



Trophic structure of benthic communities in the Cabo Frio upwelling system (southeastern Brazilian shelf): a temporal study using stable isotope analysis

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ABSTRACT: In Brazil, coastal upwelling is observed in 7 areas along the southeastern/southern region and is most pronounced near Cabo Frio, Rio de Janeiro. This region is exposed to moderate seasonal Ekman-driven upwelling that brings cold water with increased nutrient levels nearshore and is more frequent and intense during the austral spring and summer, primarily due to the prevalence of northeasterly winds. Our aim was to verify the influence of this upwelling on the benthic trophic structure of the inner and outer shelf off Cabo Frio through measurements of stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes. We identified 1 main pathway of organic matter (OM) transfer from the base to the top of the food web, as observed from the tendencies of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The isotopic signatures of benthic consumers exhibited temporal and spatial variability, with no interaction between them. As the result of a time lag, only consumers (mostly decapod carnivores) appeared to reflect the assimilation of ^{15}N -depleted and ^{13}C -enriched OM produced and deposited during strong upwelling that occurred 4 mo earlier. Therefore, the intensity and period of the upwelling phenomenon were important for detecting upwelling in benthic food webs. Lighter nitrogen and heavier carbon isotopes were found on the inner shelf. Consumers may have exploited OM of different quality on the inner and outer shelf due to differences in sediment, hydrodynamics, mineralisation and assimilation of ^{13}C -enriched microphytobenthos. Nevertheless, 4 trophic levels were estimated in the benthic communities of the continental shelf off the Cabo Frio upwelling system, independent of period or area.

KEY WORDS: Stable isotope ratios · Food web · Benthos · Continental shelf · Upwelling · Temporal variation · SE Brazil

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INTRODUCTION

The sedimentation of particulate organic matter (POM) produced in the euphotic zone supplies continental shelf bottom communities (Graf 1992). Oceanographic processes, such as upwelling or seasonal stratification and mixing, which fertilise the euphotic layer, control the rates of deposition on the sea floor (Bode et al. 2006). The assessment of the major food sources supporting benthic-demersal communities

and their pathways through communities is important for understanding the functioning of continental shelf ecosystems and for their management (Peterson 1999, Fry 2006, Michener & Kaufman 2007).

In Brazil, coastal upwelling is observed in 7 areas along the southeastern/southern region and is most pronounced near Cabo Frio, Rio de Janeiro State (23° S, 42° W; Fig. 1; Coelho-Souza et al. 2012). Both coastline geometry and oceanic bottom topography influence the magnitude of upwelling (Rodrigues &

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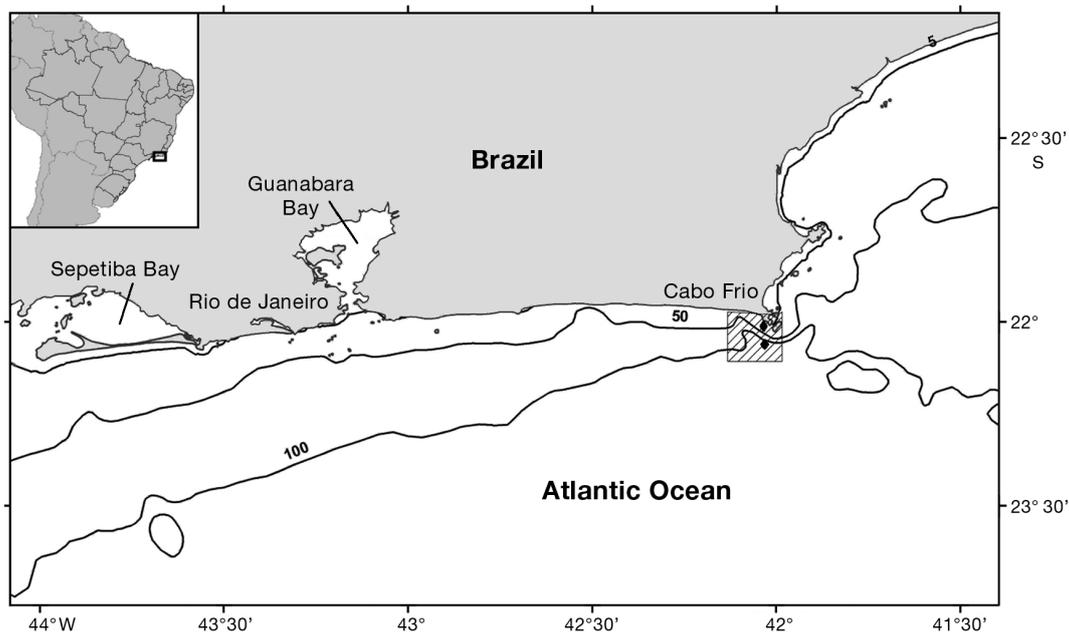


Fig. 1. Location of the 2 sampling areas (black points) on the Cabo Frio continental shelf. Inner shelf: 40 m depth, outer shelf: 100 m depth. Hatching indicates the study area of DEPROAS Project

Lorenzetti 2001). Primary productivity in this area ranges from 2 to 14 mg C m⁻³ h⁻¹, which is low compared to similar systems elsewhere (Valentin 2001).

Nevertheless, upwelling is responsible for high biological productivity in the Cabo Frio region, supporting fishery species, such as sardines and squid, that use the area for recruitment and feeding (Costa & Fernandes 1993, Matsuura 1996), with significant economic consequences since this coastal region is one of the main sardine production centres in Brazil. Despite the importance of the fishery, there is little knowledge regarding the food web structure and production base in this region, limiting appropriate fishery management measures (Coelho-Souza et al. 2012).

One approach for understanding food webs is assessment of the stable carbon and nitrogen isotope composition. Consumers are enriched in heavy isotopes compared to their diet, and this enrichment allows quantification of the relative contributions of different food types in a consumer's diet (Peterson 1999, Fry 2006). In relation to carbon, which is more conservatively transferred, differences in isotopic values within primary consumers provide evidence of specific food sources. Determination of the nitrogen isotope ratio permits the discrimination of trophic levels, with consumers usually being enriched in ¹⁵N by 2 to 5‰ in relation to their diets (Peterson & Fry 1987).

Studies of food webs at upwelling sites using stable N and C isotopes have mainly focused on the water column (Mullin et al. 1984, Libes & Deuser 1988,

Lindsay et al. 1998, Wu et al. 1999, Bode et al. 2003). In terms of δ¹⁵N, the composition of settling particles records changes in surface production in regions of the ocean where nutrients are periodically supplied to the photic zone (Holmes et al. 1998, 2002, Wu et al. 1999). In plankton and sedimenting POM, δ¹⁵N is regulated by both the supply of nitrate and the δ¹⁵N of the nitrate reservoir (Wu et al. 1999). Low δ¹⁵N values are observed for phytoplankton from nitrate-rich waters because of the preferential uptake of nitrate containing the lighter isotope (¹⁴N) (Wada & Hattori 1991). In contrast, high δ¹⁵N values may be found in plankton from nutrient-depleted waters due to the utilisation of regenerated ammonia. Low δ¹³C values in plankton are commonly attributed to the dominance of nanophytoplankton, low primary productivity and high [CO_{2(aq)}], allowing maximal photosynthetic fractionation (Wu et al. 1999). The growth and dominance of diatoms in nutrient-rich waters are likely to be responsible for enrichment of the heavy carbon isotope in POM (Fry & Wainwright 1991).

