Aquat. Living Resour. 2025, 38, 20
© E. Janowski et al., Published by EDP Sciences 2025
https://doi.org/10.1051/alr/2025017

Aquatic Living Resources
Available online at:
www.alr-journal.org

RESEARCH ARTICLE

Seasonal changes in the diet of the bloody cockle (*Senilia senilis*) along the Sine Saloum inverse estuary

Eva Janowski[1,*], Babacar Sané[1], Fany Sardenne[1], Margaux Mathieu-Resuge[1,2], Manon Buscaglia[1], Loïc Harrault[1], Jean-Marie Munaron[1], Malick Diouf[3] and Yoann Thomas[1,*]

[1] IRD, Univ Brest, Ifremer, CNRS, LEMAR, F-29280 Plouzané, France
[2] Univ Brest, Ifremer, BEEP, F-29280 Plouzané, France
[3] Université Cheikh Anta Diop, département de biologie animale, Dakar, Sénégal

Received 8 April 2025 / Accepted 29 September 2025

Handling Editor: Pierre Boudry

Abstract – This study investigates the food sources of *Senilia senilis* along the Sine Saloum estuary during the monsoon and dry seasons by combining isotopic and lipid analysis. We analyzed the fatty acids (FA) and sterol composition of digestive glands, and the carbon and nitrogen isotopic composition of muscles from 180 individuals sampled at four stations distributed along the estuary and during both seasons. Our findings reveal a spatiotemporal structure of the diet of *S. senilis*. In the upper estuary, *S. senilis* relies probably more on bacteria and zooplankton (higher proportions of 17:0, anteiso 17:0 and 15:0, 20:1 and 22:1) than downstream, where it locally finds the most homogeneous habitat (lowest isotopic diversity). The sources of nitrogen and carbon supporting planktonic communities appear to be more heterogeneous upstream, as indicated by the greater isotopic diversity at station 2. During the dry season, *S. senilis* relies more on dinoflagellates (higher proportions of 22:6n-3 and 18:4n-3) than during monsoon. However, during the monsoon, it has a greater diversity of FA, and therefore probably of food taxa, and relies more on diatoms (higher proportions of 16:1n-7 and 20:5n-3), likely from benthic origin. Together, these results highlight the trophic plasticity of *S. senilis* in response to the Sine Saloum estuary's inverse dynamics. Such changes in the environment may also modify physiological need, as revealed by non-methylated interrupted (NMI) FAs present in the individuals sampled in the part of the estuary undergoing the most brutal environmental changes.

Keywords: West Africa / fatty acids / stable isotopes / sterols / trophic ecology / filter feeders

1 Introduction

In the estuaries and lagoons of West Africa, the bloody cockle (*Senilia senilis*, Linné, 1758; valid name for *Anadara senilis* or *Arca senilis*) is the dominant mollusk species, both in terms of abundance and biomass (Collignon, 1950; Honkoop et al., 2008; Zabi and Le Loeuff, 1994). This is especially the case in the Sine Saloum delta (Senegal) where *S. senilis* has been exploited and consumed by local communities for thousands of years (Carré et al., 2022; Hardy et al., 2016). This exploitation is currently carried out by women's communities, who manually collect cockles from the sediment-water interface in intertidal and shallow subtidal zones. *S. senilis* is a filter-feeding organism and is considered as a primary consumer, feeding on sedimentary and particulate organic matters and microphytobenthos (Honkoop et al., 2008; Wolff et al., 1993a, 1993b). Filter-feeding organisms have generally little capacity to move and depend on the conditions of their immediate environment to access their food resources (Marchais et al., 2013). They are therefore subject to spatial and temporal variations in their food sources (Mathieu-Resuge et al., 2019a; Nerot et al., 2015; Purroy et al., 2018), reflecting the ecological processes occurring at the lowest trophic levels (Marchais et al., 2013).

The Sine Saloum is a dynamic interface between the marine and terrestrial environments with a high diversity of ecosystems, including extensive mangroves that are particularly prominent in the downstream regions. This region is subject to significant variations in climatic conditions, which led to a major drought in the 1950s and a marked return to rainfall in recent years (Descroix et al., 2020). *S. senilis* is subject to major variations of the environmental conditions as the delta is an inverse estuary all year long, i.e., its salinity is higher upstream, and the region is subject to the climate regime

*Corresponding author: eva.janowski@univ-brest.fr; Yoann.Thomas@ird.fr

Table 1. Non-exhaustive list of FAs and sterols with their designations, names and uses as trophic biomarkers.

Designation	Biomarker for	References
Bacteria	Branched FAs (*iso/anteiso*) Odd FAs (*15:0*, *17:0*)	(Bartsch et al., 2017; Connelly et al., 2014; Desvilettes et al., 1997; Iverson, 2009)
Diatoms	16:1n-7 16:4n-1 20:5n-3 Desmosterol	(Dalsgaard et al., 2003; Pepin et al., 2011; Volkman, 2003; Volkman et al., 1989)
Zooplankton	C20-C22 (n-11)	(Alfaro et al., 2006; Parrish, 2013; Tocher, 2003)
Rhodophyceae	20:4n-6	(Kelly and Scheibling, 2012; Parrish, 2013)
Dinoflagellates	22:6n-3 18:4n-3 Lanosterol	(Bergé and Barnathan, 2005; Giner, 1993; Kelly and Scheibling, 2012; Nerot et al., 2015; Parrish, 2013)
Vascular plants (*seagrass*, *mangrove*)	18:2n-6 18:3n-3 Stigmasterol Campesterol	(Kelly and Scheibling, 2012; Parrish, 2013; Pepin et al., 2011; Valitova et al., 2016; Volkman, 2003)
Microalgae	22:5n-3	(Delaunay et al., 1993; Volkman, 2003)

of the monsoon (Descroix et al., 2020). From June to September, the Sine Saloum undergoes a monsoon season characterized by high rainfall, especially in August (97 to 379 mm of rain) and relatively high temperatures, especially in July (19 to 30 °C) (Doumouya et al., 2016). From October to May, the Sine Saloum is subject to a dry season the lack of freshwater input and the high temperature (up to 39 °C from Mars to June, Doumouya et al., 2016) support evaporation leading to an increased salinity in the delta. A study by Descroix et al. (2020) showed that maximum salinity values are always reached in the most upstream part of the estuary, where they can exceed 100 PSU (Bousso, 2000; Simier et al., 2004). Changes in environmental parameters (temperature and salinity) influence the structure of communities, with cascading effects on trophic relationships among species (Gibert, 2019; Gning et al., 2010; Villanueva, 2015; Whitfield et al., 2006). Therefore, salinity and temperature changes over the course of the year and the estuary should modify the dietary resources available to *S. senilis* and generate environmental stress.

