A number of studies of variability in the $\delta^{13}\text{C}$ signatures of marine phytoplankton ascribe lower values to colder water temperatures and increased solubility of CO_2 (Arthur et al. 1985, Fry 1996), and this is supported by evidence of depleted carbon values in Antarctic plankton relative to plankton from equatorial waters (Rau et al. 1989). In the present study however, although we have no information on the composition of the phytoplankton in nearshore and offshore SPM, it is unlikely that such an effect would be caused by a steep CO_2 gradient existing on a scale of 10 km. Therefore, differences in $\delta^{13}\text{C}$ between nearshore and offshore SPM are attributed to different carbon sources in terms of phytoplankton and macroalgae. Consequently, unless nearshore (intertidal, 0 km) water contains different phytoplankton communities to water 10 km offshore, this overall reliance on nearshore primary production suggests that overall, mussels are feeding unselectively, and emphasizes the dietary importance of macroalgal detritus for mussels in the intertidal zone.

It is unrealistic to expect SPM samples to reflect a single macroalgal signature when SPM contains a variable composition of detritus from numerous seaweeds and consequently the links between mussel diet and macroalgae remain unclear. No clear, consistent relationship was obvious between living macroalgae and mussel diet or nearshore SPM. A study exploring the effects of seaweed degradation on isotopic signatures may illuminate the links between living macrophytes, mussel diet and nearshore waters and is currently being investigated (J. M. Hill & C. D. McQuaid unpubl.).

SUMMARY AND CONCLUSIONS

Overall $\delta^{13}\text{C}$ depletion trends between nearshore and offshore water were seen along the entire coastline, representing changes from nearshore carbon sources that include a component of macrophyte detritus to offshore pelagic carbon sources. Geographically, nearshore SPM became enriched moving from the east to the south coast, while offshore waters remained relatively constant, and the extent of mixing of the 2 carbon sources and the protrusion of nearshore into

offshore waters seemed to be closely related to hydrographic features or events along the coastline (i.e. shelf width, pulses, current position and upwelling cells).

Mussel tissue demonstrated geographic variation, particularly in carbon, with differences between the east, south and west coasts. Although it was difficult to relate these trends in $\delta^{13}\text{C}$ values or carbon values of near-offshore SPM with distinct sources of production, the linear mixing model revealed a high carbon and nitrogen dependence on nearshore, rather than offshore, SPM, suggesting that nearshore detritus plays a crucial role in mussel diet. This reliance on nearshore SPM is of further significance if we consider that mussels are a major component of the intertidal biota and are the prey of a wide range of species (Griffiths & Hokey 1987), playing a major part in retaining nearshore primary production that might otherwise be exported. As the importance of autochthonous primary production to intertidal filter feeders is clarified, it becomes important to focus on regional geographic differences in primary production along the southern African coastline to elucidate changes in SPM composition. Further studies into isotopic signatures of water in the Benguela current system and an investigation into the effect of degradation on macroalgal isotopic ratios may help to unravel the links between SPM and intertidal consumers.

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