The variation of the surface-generated stable nitrogen isotope signal is mirrored in sinking particles and transferred to the sediments below (Altabet & Francois 1994), as observed in the Benguela upwelling system and on the Peruvian shelf (Libes & Deuser 1988, Holmes et al. 1998, 2002). This phenomenon was also observed in regard to the carbon signal in sedimented POM at an upwelling site off Vancouver Island, Canada (Wu et al. 1999).

The usefulness of dual stable isotope results for elucidating sources of carbon and trophic levels within the food webs of continental shelf ecosystems has been evaluated in many studies conducted since Fry (1988). Isotopic characterisations of potential food sources and benthic invertebrates in terms of carbon and nitrogen suggest that the benthic trophic web is mostly based on the organic matter in surface sediments, which interacts closely with suspended POM and sedimented organic matter (Davenport & Bax 2002, Carlier et al. 2007, Le Loc'h et al. 2008). Nearshore versus offshore variation of the nitrogen isotope signature of fishes and invertebrates may reflect alterations in productivity regimes over the Newfoundland and Labrador continental shelf (Sherwood & Rose 2005). Seasonal $\delta^{13}\text{C}$ variability in suprabenthic fauna is possibly related to primary production at the surface, with a peak in spring resulting in increased lipid storage at the base of the trophic web in the western Mediterranean (Madurell et al. 2008). Differences in regional water column productivity in the southern Chukchi Sea with respect to the isotope signature of POM are reflected in the benthic food web (Iken et al. 2010). On the North Atlantic shelf, spatial and temporal differences in the isotopic baselines of suspension and deposit feeders have been found, and higher trophic levels also follow this trend (Kürten et al. 2013). Moreover, stable isotope analysis reveals the relative importance of spatial variation in phytodetritus and microphytobenthos resources supporting benthic food webs on the inner continental shelf of Louisiana (Grippio et al. 2011). Studies in tropical marine shelf systems have mainly been conducted nearshore on hard substrates or coral reefs (revision in Mallela & Harrod 2008). In SE Brazil off Ubatuba, a subtropical region, only the marine coastal area was evaluated (Matsuura & Wada 1994, Corbisier et al. 2006).

In contrast to pelagic studies, little stable isotope-based research has been conducted on benthic communities in upwelling areas. On the coast of Galicia (NW Spain), stable isotope data indicate a dominant role of marine sources of nutrients supporting littoral benthic food webs, with a large influence of phytoplankton (Bode et al. 2006). In areas receiving river inputs and in upwelling areas, significant spatial and temporal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for benthic and pelagic organisms have been found in the Bay of Biscay, a temperate ecosystem (Chouvelon et al. 2012). In contrast, in the KwaZulu-Natal Bight in South Africa, under topographically induced upwelling, riverine total suspended solids are the dominant source of organic matter (OM) for the marine

sediments across most of the bight, representing an important source of OM for the demersal ecosystem, with oceanographic processes playing a minor role (De Lecea et al. 2013). These examples suggest that seasonal upwelling leads to strong and quite variable shifts in production sources that cascade up the food webs in the region and that stable isotope analysis offers a reliable approach for defining these changes.

The SW Atlantic Continental Shelf Ecosystem Dynamics (DEPROAS) project investigated the seasonal influence of the upwelling of the cold, nutrient-rich South Atlantic Central Water (SACW) in the Cabo Frio area off the Brazilian coast. As part of that study, we used stable isotopes to examine to what extent the temporal variation of the upwelling alters the trophodynamics of the benthic food web off Cabo Frio, focusing on the potential differences between the inner and outer shelves.

MATERIALS AND METHODS

Study area

The study area is situated over the inner (~40 m isobath) and outer shelf (~100 m isobath) off Cabo Frio, east of Rio de Janeiro State (~22° 58.5' S, 42° 03.3' W and 23° 04.5' S, 42° 00.9' W, respectively, Fig. 1), in the Southeastern Brazilian Bight (SEBB). This area is characterised by a relatively narrow shelf (ca. 50 km in length), where the 50 and 100 m depth lines are close to shore (<5 km), and shows an abrupt change in coastline direction (from NE–SW in the northern portion to E–W in the southern portion). The continental shelf, down to the 50 m isobath, exhibits a predominance of oligotrophic warm waters with low salinity and is influenced by a continental flux, referred to as Coastal Water (CW). High-nutrient colder water with low salinity, viz. the SACW, originates at the Sub-Tropical Convergence at ~30° S and flows near the bottom of the shelf break around the 200 m isobath (Castro et al. 1987). Due to climatic and topographic aspects of the local coast, there is a seasonal eutrophication effect of the upwelling of the SACW to the surface. This phenomenon is driven by Ekman forcing during the spring–summer period (Valentin et al. 1987, Campos et al. 1996). Two main austral seasons can be defined: (1) spring–summer (September to April), when the tropical maritime anticyclone becomes established and the prevailing E–NE winds are favourable to upwelling, and (2) autumn–winter (June to August), when there are frequent passages of colder polar fronts and rapid suc-

cession of changing wind cycles that are unfavourable to upwelling (Valentin et al. 1987). Upwelling events are activated whenever upwelling winds are favourable and are not restricted to summer months (Matsuura 1986).

Dissolved inorganic nitrogen (DIN) is the main limiting nutrient ($<1 \mu\text{M}$), but phosphate and, to a lesser degree, iron and molybdenum are also important in the regulation of phytoplankton biomass growth (Gonzalez-Rodriguez 1991). When the cold water reaches the surface in the coastal segment, the highest nitrate and phosphate concentrations are observed ($>10 \mu\text{M}$ and $>0.5 \mu\text{M}$, respectively), which occur below the thermocline ($<18^\circ\text{C}$) (Valentin et al. 1987). Chl *a* concentrations reported in the main upwelling area vary from 0.5 to 6.0 mg m^{-3} , with a high of 21 mg m^{-3} being recorded during a microalgal bloom (Gonzalez-Rodriguez et al. 1992).

Benthic communities

Previous studies conducted on the Cabo Frio shelf revealed that the benthic assemblages are spatially structured along a depth/sediment gradient, with the 45 m isobath representing a transition zone for bivalves (Soares-Gomes & Fernandes 2005), anomurans (Gama & Fernandes 1994), echinoderms (Ventura & Fernandes 1995) and benthic and demersal fishes (Fagundes-Netto & Gaelzer 1991). The macrofaunal species composition differs between the inner and outer shelf and shows temporal changes due to the input of organic matter to the sea floor (Gomes 2006). The impact of the SACW on the inner shelf also leads to a change in the megabenthic community, with high dominance of benthic carnivores, such as the crab *Achelous spinicarpus* and the sea star *Astropecten brasiliensis*, both of which account for most of the megabenthos biomass (De Leo & Pires-Vanin 2006).

Sample collection and processing

Because of oceanographic and community differences, we analysed the benthos separately on the inner (IS) and outer (OS) shelf. Samples were collected in summer (S1) and winter (W1) 2001 (February and July, respectively) and summer 2002 (S2, February) on board the RV 'Prof. W. Besnard' of the University of São Paulo. The sampling stations were located across-shelf above the IS and OS, around depths of 40 and 100 m (Fig. 1).