To provide elements to ensure the sustainability of *S. senilis* harvesting, it is therefore essential to assess how the salinity conditions of the Sine Saloum estuary impact the trophic ecology of this species throughout the year. The aim of this study was to characterize how seasonal variations in salinity conditions along the Sine Saloum estuarine gradient influence the food resources assimilated by *S. senilis*.

The trophic ecology of bivalves can be investigated through various methods, including the use of trophic biomarkers such as stable isotopes, fatty acids, and sterol compositions as proxies for assimilated food sources (Nerot et al., 2015; Vander Zanden et al., 2015). However, combining several biomarkers enhances the characterization of food sources assimilated by bivalves (Chikaraishi, 2006; Mathieu-Resuge et al., 2019b, 2019a). Studied on consumers, these biomarkers provide an integrative view of the food resources actually assimilated over a time frame of a few days to weeks depending on the turnover of the tissue under consideration: few days for lipids (fatty acids and sterols) in the digestive gland to few weeks to months for stable isotopes in bivalve muscle (Lefebvre et al., 2009; Lorrain et al., 2002; Marchais et al., 2013; Pazos et al., 2003). The carbon isotopes ratio (expressed as $\delta^{13}C$ values) is a proxy for the spatial origin of an organism's food resource (e.g., terrigenous *vs.* oceanic input), while the nitrogen isotopes ratio (expressed as $\delta^{15}N$ values) is a tool for determining an organism's trophic position (Fry, 1988; Jackson et al., 2011). Fatty acids (FAs) are lipid compounds with multiple roles in organisms: they can be stored as energy reserve, and like sterols, they have a structural or functional roles in cell membranes or as hormone precursor (Alfaro et al., 2006; Pazos et al., 2003; Tocher, 2003). Some FAs are only produced by a few groups of primary producers and are conserved with few modifications during trophic transfer within food webs (Alfaro et al., 2006; Dalsgaard et al., 2003). For example, the increased presence of 22:6n-3 (Docosahexaenoic acid, DHA) or 20:5n-3 (Eicosapentaenoic acid, EPA) in a consumer generally indicates direct or indirect consumption of dinoflagellates or diatoms, respectively (Budge and Parrish, 1998; Parrish et al., 2000). Thus, certain FAs are good trophic markers, as described in Table 1, and the FAs composition of a consumer is changing according to its diet (Alfaro et al., 2006; Nerot et al., 2015; Richoux et al., 2014). In mangroves, omnivore and mixed feeding strategies seem to be preferred by the mangrove benthic fauna (Alfaro et al., 2006; Bouillon et al., 2008); thus the use of FAs to identify and distinguish the different carbon sources used by organisms in these ecosystems is fairly reliable (Guo et al., 2020; Meziane et al., 2006; Meziane and Tsuchiya, 2002). The sterol profiles of animals are less diverse than those of plants and characterized by high levels of cholesterol and small amounts of other sterols (Martin-Creuzburg and Elert, 2009). Therefore, the capacity of bivalves to synthesized sterols *de novo* appears to be very low, or even non-existent (Martin-Creuzburg and Elert, 2009; Volkman, 2003). The sterol composition of bivalves will therefore be mainly of dietary origin and can also be used as trophic markers (Mathieu-Resuge et al., 2019a; Soudant et al., 1996).

This study hypothesizes that the spatial gradient (upstream-downstream) associated with the inverse estuary and the seasonal variations driven by monsoon events in the Sine Saloum influence the diversity and quality of food resources available to *S. senilis*. To assess this impact, we used a multibiomarker approach to characterize how these environmental changes affect the food resources of *S. senilis*.

2 Materials and methods

2.1 Sampling of *S. senilis* and measures of environmental parameters

A total of 180 individuals of *S. senilis* were collected in April 2022 (dry season) and October 2022 (monsoon season) along a 55 km upstream-downstream gradient of the Sine Saloum estuary. Sampling in April 2022 was carried out at two stations located *ca.* 55 km upstream and close to the river mouth, respectively (Station 1 and Station 4, see Fig. 1). In October 2022, four stations were sampled: stations 1 and 4, as well as two intermediate stations (Station 2 and Station 3, see Fig. 1). At each station and season, bivalve sampling was carried out over an area with an approximate radius of 10 to 20 meters. All the stations were located in the intertidal zone. As the tidal range is relatively small in the study area, with a maximum of 1.2 m, differences in water depth between stations were considered to be minimal. The digestive gland was taken and preserved in approximately 6 mL of a chloroform: methanol solvent mixture (2:1, v/v) at −20 °C for lipidic analysis. The adductor muscle of the organisms was frozen at −20 °C and then freeze-dried (alpha 1–4 L5C basic freeze-dryer, 72h) for isotopic analysis.

Environmental variables were measured at each sampling site. Water temperature (°C) and salinity (PSU) were measured using a CTD-DIVER probe (Van Essen Instruments). A WiMo probe (NKE instruments) measured the pH, dissolved oxygen concentration ($mg.L^{-1}$), water oxygen saturation (%), turbidity (NTU) and chlorophyll-*a* concentration. Chlorophyll-a values are reported in arbitrary units (AU), as they are based on raw fluorescence signals not calibrated against absolute concentrations (e.g., $\mu g.L^{-1}$), in order to reflect relative differences among sites and avoid misinterpretation. The distance to the mouth of the river of each station and the minimum distance to adjacent mangrove were determined using QGis software (version 3.16.0). The granulometry of the sediment was categorized visually as sandy-muddy, sandy, or coarse sand. Finally, to measure the diversity and abundance of phytoplankton organisms present in the most upstream (Station 1) and downstream (Station 4) stations at both seasons, taxonomic analyses were done using 250 mL of seawater taken from the surface and fixed with 1 mL of Lugol. A 50ml subsample was settled and analyzed using the Utermöhl method to assess the abundance of the main families (Karlson et al., 2010). The subsample volume was limited due to high particulate load in the water column, which would have impeded accurate microscopic identification and enumeration.