Sampling

Water samples from the surface layer (above the thermocline) and close to the bottom (below the thermocline) and at the thermocline (only on the OS) were collected in Niskin bottles. The depth of the thermocline was verified using a CTD probe. Suspended particulate matter (SPM) was obtained by filtering seawater samples on pre-combusted (500°C , 2 h) glass fibre filters (GF/F, nominal pore size $0.7 \mu\text{m}$) and subsequently stored frozen at -20°C .

Zooplankton were collected through vertical tows of ring nets with a closer ($300 \mu\text{m}$ net) above and below the thermocline, on the IS and OS, as well as in the thermocline zone on the OS. Zooplankton samples were placed in filtered seawater for 6 h to allow gut clearance, then filtered on previously combusted GF/F (nominal pore size $0.7 \mu\text{m}$) and preserved frozen at -20°C .

Sediment was sampled with a box-corer and a van Veen grab, then washed and sieved (1 mm mesh size). Small invertebrates (mainly polychaetes, molluscs, crustaceans and echinoderms) were separated and maintained alive in small buckets with filtered, aerated seawater for 24 h or more to allow gut clearance. Subsequently, the organisms were frozen, either individually or with species being pooled.

Megabenthic invertebrates, fishes and cephalopods were collected with an otter trawl (2 to 3 tows at 2 knots for 30 min). A beam trawl was used to collect some megabenthic invertebrates. Organisms were sorted, identified and frozen in plastic bags at -20°C .

Bulk surface sediment samples were obtained from the top layer of a box-corer and stored frozen prior to freeze-drying. Terrestrial plant detritus and macroalgae collected by trawling were rinsed with distilled water and stored at -20°C .

Laboratory processing

Muscle tissue was collected from crustacean decapods, molluscs and fishes. Whole individuals of echinoderms and small invertebrate species (polychaetes, sipunculans, echinoderms, amphipods) were processed when dissection was not possible. Tissue samples were washed carefully with distilled water and stored individually frozen, or as composite samples for small invertebrates. All samples were freeze-dried at -60°C for 24 to 48 h. Each sample was ground into a fine powder using a mortar and a pestle and stored dried.

Invertebrates with carbonates on their carapaces (small crustaceans, echinoderms) and sediment samples were treated with concentrated (12 M) HCl fumes in a desiccator to remove inorganic carbonates (Harris et al. 2001). Samples for $\delta^{15}\text{N}$ were analysed before decalcification, since this process negatively affects $\delta^{15}\text{N}$ (Jacob et al. 2005). SPM and zooplankton samples were not acidified. Because of high calcium carbonate content (>40%), most of the obtained sediment C isotopic results of the samples from the shelf were not acceptable. Lipid contents, which may interfere in the measurement of $\delta^{13}\text{C}$ values in tissues, were not extracted prior to analysis, as the great majority of the collected benthic consumers presented a low lipid content (C:N < 4.0) (Post et al. 2007). Removal of lipids can potentially alter $\delta^{15}\text{N}$ values (Mintenbeck et al. 2008, Boecklen et al. 2011). Powdered samples were weighed out according to the sample type (2.0 mg dry weight for animals and plants and 8.0 mg dry weight for sediments and glass filters) and stored in tin capsules for isotope analyses.

Stable isotope measurements

The abundance of natural carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes (SIs) was measured using a continuous flow isotope mass spectrometer (Europa Hydra 20/20) coupled with an elemental analyser at the Stable Isotope Facility of the University of California, Davis, CA, USA. The standard reference material was Pee Dee Belemnite (PDB) for $\delta^{13}\text{C}$ and atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$. An internal standard was included after every 12th sample, and the analytical precision based on the obtained standard deviation was 0.10 for carbon and 0.20 for nitrogen.

SI ratios are conventionally presented as the deviation from a standard material in parts per thousand (‰), as follows: $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

The trophic level (TL) of consumers was estimated using the following formula:

$$\text{TL} = [(\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{primary consumer}})/3.4] + 2$$

where 3.4‰ is the assumed ${}^{15}\text{N}$ enrichment factor between one trophic level and the next (Minagawa & Wada 1984, Post 2002). For trophic level estimates, the mean $\delta^{15}\text{N}$ value for primary consumer suspension feeders (bivalves and/or Ampeliscidae amphipods) from each area and period was used as the baseline reference (Vander Zanden & Rasmussen 2001), since they present a greater longevity and reflect a longer mean time of assimilation than phytoplankton (Mina-

gawa & Wada 1984). A value of 2 in the formula represents the trophic level of a primary consumer.

Each species/family of macrofauna and megafauna was assigned to one of the following functional feeding groups: suspension feeder, surface deposit feeder, subsurface deposit feeder, omnivore, or carnivore and/or scavenger (references in Corbisier 2006). The functional feeding groups of close taxonomical groups were used when no information was available.

We tested the temporal and spatial (IS versus OS) effect on $\delta^{15}\text{N}$ of the organisms by analysis of covariance (ANCOVA), using the General Linear Model routine of Minitab® 16 software. The model included the $\delta^{15}\text{N}$ as the independent variable, $\delta^{13}\text{C}$ values as covariates and periods and areas as fixed factors. Analysis of $\delta^{13}\text{C}$ values with $\delta^{15}\text{N}$ as the covariate was also conducted. Pairwise comparisons among samples were performed with Tukey 95% simultaneous confidence intervals. The dataset included individual samples of all benthic organisms (except fishes), and zooplankton were used as the baseline for the food webs. Spatial and temporal variations of isotope signatures in trophic groups were tested for statistical differences using 1-way ANOVA with area (IS and OS) and period (S1, W1 and S2) as factors, with post hoc comparisons (Tukey HSD). Only zooplankton, surface deposit feeders and decapod carnivores (excluding *Dardanus insignis*) were compared, as 3 data from each trophic group were not always available for multiple comparisons.

RESULTS

Hydrographic conditions and sediment type

The DEPROAS Project provided substantial background information on the oceanographic conditions during the study period (Silveira et al. 2002). Hydrographic data from a mesoscale cruise conducted a week before the first sampling showed that the SACW thermal front lasted for 2 d (February 2001). During winter 2001, the front retreated to the OS. A higher near-bottom temperature (22.5°C) was observed for the 40 m isobath station, indicating the presence of CW within the coastal zone. During summer 2002, the thermal front was located on the bottom of the IS, showing a temperature of ~14°C at Cabo Frio (Table 1). Upwelling occurred 15 d before the cruise in summer 2001 and a month before the cruise in winter 2001. In contrast, during summer 2002, CW was found in the upper layer of water over the IS, and oligotrophic conditions prevailed (Kampel 2003, Sum-

ida et al. 2005). In summer 2001, nitrate and phosphate levels were higher than in winter 2001 (Kampel 2003) (summarized in Table 1). This variation in the oceanographic regime allowed us to compare the effects of pelagic enrichment on the benthic food webs.

The sediments consisted of well-sorted fine sand on the IS and poorly sorted fine-to-median silt on the OS off Cabo Frio. The concentrations of both chl *a* and phaeopigments in the first 2 cm of the sediments were higher at the IS and OS stations in summer 2001 than in winter 2001 (2.4 to 6.6-fold greater; Table 1).