2.2 Fatty acids and sterols analysis of *S. senilis*

Fatty acid and sterol compositions of total lipids were analyzed on the digestive gland tissues of 179 individuals (1 individual from Station 1 collected in April was found to be empty).

All samples (i.e., digestive gland) stored in chloroform: methanol (2:1, v/v) were sonicated to improve lipid extraction. After adding an internal standard (tricosanoic acid C23:0, 2.3 μg), the lipid extracts were saponified and then trans esterified as described in Mathieu-Resuge et al. (2023). Briefly, 1 mL of KOH MeOH (0.5 M) was added to the evaporated extract and heated in a dry bath for 30 min at 80 °C; after cooling at room temperature, 1.6 mL H_2SO_4:MeOH mixture (3.4%, v:v) was added and heating for 10 min at 100 °C. The fatty acid methyl esters (FAME) and sterols were then recovered in hexane and rinsed 3 times with hexane-saturated water. The upper organic phase containing FAME and sterols was recovered for gas chromatography analysis.

FAME and sterols were analyzed by gas chromatography coupled to a flame ionization detector (GC-FID; TRACE 1300 Thermo Scientific) equipped with two columns of different polarities to ensure a correct identification of compounds (ZB-WAX and ZB-5HT columns, both 30 m x 0.25 mm ID x 0.2 μm, Phenomenex). The oven temperature was rise from 60 °C to 150 °C at a rate of 50 °C/min; from 150 °C to 170 °C at a rate of 3.5 °C/min; from 170 °C to 185 °C at a rate of 1.5 °C/min; from 185 °C to 225 °C/min at a rate of 2.4 °C/min; and finally, a rise from 225 °C to 250 °C at a rate of 5.5 °C/min followed by a plateau at 250 °C for 20 min (run of 94 min).

FAME and sterols identifications were carried out by comparing with an external standard (Supelco 37 Component FAME Mix and PUFA No.3 for fatty acids, and a sterol mix from the laboratory), and using mass spectrometry analysis when necessary (GC-MS TRACE 1300 coupled to an ISQ 7000 single quadrupole mass spectrometer, equipped with the same ZB-WAX column and using the same temperature program as for the GC-FID, scan 40–600 mz, electron impact ionization (EI+), ion source temperature of 200 °C, electron energy of 70 eV, electron lens voltage of 5 V). The relative proportions of fatty acids and sterols were expressed as a percentage (%) of the total fatty acids and the total sterols, respectively. A total of 68 FAs and 10 sterols were identified.

2.3 Stable isotopes analysis ($\delta^{13}C$ and $\delta^{15}N$ values) of *S. senilis*

S. senilis adductor muscle tissues were analyzed for stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). After freeze-drying, tissues were ground to a powder using a ball mill (Restch MM400). Powders were weighed (400 ± 100 μg) in tin capsules (Elemental Micro Analysis D1800, 8 × 5 mm or Elemental Micro Analysis D1104 10.5 × 9 mm) using a microbalance accurate to 1 μg.

Samples were analyzed by continuous flow on a Flash EA2000 elemental analyzer coupled to a Delta V Plus isotope ratio mass spectrometer (EA-IRMS, Thermo Fisher scientific) at the Pôle Spectrométrie Ocean, University of Brest, France.

Calibrations and isotopic corrections were based on reference materials (USGS-61, USGS-62 and USGS-63) and on an in-house standard Thermo-Acetanilide.

Results were reported in the δ unit notation and expressed as parts per thousand (‰) relative to the international standards (atmospheric N_2 for nitrogen and Vienna- Pee Dee Belemnite for carbon). Analytical precision was <0.10 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values, based on replicate measurements of a Thermo-Acetanilide standard analyzed after every six