Sources of OM

The potential food sources differed in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The mean $\delta^{13}\text{C}$ values of SPM ranged from -24.17 to -20.26‰ and the $\delta^{15}\text{N}$ values from 5.24 to 8.55‰ for the IS and OS off Cabo Frio (Table 2).

Detached macrophytes were found only on the IS. Their $\delta^{13}\text{C}$ values ranged from -15.66 to -14.31‰ for macroalgae in the summer, and their $\delta^{15}\text{N}$ values from 5.38 to 7.67‰ (Table 2). The sea-grass *Halodule* sp. presented the highest $\delta^{13}\text{C}$ value (-13.50‰) and the lowest $\delta^{15}\text{N}$ value (4.16‰).

Only 2 $\delta^{13}\text{C}$ values for surface sediment particulate matter (SSPM) were obtained on the IS (-21.95 and -20.78‰). No $\delta^{13}\text{C}$ isotopic signatures were obtained on the OS due to the high percentage of calcium carbonates. The $\delta^{15}\text{N}$ values varied from 7.90 to 9.39‰ on the IS and from 5.33 to 10.46‰ on the OS (Table 2).

Consumers

Pelagic

Zooplankton were enriched in ^{13}C in relation to SPM. The $\delta^{13}\text{C}$ mean values for zooplankton ranged from

Table 1. Temperature, salinity and water mass at the bottom, nutrients in the water column and sediment characteristics of the areas sampled in the 3 study periods. IS: inner shelf; OS: outer shelf; CW: coastal water; SACW: South Atlantic Central Water

	Summer 2001	Winter 2001	Summer 2002
Bottom water			
Temperature (°C)			
IS	18.70	22.50	13.75
OS	15.47	17.85	13.56
Salinity			
IS	35.77	35.71	35.32
OS	35.45	36.22	35.29
Water mass			
IS	SACW	CW	SACW
OS	SACW	SACW	SACW
Water column^a (min.–max.)			
Chl <i>a</i> (mg m ⁻³)	0.01–0.96	0.09–2.15	–
Primary production (g C m ⁻² d ⁻¹)	0.39–1.48	0.11–1.91	–
NH ₄ ⁺ (μM)	<0.05–4.01	<0.05–3.20	–
NO ₂ ⁻ (μM)	<0.05–1.11	<0.05–0.13	–
NO ₃ ⁻ (μM)	<0.05–11.93	<0.05–2.9	–
PO ₄ ³⁻ (μM)	<0.03–6.53	<0.3–3.45	–
Sediment^b			
IS	Well sorted fine sand		–
OS	Poorly sorted fine to median silt		–
Phytoplankton^b (mean ± SD)			
Chl <i>a</i> (mg m ⁻²)			
IS	24.8 ± 5.4	8.4 ± 4.0	–
OS	51.9 ± 37.6	9.0 ± 0.3	–
Phaeopigments (mg m ⁻²)			
IS	55.1 ± 34.6	8.4 ± 7.2	–
OS	144.9 ± 75.4	59.8 ± 11.5	–

^aKampel (2003); ^bCorbisier (2006)

Table 2. Mean ± SD $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values for potential food sources (n: number of samples analysed; SPM: suspended particulate matter; SSPM: surface sediment particulate matter; IS: inner shelf; OS: outer shelf; S1: summer 2001; W1: winter 2001; S2: summer 2002; Unident.: unidentified) on the Cabo Frio continental shelf

Food sources	Area	Period	n	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$
Marine SPM	IS	S1	6	-21.30 ± 1.54	6	5.24 ± 1.32
		W1	2	-22.32 ± 0.10	1	8.55
		S2	4	-20.26 ± 0.28	4	5.98 ± 0.93
	OS	S1	6	-20.79 ± 0.88	3	7.68 ± 1.96
		W1	3	-24.17 ± 1.48	3	5.82 ± 1.80
		S2	5	-21.06 ± 0.76	5	6.52 ± 1.18
Macrophytes	IS	S2	2	-15.66 ± 0.23	2	6.77 ± 1.13
		S1	1	-14.50	1	7.67
		S2	1	-15.66	1	5.81
	Unident. Rhodophyta	S1	1	-14.49	1	6.98
		S2	1	-14.31	1	5.38
		W1	1	-13.50	1	4.16
Sediment (SSPM)	IS	S1	–	–	–	–
		W1	1	-21.95	2	9.39 ± 0.28
		S2	1	-20.78	3	7.90 ± 3.23
	OS	S1	–	–	1	10.46
		W1	–	–	3	5.64 ± 0.23
		S2	–	–	3	5.33 ± 1.95

–20.71 to –19.17‰, while the $\delta^{15}\text{N}$ values ranged from 6.40 to 9.59‰ (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m512p023_supp.pdf).

Benthic

A total of 66 different consumers (49 and 36 for the IS and OS, respectively) were analysed to determine the SI ratios of the benthic communities (Tables S1 & S2 in the Supplement). They were the most abundant species during sampling and represent the benthic fauna of the shelf. They exhibited a wide range of SI ratios, presenting $\delta^{13}\text{C}$ values of –20.21‰ (Ampeliscidae amphipod) to –12.53‰ (sea star *Astropecten brasiliensis*) and $\delta^{15}\text{N}$ values of 6.27‰ (surface deposit-feeding echinuran) to 14.50‰ (the carnivore anomuran *Dardanus insignis*). Sea stars displayed more enriched $\delta^{13}\text{C}$ values overall, most likely because the applied acidification was insufficient to remove all carbonates. Nevertheless, the obtained $\delta^{15}\text{N}$ values were precise, as they were determined from a separate sample.

In general, the mean values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were in agreement with the postulated trophic groups (Fig. 2, Tables S1 & S2). Benthic suspension feeders presented $\delta^{13}\text{C}$ values ranging from –20.21 to –16.62‰ and $\delta^{15}\text{N}$ values between 6.33 and 9.17‰. They were represented by bivalves on the IS and the bivalve *Corbula patagonica* and Ampeliscidae amphipods on the OS. In general, they had higher $\delta^{15}\text{N}$ values on the OS (Table S2).

The $\delta^{13}\text{C}$ values of deposit feeders ranged from –21.27 to –15.19‰ on the IS and from –19.59 to –14.74‰ on the OS. The $\delta^{15}\text{N}$ values showed wider variation than suspension feeders, from 6.27 to 11.61‰ on the IS and from 7.90 to 12.75‰ on the OS. The $\delta^{15}\text{N}$ values for surface deposit feeders ranged from 6.27 to 10.85‰. The burrowers and subsurface deposit feeders (Capitellidae, Orbiniidae and Maldanidae polychaetes, amphipods) exhibited higher $\delta^{15}\text{N}$ values than the surface deposit feeders (from 8.80 to 12.75‰).

Benthic invertebrate carnivores, scavengers and omnivores ($\delta^{13}\text{C}$ values between –18.50 and –12.97‰) presented $\delta^{15}\text{N}$ values between 9.15 and 14.50‰ (except for the value of 8.08‰ obtained for a small nemertean). The highest mean $\delta^{15}\text{N}$ values (>13.00‰) observed on the IS were for the anomuran *D. insignis* and the sea stars. On the OS, more species had higher mean $\delta^{15}\text{N}$ values: the cephalopod *Octopus* spp., the gastropod *Zidona*

dufresnei, the crab *Stenocionops spinosissimus*, the anomuran *D. insignis* and the sea star *A. brasiliensis* (Table S2).

Benthic-feeding fishes (*Cynoscion guatucupa*, *C. jamaicensis*, *Merluccius hubbsi*, *Porichthys porosissimus* and *Trachurus lathami*) exhibited a narrow range of values: mean $\delta^{13}\text{C}$ from –18.63 to –17.43‰ on the OS and from –17.32 to –16.51‰ on the IS. Their mean $\delta^{15}\text{N}$ values varied from 12.08 to 14.39‰ for the IS and the OS. These fishes were less enriched in $\delta^{15}\text{N}$ in the summer (S1 and S2) than in W1.

There was a tendency toward an increase in $\delta^{15}\text{N}$ values from suspension feeders, through deposit feeders, subsurface deposit feeders, burrowers and omnivores, to carnivorous invertebrates and benthic-feeding fishes in both areas and in the 3 periods (Fig. 2). This trend was less clear for $\delta^{13}\text{C}$, although the 2 ratios had a significant correlation in both areas and periods ($p < 0.05$, Fig. 3). The communities seemed to rely mostly on one source of OM.

The benthic trophic network in Cabo Frio was composed of 4 trophic levels (Fig. 2). Depending on the trophic group, benthic invertebrates extended from trophic level 2.0 to 4.2, whereas fishes belonged to trophic levels between 3.5 and 4.3.

We found significant statistical $\delta^{15}\text{N}$ differences among samples, even after adjusting for $\delta^{13}\text{C}$ (ANCOVA, Table 3, Fig. 3). Comparing periods, on the IS the lowest $\delta^{15}\text{N}$ values of benthic consumers were found in S2, and the highest in S1. On the OS, similar temporal variation was observed, although S1 was similar to W1, and both had $\delta^{15}\text{N}$ values higher than S2. There were also significant differences between the IS and OS in each period (Fig. 3). The $\delta^{15}\text{N}$ values were always lower on the IS than on the OS; in contrast, the $\delta^{13}\text{C}$ values were higher on the IS. There was no interaction between period and area for both isotopes (Table 3).

Regarding particular trophic groups of consumers (Fig. 4), $\delta^{15}\text{N}$ values for zooplankton differed between periods ($p = 0.039$), being significantly higher on the OS in S1 than on the OS in S2; $\delta^{13}\text{C}$ values did not differ ($p = 0.372$). Surface deposit feeders differed in $\delta^{15}\text{N}$ values ($p = 0.003$), with lower values in S1 and S2 on the IS, and did not differ in $\delta^{13}\text{C}$ values ($p = 0.372$). The $\delta^{15}\text{N}$ values of carnivore decapods showed significant differences ($p < 0.001$) among periods, with lower values in S2 (IS and OS) than other areas/periods. $\delta^{13}\text{C}$ values also differed ($p < 0.001$) but not in the same way. The differences were more pronounced between IS and OS.

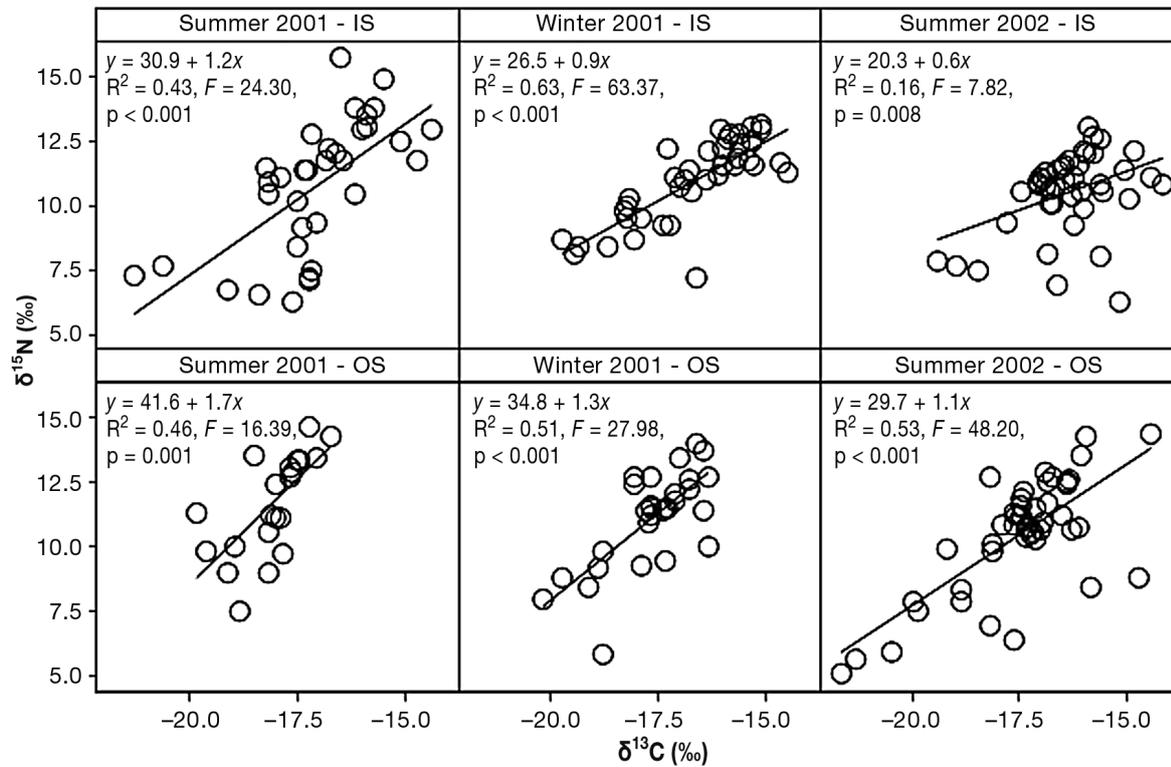


Fig. 3. Relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of benthic organisms and zooplankton according to the area and period of sampling. IS: inner shelf; OS: outer shelf. Fishes were not included

Table 3. Analyses of covariance for the effects of $\delta^{13}\text{C}$, period (S1: summer 2001, W1: winter 2001, S2: summer 2002), and area (IS: inner shelf, OS: outer shelf) on $\delta^{15}\text{N}$ signatures of consumers of the food web of Cabo Frio continental shelf. Results of $\delta^{13}\text{C}$ with $\delta^{15}\text{N}$ as covariate are also presented, as are the results of grouping information using the Tukey method and 95% confidence for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of consumers

	df	F	p	Period	Area	n	Mean $\delta^{15}\text{N}$	Grouping
Covariate				S1	OS	21	12.6	A
$\delta^{13}\text{C}$	1	158.32	0.001	W1	OS	29	11.7	A B
				S2	OS	45	10.9	B C
				S1	IS	34	10.7	B C D
Effects								
Period	2	13.13	0.001	W1	IS	40	10.5	C D
Area	1	36.03	0.001	S2	IS	43	9.8	D
Period×Area	2	1.17	0.311					
Total df	211							
	df	F	p	Period	Area	n	Mean $\delta^{13}\text{C}$	Grouping
Covariate				S2	IS	43	-16.3	A
$\delta^{15}\text{N}$	1	158.32	0.001	W1	IS	40	-16.7	A B
				S1	IS	34	-17.0	B C
				S2	OS	45	-17.4	C D
Effects								
Period	2	14.09	0.001	W1	OS	29	-17.8	D E
Area	1	74.65	0.001	S1	OS	21	-18.4	E
Period×Area	2	0.41	0.665					
Total df	211							