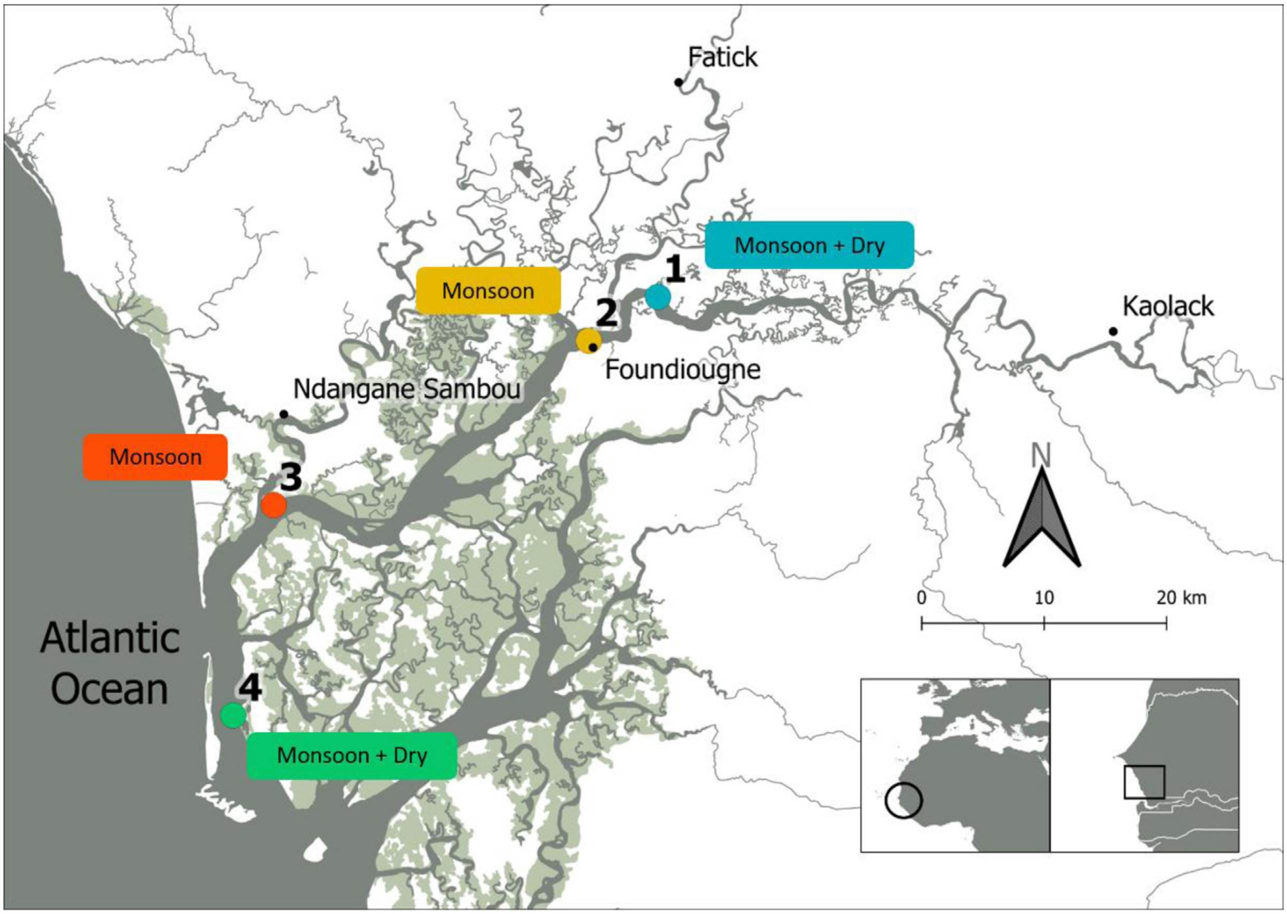

Fig. 1. Locations of the sampling stations in the Sine Saloum delta, Senegal. Stations are identified by colored dots (blue for station 1, yellow for station 2, red for station 3 and green for station 4) along with nearby towns in black dots and mangrove in light grey (Shapefile obtained using Géo Senegal). The season at which sampling took place are indicated in colored squares.

samples. All the C:N values were below 3.5 and the δ^{13}C values were therefore not corrected for lipid content.

2.4 Suspended particulate organic matter (SPOM) and surface sediment analysis

To characterized the trophic composition of potential food sources, environmental samples of SPOM and surface sediment were collected at the four stations. For SPOM, 500ml of prefiltered water (on a 240 μm mesh to remove larger debris) was filtered onto a pre-combusted glass fiber filter (Whatman GF/F, 0.7μm). Two filters were collected per station in April 2022 and October 2022. The surface sediment (top 1cm) was sampled in October 2022, with two replicates per station.

In total, 24 environmental samples were obtained. One whole filter was stored in chloroform: methanol (2:1, v/v) and used for lipid analyses (fatty acid and sterols) using the same method as for the digestive glands of *S. senilis*, while the second was split into two halves for stable isotope analysis. One was analyzed directly for δ^{15}N, and the other was acidified with nitric acid fume prior to δ^{13}C analysis to remove inorganic carbon.

Lipid profiles and stable isotopes (δ^{13}C and δ^{15}N) values obtained from SPOM and the surface sediment are provided in the supplementary material (Supplementary 2) for reference. They were not included in the statistical analyses due to the lack of replication necessary for robust quantitative comparisons.

2.5 Data analysis

All statistical analyses were performed using R software (R Core Team, 2022). We determined the FAs and sterols responsible for 80% of the dissimilarity between the groups (season and station), corresponding to 24 FAs using the *simper* function in the vegan package (Oksanen et al., 2022). All the sterols were retained for further analysis.

A permutation multivariate analysis of variance (PERMANOVA) was then performed using the *adonis2* function in the vegan package (Oksanen et al., 2022), to determine whether there were significant differences in FAs proportions according to season, station or the interaction of the two factors. The PERMANOVA was followed by a *pairwise.adonis* post hoc test from the pairwiseAdonis package (Martinez Arbizu and Pedro, 2020) in order to specify the differences between the two seasons and between the four stations.

A Principal Component Analysis (PCA) was performed using the Factoshiny package (Vaissie et al., 2021) in order to visualize the entire dataset (environmental parameters, FAs and sterols compositions, stable isotopes values) by positioning the observations in the space of the studied variables.

As the conditions of normality and homogeneity of variances were not always met for the $\delta^{13}C$ and $\delta^{15}N$ values, a non-parametric univariate test (Scheirer-Ray-Hare test) was carried out to test the effects of season and station. This non-parametric test was followed by a Wilcoxon post hoc test to determine the relationship between the two seasons and among the four stations.

Food source diversity was estimated using a method developed by Layman et al. (2007) and implemented in R software coupled with the JAGS program through the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. (2011)). For each station and season, diversity in food sources was estimated using Bayesian standard ellipse areas (SEAb), which were obtained from the coordinates of the first two dimensions of the PCA and biplots of $\delta^{13}C$ and $\delta^{15}N$ values. The SEAb represent the distributions of 4,000 iterations of posterior estimates for the ellipse areas of each group (station x season) and are unbiased with respect to sample size (Jackson et al., 2011). This enables comparisons to be made between groups with regard to food source diversity.

3 Results

3.1 Environmental parameters

A marked spatial and seasonal variability of salinity and temperature was observed (Tab. 2). During the dry season, the upper estuary was hypersaline (45.6 PSU and 42.0 PSU at stations 1 and 2, respectively) and presented high water temperatures (26.4 °C and 26.5 °C at stations 1 and 2, respectively. The downstream stations showed slightly lower salinity and temperature values than those upstream (35.9 PSU and 31.9 PSU and 25.5 °C and 23.6 °C at stations 3 and 4, respectively). During the monsoon, the water masses became more homogenous both in terms of salinity and water temperature, with mean values over the four stations of 19.9 ± 0.8 PSU and 30.9 ± 0.1 °C, respectively.

The turbidity increased along the estuary, from the upstream stations to the downstream ones during both seasons. During the dry season, chlorophyll-a concentrations showed a general increasing trend from station 1 to station 4, with values of 50.8 ± 17.5 au, 61.4 ± 46.3 au, 79.9 ± 51.6 au and 80.3 ± 44.8 au, respectively, and 44.8 ± 14.5 au, 35.1 ± 29.1 au, 61.3 ± 3.5 au and 96.7 au during the monsoon, respectively.