DISCUSSION

Potential food sources

The assessment of the transfer of autotrophic production using SIs relies on the assumption that organic sources at the base of the food web exhibit distinct isotope signatures (Peterson 1999). In the present study, the obtained $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separated potential food sources.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values recorded for the isotope ratios of SPM were similar to those found in the coastal shelf zone in the subtropical sector of the southeastern coast of Brazil, under the seasonal intrusion of SACW (-21.7 to -20.5‰ and 6.9 to 9.6‰ , respectively; Matsuura & Wada 1994). The SPM isotope values reflected the immediate processes that occurred in the water column. Despite the constant presence of SACW over the bottom of the shelf, upwelling events were vari-

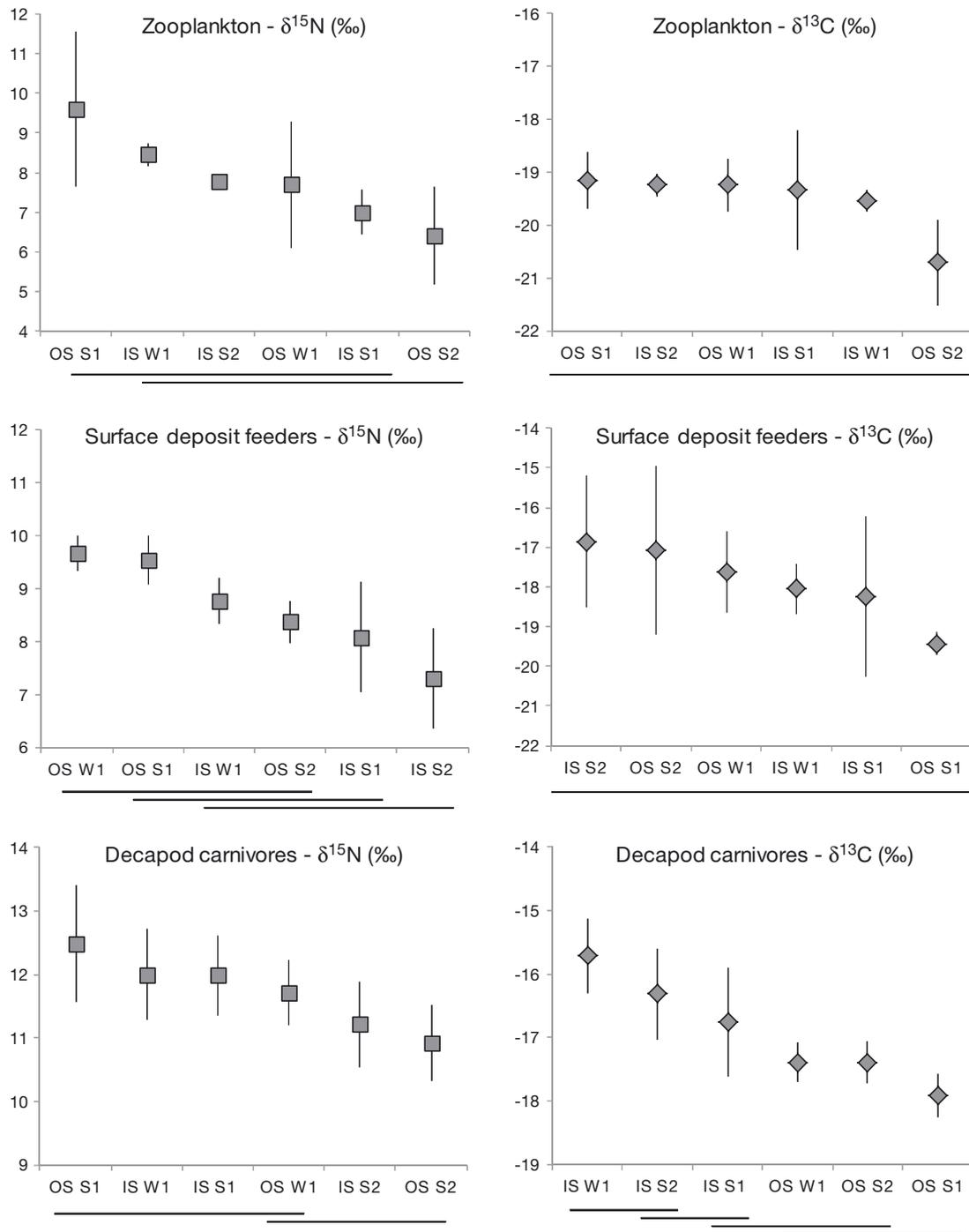


Fig. 4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (‰, mean \pm SD) of zooplankton, deposit feeders and carnivores (decapod crustaceans) and ANOVA with Tukey multiple comparisons for areas and periods ($p < 0.05$). IS: inner shelf; OS: outer shelf; S1: summer 2001; W1: winter 2001; S2: summer 2002. Horizontal black lines below the x-axes link means that are not significantly different

able during the sampling period (Kampel 2003, Sumida et al. 2005), and the SI measurements were not continuous, not reflecting these events. Consequently, they are presented only as an indication of SPM isotope values on the shelf.

The $\delta^{13}\text{C}$ values recorded for sedimented organic matter (SSPM) on the IS were in the range of those found for continental shelf sediments along the northern sector of the southeastern coast of Brazil (from -22.1 to -20.0 ‰; Matsuura & Wada 1994,

Mahiques et al. 1999, 2004). These values were close to those obtained for SPM. The $\delta^{15}\text{N}$ values varied from 5.33 to 10.46‰ off Cabo Frio and were slightly higher than those found off Ubatuba on the south-eastern continental shelf, where $\delta^{15}\text{N}$ signatures are reported to vary from 4.1 to 6.4‰ (Matsuura & Wada 1994, de Mahiques et al. 1999, Corbisier et al. 2006).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for macroalgae were in the range found in the Flamengo Inlet, Ubatuba, of -17.6 to -11.2 ‰ and 6.2 to 8.1 ‰, respectively (Corbisier et al. 2006). As expected for C_4 plants, the $\delta^{13}\text{C}$ values for the seagrass *Halodule* sp. were ^{13}C enriched, in agreement with the literature (Sackett 1989).

Pelagic consumers

The mean $\delta^{13}\text{C}$ values for zooplankton were slightly higher than those found in the coastal shelf zone of the Ubatuba region (-21.9 to -20.0 ‰) during autumn, while the $\delta^{15}\text{N}$ values were within the range observed under those conditions (7.0 to 9.5 ‰; Matsuura & Wada 1994). The isotope values of zooplankton were specific to the time and did not reflect the prevailing oceanographic conditions. They were considered in the analysis of trophic interactions only as a baseline of pelagic OM for the Cabo Frio upwelling benthic communities.

Temporal and spatial variations of the benthic food web

Food web

The range of $\delta^{13}\text{C}$ values obtained for benthic consumers was linked to SPM, zooplankton and SSPM, suggesting that the other analysed potential food sources were not utilised on the shelf off Cabo Frio.