These spatio-temporal trends in chlorophyll-*a* were also observed for several phytoplankton family abundances (Tab. 2): during the dry season, higher abundances were measured downstream (station 4) compared to upstream (station 1) for Bacillariophyceae, Dinoflagellates and Nanophytoplankton. Just like the Nanophytoplankton, the Euglenophyceae family was absent upstream during the dry season. During the monsoon, the minimums abundances were obtained upstream (mainly represented by Bacillariophyceae, Dinoflagellates, and Cyanophyceae) and the maximum abundances downstream (mainly represented by Nanophytoplankton, Dinoflagellates, Cyanophyeae, and Chlorophyceae). Finally, when the Nanophytoplankton were absent, the Bacillariophyceae showed the highest abundances (downstream during the dry season and upstream during the monsoon season). The abundances of the various phytoplankton families were all higher during the dry season, in the upstream part of the estuary (except for the Cyanophyceae), while in the downstream part, only the Euglenophyceae and Dinoflagellates families were more abundant in the dry season rather than during the monsoon.

3.2 Spatial and season variations in fatty acid and sterol compositions

Twenty-four FAs were responsible for 80% of the dissimilarity between the samples: TMTD, 14:0, 16:0, 16:0 DMA, 16:1n-7, 17:0, anteiso 17:0, 18:0, 18:0 DMA, iso 18:0, anteiso 18:0 DMA, 18:1n-7, 18:2n-6, 18:2n-7, 18:4n-3, 20:1n-11, 20:4n-6, 20:5n-3, 22:1n-11, 22:2i, 22:2j, 22:4n-6, 22:5n-3, 22:5n-6, 22:6n-3 (Tab. 3). Ten sterols were identified in *S. senilis* digestive glands: brassicasterol, campesterol, cholestanol, cholesterol, desmosterol, lanosterol, lathosterol, norcholesterol and stigmasterol (Tab. 3).

The PCAs illustrated the spatial and temporal structuring of lipid composition in FAs and sterols (Fig. 2). Dimension 1 explained 32.1% of the variability and separated individuals according to their station, with stations 1 and 2 on the right-hand side of the axis, and stations 3 and 4 were found on the left-hand side of the axis (Fig. 2A). In addition, dimension 1 showed a total overlap of the ellipses of individuals sampled at stations 3 and 4. These overlaps indicated that the individuals at these stations had relatively similar FA and sterol compositions, distinguishing the upstream stations from the downstream stations. The FAs: 17:0, anteiso 17:0, iso 18:0, anteiso 18:0 DMA, 18:2n-7, 22:1n-11 and 22:5n-6; as well as the sterols: norcholesterol, cholesterol, desmosterol, cholestanol, and lanosterol are positively correlated on the dimension 1 axis and were therefore more characteristic of the station 1 and 2. The FAs: 16:1n-7, 18:1n-7, 18:4n-3, 20:4n-6, 20:5n-3 and 22:5n-3 as well as the sterols: stigmasterol, campesterol and brassicasterol, which varied negatively on the dimension 1 axis, were characteristic of the stations 3 and 4. Dimension 2 explained 14.4% of the variability and described interindividual variations but discriminated relatively little between the seasons and stations. The proportions of 18:1n-7 varied positively along the dimension 2 while 22:4n-6 varied negatively along the dimension 2. Finally, dimension 3 explained 6.9% of the variability and separated individuals according to the season (Fig. 2B). Individuals sampled in April, during the dry season, were found on the negative side of the axis and those sampled in October during the monsoon were found on the positive side. The FAs: 17:0, 18:0, iso 18:0, 18:1n-7, 18:2n-6, 20:1n-11, 22:1n-11, 22:4n-6, 22:5n-6 as well as the sterols: brassicasterol, cholestanol, desmosterol, and stigmasterol varied positively along dimension 3 and relate to individuals sampled in October. The 18:2n-6, 18:4n-3, 20:4n-6, 22:5n-3, 22:6n-3, campesterol, lanosterol, cholesterol, and norcholesterol varied negatively along the dimension 3, in relation to the individuals sampled in April.

Table 2. Mean (± standard deviation) environmental measurements (granulometry, distance to the mouth of the river (km), distance to a mangrove (km), water temperature (°C), salinity (PSU), pH, dissolved oxygen (mg.L^{-1} and %), turbidity (NTU), chlorophyll-a concentration (expressed by arbitrary units, AU) and abundance of different phytoplankton families (cell.L^{-1}), no data (ND) were obtained at the stations 2 and 3) at stations 1, 2, 3 and 4 in April and October 2022 along the upstream-downstream gradient of the Sine Saloum estuary, Senegal. For some environmental parameters at station 4 during the monsoon season, only two values were available due to sensor malfunction, and thus no standard deviation could be calculated, those are indicated by (−).

Station	Granulometry	Distance to the mouth of the river (km)	Distance to a mangrove (km)	Season	Water temperature (°C)	Salinity (PSU)	pH	Dissolved oxygen (mg.L^{-1})	Dissolved oxygen (%)	Turbidity (NTU)	Chlorophyll-*a* (expressed by arbitrary units, AU)	Bacilleriophycea (cell.L^{-1})	Dinoflagellates (cell.L^{-1})	Chlorophycae (cell.L^{-1})	Cyanophycae (cell.L^{-1})	Euglenophycae (cell.L^{-1})	Nanophytoplancton (cell.L^{-1})
1	Coarse sand (shell debris)	54.7	0.6	Dry	26.4 (±0.2)	45.6 (±0.2)	8.2 (±0.4)	4.8 (±0.2)	81.4 (±2.7)	8.5 (±0.5)	50.8 (±17.5)	$1.99 \times 10^{+5}$	$1.05 \times 10^{+4}$	0	$4.00 \times 10^{+1}$	0	$2.02 \times 10^{+6}$
				Monsoon	30.8 (±0.0)	19.5 (±0.4)	8.3 (±0.0)	6.9 (±0.3)	94.1 (±3.9)	11.6 (±0.6)	44.8 (±14.5)	$2.01 \times 10^{+4}$	$2.80 \times 10^{+2}$	0	$1.60 \times 10^{+2}$	0	0
2	Sandy	46.6	1.6	Dry	26.5 (±0.2)	42.0 (±0.3)	8.0 (±0.0)	6.4 (±0.1)	88.6 (±0.8)	6.5 (±0.5)	61.4 (±46.3)	ND	ND	ND	ND	ND	ND
				Monsoon	30.7 (±0.0)	19.2 (±0.0)	8.2 (±0.0)	7.0 (±0.1)	92.7 (±0.7)	12.7 (±0.7)	35.1 (±29.1)	ND	ND	ND	ND	ND	ND
3	Sandy-muddy	12.9	0.2	Dry	25.5 (±0.0)	35.9 (±0.1)	8.0 (±0.0)	7.9 (±0.1)	95.1 (±0.5)	9.4 (±0.6)	79.9 (±51.6)	ND	ND	ND	ND	ND	ND
				Monsoon	30.9 (±0.1)	19.8 (±0.0)	7.7 (±0.0)	6.1 (±0.2)	80.8 (±2.0)	24.6 (±3.5)	61.3 (±3.5)	ND	ND	ND	ND	ND	ND
4	Sandy	7.4	0.4	Dry	23.6 (±0.0)	31.5 (±0.0)	7.9 (±0.0)	6.6 (±0.3)	90.7 (±3.0)	8.4 (±0.3)	80.3 (±44.8)	$1.81 \times 10^{+4}$	$5.80 \times 10^{+3}$	0	$4.00 \times 10^{+1}$	$4.00 \times 10^{+1}$	0
				Monsoon	31.0 (±0.3)	21.1 (±0.1)	8.1 (−)	7.7 (−)	108.9 (−)	13.6 (−)	96.7 (−)	$2.66 \times 10^{+4}$	$2.50 \times 10^{+3}$	$8.00 \times 10^{+1}$	$1.28 \times 10^{+3}$	0	$9.22 \times 10^{+5}$