Macrophytes were more ^{13}C enriched compared to primary consumers, and our results did not support their contribution to the basis of the food web. Additionally, although many algae, such as *Ulva* sp. and *Sargassum* sp., reach a higher biomass on rocky shores along the coast of Rio de Janeiro State during upwelling (Coelho-Souza et al. 2012), detached macroalgae were not abundant on the IS bottom during the sampling period. The macrophyte *Halodule* sp. is found along sheltered shores and within coastal lagoon systems along Rio de Janeiro State, although it does not grow on the IS because of the high hydrodynamics (Oliveira et al. 1983). There is a lack of considerable fluvial input to the Cabo Frio shelf

(Mahiques et al. 1999, 2004), and terrestrial OM inputs are generally highly ^{13}C depleted ($\delta^{13}\text{C} < -26$ ‰); thus, they do not contribute as a source of OM in the Cabo Frio shelf communities.

Suspension and surface deposit feeders could not be clearly distinguished by their isotope ratios. Slightly higher $\delta^{15}\text{N}$ values were found for surface deposit feeders, although some of these species presented values similar to the former group. The distinction of suspension feeders from surface deposit feeders according to anatomical and functional characteristics is not always easy and accurate (Arruda et al. 2003). Species of *Corbula* are classified as suspension feeders; nevertheless, their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were close to that of surface deposit feeders. In addition, it appeared that some of these primary consumers exploit the same food source, as verified by Le Loc'h et al. (2008), such as a mixture of detrital material originating from pelagic OM recently sedimented or from benthic detrital secondary production.

^{15}N enrichment of approximately 2 to 4‰ was observed among subsurface deposit feeders in relation to suspension and surface deposit feeders. Similar results have been found in other shelf systems (Davenport & Bax 2002, Darnaude et al. 2004, Carlier et al. 2007, Le Loc'h et al. 2008). Subsurface deposit feeders are primary consumers that exploit a food source resulting from the degradation of POM deep in the sediment; under anoxic conditions in the sediment, denitrification results in an increase in $\delta^{15}\text{N}$ in the remaining nitrate (Sweeney & Kaplan 1980) and may also contribute to a significant ^{15}N enrichment of POM deep in the sediment, leading to enriched food sources resulting from the degradation of sedimented particulate matter. Burrowers such as Capitellidae and Orbiniidae polychaetes or phoxocephalid amphipods are non-selective deposit feeders (Fauchald & Jumars 1979, Chiesa & Alonso 2011) and may also ingest sediment from the anoxic layer and present high $\delta^{15}\text{N}$ values.

The secondary benthic consumers were composed of carnivore species with diverse strategies, feeding on small invertebrates. On the other hand, the top benthic predators included mostly large decapod crustaceans, such as the anomuran *Dardanus insignis*, the brachyurans *Libinia spinosa*, *Persephona mediterranea* and *Stenocionops spinosissimus*, in addition to the gastropod *Zidona dufresnei* and octopods, the polychaete *Aphrodita* sp. and the sea stars *Astropecten brasiliensis* and *Luidia* spp., which were even more ^{15}N -enriched than the benthic-feeding fishes.

The demersal fishes, including the Argentine hake *Merluccius hubbsi*, the striped and Jamaica weak-

fishes *Cynoscion guatucupa* and *C. jamaicensis*, *Porichthys porosissimus* and the rough scad *Trachurus lathami*, feed on pelagic fish and crustaceans (copepods, euphasids), peracarid crustaceans, shrimp, polychaetes and/or squid in various proportions (Muto 2004, Muto & Soares 2011). The mean SI signatures were in agreement with diets based on benthopelagic prey. The highest trophic level occupied by invertebrates was similar to that found in many benthic continental shelf communities (Davenport & Bax 2002, Sherwood & Rose 2005, Carlier et al. 2007, Le Loc'h et al. 2008, Kürten et al. 2013). The estimated 4 trophic levels of the benthic communities taking the trophic position of primary consumers as baseline did not reflect the differences in species composition between areas and periods.

Temporal variation

The $\delta^{15}\text{N}$ isotope values for IS or OS benthic consumers did not differ between S1 and W1, in contrast to the lower values found in S2. $\delta^{13}\text{C}$ values varied inversely. The phytoplankton primary production seemed largely to be the main source of OM to the shelf communities, and its temporal variation should be the source of observed differences between sampling periods. These differences should be linked to processes related to oligotrophic or upwelling conditions, and may be an indication of temporal variations in processes occurring at the level of DIN utilisation and availability, potentially leading to changes in DIN $\delta^{15}\text{N}$ values that may be transmitted up the food web, as described by Sherwood & Rose (2005) and Chauvelon et al. (2012). During upwelling, a high supply of nitrate favours the uptake of ^{15}N -depleted nitrogen sources by phytoplankton (Wu et al. 1999), and low $\delta^{15}\text{N}$ values are observed for phytoplankton (Wada & Hattori 1991). In addition, low $\delta^{13}\text{C}$ values in plankton are commonly attributed to the dominance of nanophytoplankton, low primary productivity and high $[\text{CO}_{2(\text{aq})}]$, allowing maximal photosynthetic fractionation (Wu et al. 1999). The growth and dominance of diatoms in nutrient-rich waters are likely to be responsible for enrichment of the heavy carbon isotope in POM (Fry & Wainwright 1991).

Nevertheless, despite the significance of the new production input mainly during S1, and with less intensity in W1, when upwelling did occur close to sampling periods (Kampel 2003, Sumida et al. 2005, our phytodetritus data in Table 1), the expected depletion of ^{15}N in phytoplankton was not propagated within the benthic trophic web at the same

time. $\delta^{15}\text{N}$ values for benthic communities did not reflect this process obviously, and higher values of $\delta^{15}\text{N}$ for consumers were found in S1 and W1 than in S2.

In contrast, oligotrophic conditions prevailed in S2. High $\delta^{15}\text{N}$ values are found in plankton from nutrient-depleted waters due to the utilisation of regenerated ammonia (Wada & Hattori 1991) and may be transmitted up the food web. Nevertheless, the benthic consumers did not reflect this condition and had lower $\delta^{15}\text{N}$ signatures than in the other 2 periods. The most plausible explanation was the assimilation of new production that occurred in spring 2001, 4 to 5 mo before S2, when 2 high peaks of sea-surface chl *a* anomalies were recorded (Sumida et al. 2005). The SIs of benthic organisms should reflect these previous conditions of spring production, as found for suprabenthic fauna isotope signatures after the main peak of spring primary production at the surface in the western Mediterranean (Madurell et al. 2008). Although biomass deposited after a change in diet will reflect the isotope composition of the new food, the relationship between diet and SI ratios in consumer tissues is not always direct and may be subjected to variability produced by differences in assimilation, fractionation among tissues and turnover rates of tissues (Suring & Wing 2009). Benthic invertebrates most likely displayed a time lag in reflecting those previous upwelling conditions probably because of the turnover rate of tissues (Tieszen et al. 1983, Bosley et al. 2002, Lorrain et al. 2002). Muscle tissue reflects a long-term dietary history and thus integrates nutrient sources more consistently (Tieszen et al. 1983, Fantle et al. 1999, Lorrain et al. 2002, Sweeting et al. 2005). The isotopic turnover rate is a combination of isotopic dilution due to growth and replacement by metabolic processes (Fry & Arnold 1982). Young, rapidly growing organisms will reach equilibrium relatively quickly, potentially losing their initial signature within a short time, while older or slower-growing organisms will take longer (Fry & Arnold 1982, Hesslein et al. 1993). The metabolic replacement rate in fish is slow (Hesslein et al. 1993, MacAvoy et al. 2001), but may be somewhat faster in crustaceans (Frazer et al. 1997, Schmidt et al. 2003). Diet-switch experiments endorse that the isotopic turnover of consumers frequently lags the isotopic turnover of their diets. The majority of studies of isotopic turnover rates in ectotherms have been conducted with small, fast-growing organisms in which growth was the largest component of turnover. Fry & Arnold (1982) studied small, fast-growing shrimp (doubling of weight in 8 to 23 d) which quickly