Table 3. The 24 FAs responsible for 80% of the dissimilarity between stations and sterols mean compositions (mean ± standard deviation), in % of total FAs and in % of total sterols, respectively, in the digestive gland of *S. senilis* and stable isotopes values of $\delta^{13}C$ and $\delta^{15}N$ (in ‰) in the abductor muscle of *S. senilis* at 4 stations and 2 seasons in the Sine Saloum estuary, Senegal.

Season	Dry	Monsoon	Monsoon	Monsoon	Dry	Monsoon
Station	1	1	2	3	4	4
	N=28	N=28	N=30	N=30	N=30	N=29
$\delta^{15}N$	5.8 ± 0.3	6.5 ± 0.4	6.6 ± 0.4	8 ± 0.5	9.2 ± 0.4	8.5 ± 0.2
$\delta^{13}C$	−20.2 ± 0.3	−19.6 ± 0.8	−20.4 ± 0.3	−20.8 ± 0.3	−18.8 ± 0.2	−19.2 ± 0.2
14:0	1.7 ± 0.4	1.6 ± 0.8	1.6 ± 0.9	2.8 ± 1.3	2.2 ± 0.9	3.5 ± 1.7
16:0	11.9 ± 1.0	12.1 ± 2.8	11.9 ± 2.6	16.5 ± 3.5	13.4 ± 2.4	18.2 ± 4.9
17:0	3.1 ± 0.2	3.0 ± 0.3	2.8 ± 0.2	2.4 ± 0.3	2.1 ± 0.2	2.3 ± 0.2
18:0	9.7 ± 0.6	9.9 ± 0.7	10.5 ± 0.4	10.5 ± 1.0	10.1 ± 0.7	11.1 ± 0.9
Total SFA	27	27.3	27.4	32.7	28.2	35.6
16:1n-7	1.5 ± 0.4	1.2 ± 0.4	1 ± 0.4	2.7 ± 0.7	2.4 ± 0.8	2.9 ± 0.9
18:1n-7	2.1 ± 0.3	1.6 ± 0.2	1.3 ± 0.2	2.2 ± 0.3	1.4 ± 0.2	2.1 ± 0.3
20:1n-11	3.5 ± 0.3	5.3 ± 0.8	5.1 ± 0.8	3.1 ± 0.7	2.7 ± 0.4	2.7 ± 0.7
22:1n-11	0.7 ± 0.3	0.7 ± 0.3	0.8 ± 0.3	0.6 ± 0.3	0.6 ± 0.3	0.4 ± 0.2
Total MUFA	12.4	13.4	13.1	13.7	11.7	12.6
18:2n-7	0.5 ± 0.1	0.7 ± 0.3	0.5 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
18:2n-6	2 ± 0.1	2.0 ± 0.3	2.3 ± 0.2	1.7 ± 0.2	1.9 ± 0.2	1.6 ± 0.2
18:4n-3	0.8 ± 0.1	0.5 ± 0.2	0.5 ± 0.2	0.7 ± 0.2	1.1 ± 0.3	0.7 ± 0.2
20:4n-6	1.1 ± 0.4	4.7 ± 0.7	5.3 ± 0.8	5.2 ± 1	5.5 ± 0.8	4.8 ± 1.4
20:5n-3	2.9 ± 0.4	2.1 ± 0.5	2 ± 0.4	6.6 ± 1.5	5.7 ± 0.9	6.6 ± 1.6
22:4n-6	0.6 ± 0.1	1 ± 0.2	1.3 ± 0.3	0.9 ± 0.2	1 ± 0.2	0.9 ± 0.3
22:5n-6	2.2 ± 0.3	2.6 ± 0.5	2.5 ± 0.7	1.3 ± 0.3	1.1 ± 0.1	1 ± 0.3
22:5n-3	0.8 ± 0.1	0.9 ± 0.6	0.9 ± 0.1	1.3 ± 0.2	1.5 ± 0.1	1.4 ± 0.2
22:6n-3	15.8 ± 1.3	10.1 ± 1.9	9.1 ± 1.1	7.5 ± 1.6	11.1 ± 0.8	7.7 ± 1.6
Total PUFA	11.9	16	16.1	19.1	18.6	18.2
TMTD	1.9 ± 0.3	1.1 ± 0.4	0.9 ± 0.4	1.4 ± 0.4	1.9 ± 0.4	1.7 ± 0.4
Anteiso 17:0	1.3 ± 0.3	1.3 ± 0.3	1.2 ± 0.2	0.8 ± 0.2	0.8 ± 0.1	0.7 ± 0.1
Iso 18:0	0.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.2 ± 0	0.2 ± 0	0.2 ± 0
Total Branched	5.3	4.7	4	2.9	3.5	3.1
16:0 DMA	0.8 ± 0.2	1 ± 0.2	1.3 ± 0.3	1 ± 0.5	1.2 ± 0.3	0.7 ± 0.3
Anteiso 18:0 DMA	0.6 ± 0.1	0.9 ± 0.2	0.7 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
18:0 DMA	7.4 ± 0.7	8.8 ± 0.7	9.9 ± 1	8.8 ± 1.8	10.2 ± 1.5	8.2 ± 1.9
Total DMA	10	12	13.1	10.8	12.4	9.6
22:2i	3.9 ± 0.5	5.3 ± 0.8	6.3 ± 0.9	3.7 ± 0.8	4.7 ± 0.6	3.4 ± 0.7
22:2j	7 ± 0.6	7 ± 0.8	6.5 ± 0.7	6.5 ± 1	6.6 ± 0.8	6.4 ± 1
Total NMI	12	13.3	13.6	11	12	10.6
Lathosterol	2.3 ± 0.4	2.6 ± 0.7	1.9 ± 0.6	0.7 ± 0.2	1.2 ± 0.3	0.8 ± 0.3
Norcholesterol	1.6 ± 0.3	1.4 ± 0.4	1.2 ± 0.3	0.5 ± 0.1	1.1 ± 0.2	0.5 ± 0.1
Cholestanol	3.6 ± 0.5	2.7 ± 0.6	2.4 ± 0.4	2.7 ± 0.5	2.1 ± 0.4	2.6 ± 0.7
Desmosterol	1.6 ± 0.8	1.2 ± 0.5	0.9 ± 0.4	0.7 ± 0.3	0.8 ± 0.3	0.7 ± 0.4
Cholesterol	12.6 ± 1.3	10.9 ± 0.8	9.8 ± 0.8	8.4 ± 0.8	9 ± 0.8	7.9 ± 0.8
Brassicasterol	46 ± 2.1	52.4 ± 2.2	52.3 ± 2.1	51.4 ± 2.2	48.7 ± 2.4	57.1 ± 2.3
Lanosterol	17.1 ± 2.4	16.5 ± 1.5	17.3 ± 1.3	16.9 ± 1.1	18 ± 1	13.6 ± 1
Stigmasterol	1.2 ± 0.6	0.7 ± 0.5	0.7 ± 0.6	1.2 ± 0.5	0.8 ± 0.4	1.2 ± 0.3
Campesterol	6.8 ± 0.8	6.1 ± 1	7.8 ± 0.9	14 ± 1.5	14.7 ± 1.6	12.2 ± 1.3
Norcholestadienol	7.4 ± 1.5	5.6 ± 1	5.8 ± 1	3.6 ± 0.6	3.6 ± 0.7	3.5 ± 1