reached an isotopic equilibrium with their diet. Frazer et al. (1997) found that reared larval krill took at least 10 wk to double their initial weight and only approached the $\delta^{13}\text{C}$ isotope composition of their new food source. The turnover of somatic carbon by krill is temperature dependent and may be higher during spring/summer. Gorokhova & Hansson (1999) revealed that the dietary $\delta^{15}\text{N}$ is mirrored in the muscle tissue of mysid crustaceans after 6 to 8 wk. In contrast, red rock lobster muscle isotope turnover rates are slow, although faster than the expected half-life of 147 d (Suring & Wing 2009), but slower than that of small crustaceans. Diet-labelled microphytobenthos experiments evidence a short time lag for polychaete or bivalve assimilation, between 4 to 21 d (Middelburg et al. 2000, Gálvan et al. 2008). On the Cabo Frio shelf, surface deposit feeders were composed mainly of polychaetes, which may have a high turnover rate, and in consequence did not clearly reflect the pre-nutrient-rich conditions. Since zooplankton has a faster development, its isotope composition is more coincident with seasonal variation in production (Rolf 2000). Therefore, our results support a time lag of around 4 to 5 mo for the shelf benthic communities to reflect isotope signatures of pelagic production associated with the upwelling, mainly for the predators, represented by decapod crustaceans.

Spatial variation

Independent of temporal variation, benthic consumers were generally more ^{15}N -enriched on the OS than on the IS, and they were slightly ^{13}C -depleted. These spatial differences may be associated with processes related not only to oligotrophic or upwelling conditions, but mostly to differences in processes linked to sedimentation, mineralisation and/or quality of OM.

Several possible explanations can be raised to elucidate these results, including the difference in depth for SPM sedimentation, the higher importance of nearshore upwelling events supplying new nutrients (nitrate) in an approximately 20 m deep layer (Valentin et al. 1987), the mineralisation process of OM in different sediments and the presence of a more complex OM source pool on the IS.

Pelagic production in upwelling conditions should reach the bottom faster on the IS than on the OS, where a thermocline forms a region of accumulation of sinking phytoplankton and organic detritus (Valentin et al. 1987). This process can alter the qual-

ity of OM during sinking, by decreasing the availability of $[\text{NO}_3^-]$ due to phytoplankton utilisation and increasing of $\delta^{15}\text{N}$ of sedimenting SPM (Altabet & Francois 1994, Wu et al. 1999).

The sediments differed between the IS and OS because of the high hydrodynamics over the IS, and the mineralisation of phytodetritus can change due to the biogeochemical nature of the sediment (Franco et al. 2008). In permeable sediments, phytodetritus accumulates near the sediment surface during upwelling and is likely rapidly mineralised, leading to a fast response of the whole system. In contrast, on the OS the extended presence of OM in fine sediments results in gradual mineralisation of phytodetritus through bacterial degradation, producing ammonia that is ^{15}N enriched, which was mirrored in the benthic consumers.

It appears that a different quality of carbon source supports the benthic consumers of IS or OS. More ^{15}N -depleted recently sedimented SPM or microphytobenthos (Currin et al. 1995, Kang et al. 2003) on the IS can be assimilated by surface deposit feeders and/or resuspended and assimilated by the suspension feeders, and this source, a mixture of SPM and SSPM, which constitutes a single pool of OM, was reflected throughout the trophic web, as verified by Carrier et al. (2007) and Le Loc'h et al. (2008). Conversely, on the OS, benthic diatoms experience less ideal conditions for growth, and the first level of consumers assimilates the mineralised sedimented pelagic production or the more refractory POM; consequently, $\delta^{15}\text{N}$ signatures are higher. Similar to our results, the importance of ^{13}C -enriched microphytobenthos in the Louisiana inner continental shelf is higher to the macrofauna in more sandy sediments, where microphytobenthos are the predominant microalgal resource, and settled phytoplankton are the primary microalgal food source in muddy sediments (Grippio et al. 2011). In addition, dominance of larger carnivores, including polychaetes, is observed on the OS, which could also be responsible for the higher $\delta^{15}\text{N}$ values in this area (Gomes 2006, De Leo & Pires-Vanin 2006).

In S2, fewer differences between consumers on the IS and OS as well as a wide range of values were recorded in the SI analysis, possibly because the quality of the OM pool in that period was different from the other examined periods in both areas.

We detected a lower sediment chl *a* concentration in W1 than in S1. Sumida et al. (2005) verified that the Cabo Frio sediments showed lower concentrations of chl *a* in S2 than in W1 on the continental shelf (1.7-fold lower). In contrast, sediment microbial bio-

mass was 4 times greater in S2 than in W1, which was explained by a time lag of 4 mo after a strong upwelling event in spring 2001 (chl *a* anomaly verified by SeaWiFS satellite images).

Nearshore enrichment of the $\delta^{15}\text{N}$ signatures of benthic invertebrates in relation to the values obtained offshore (shelf edge) has been found in the Newfoundland and Labrador continental shelf food web (Sherwood & Rose 2005), in contrast to our results. This difference has also been hypothesised to be an indication of spatial variations in processes occurring at the level of DIN utilisation and availability, with a constant supply of new nutrients (i.e. nitrate) that may be associated with lower $\delta^{15}\text{N}$ signatures for producers at the shelf edge that may be transmitted up the food web. In addition to processes occurring in the ocean, enrichment of $\delta^{15}\text{N}$ in nearshore food webs may result from anthropogenic inputs, which is a condition that does not occur at Cabo Frio. In the Bay of Biscay there is also a gradient from inshore to offshore organisms, with a decrease in $\delta^{15}\text{N}$ values, which was linked to oligotrophic or upwelling conditions (Chouvelon et al. 2012).

This study evidenced the importance of considering temporal and spatial variations in the food webs under variable oceanographic conditions and linking them to isotope analysis to understand the trophodynamics of the benthic system under variable upwelling. There was one main pathway of OM transfer from the base to the top of the food web, as observed from the tendencies of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. A time lag of around 4 to 5 mo for the shelf benthic communities, reflecting isotope signatures of pelagic production associated with the upwelling, was corroborated by our results. This was more evident for the benthic top predators represented by decapod crustaceans. Spatial differences between the IS and OS may be associated with processes related mostly to differences in processes linked to sedimentation, mineralisation and/or quality of OM.

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