SFA, Saturated Fatty Acids; MUFA, Monounsaturated Fatty Acids; PUFA, Polyunsaturated Fatty Acids; DMA, Dimethyl Acetal Fatty Acids; NMI, Non-Methylene-Interrupted Fatty Acids.

FA and sterol profiles varied significantly according to season, station, and the interaction of these two factors (Tabs. 4 and 5). For instance, 20:1n-11 was 1.3-times significantly higher in October than in April (4.1% *vs.* 3.1%, respectively) and 1.6-times significantly higher upstream than downstream (4.7% *vs.* 2.8 %, respectively). The same trend was observed for the sum of branched FAs (3.7% in October *vs.* 4.4% in April; 4.7% upstream *vs.* 3.2% downstream) and for the norcholestadienol (6.3% *vs.* 3.6% upstream and downstream, respectively). On the contrary, the proportions of 20:5n-3 and campesterol were significantly higher downstream than upstream (6.3% *vs.* 2.3% for 20:5n-3 and 13.6% *vs.* 6.9% for campesterol, respectively).

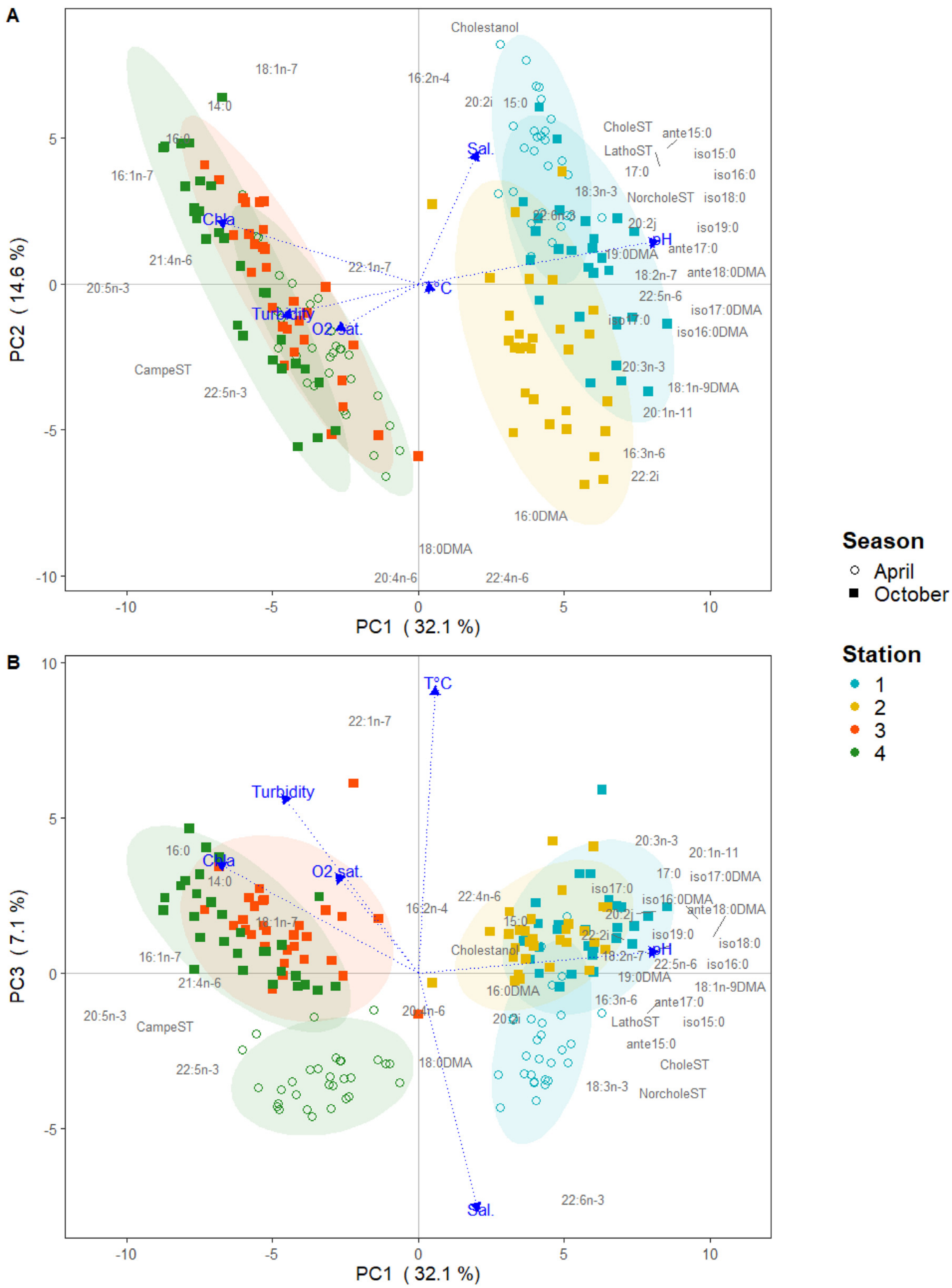

Fig. 2. Principal Component Analysis (PCA) of the sterol and FA composition (%) of the *S. senilis,* collected at 4 stations and 2 seasons in the Sine Saloum delta, Senegal. The analysis also included environmental parameters and stable isotopes values ($\delta^{13}C$ and $\delta^{15}N$ values). Only the compounds best represented on the first three axes of the PCA (i.e., $\cos^2 > 0.35$) are shown in the figure. The graph of individuals and the relative contributions of variables are shown on dimensions 1 and 2 (Fig. 2A) and 1 and 3 (Fig. 2B). The colors indicate the stations (blue for station 1, yellow for station 2, red for station 3, and green for station 4) while the shape of the points varies according to the season (empty circles for April and full squares for October). Blue arrows represent environmental parameters: T °C corresponds to water temperature, Chla to chlorophyll-a concentration (expressed by arbitrary units, AU), O2 sat. to water oxygen saturation, and Sal. to salinity. ST to sterols.

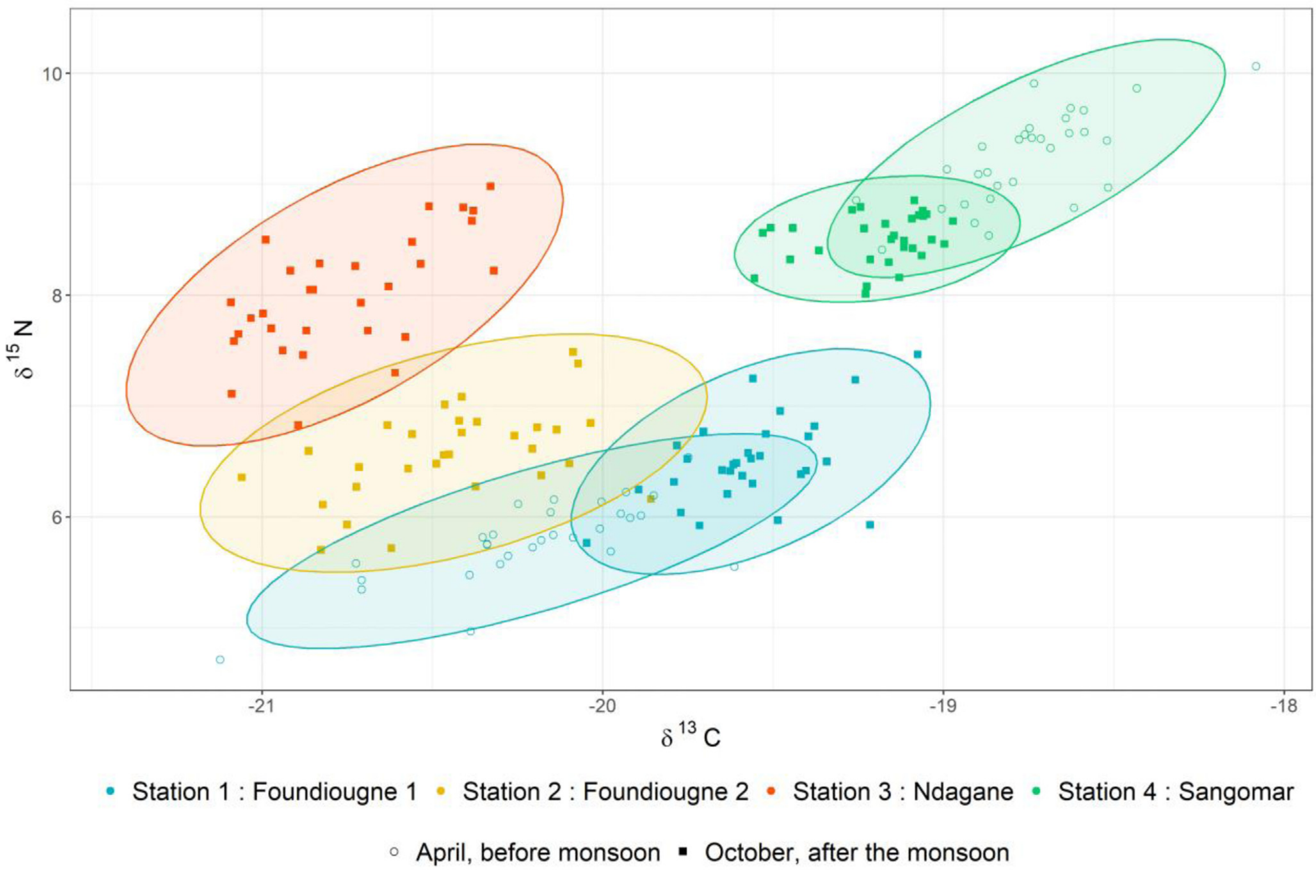

Fig. 3. Carbon and nitrogen isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$, ‰) of *S. senilis* (n=179) collected at 2 seasons and 4 stations located along the Sine Saloum delta, Senegal. The ellipses at the 95% confidence interval of the bivalves are represented by colors varying according to the stations (blue for station 1, yellow for station 2, red for station 3, and green for station 4), and the shape of the points varies according to the season (empty circles for April and full squares for October).

During the monsoon, the 20:5n-3 / 22:6n-3 ratio rose to 0.9 ± 0.2 and 0.9 ± 0.3 downstream (stations 3 and 4, Supplementary 3), above the 0.2 ± 0.0 observed upstream (stations 1 and 2, Supplementary 3). Despite lower average values, this pattern was also observed during the dry season (0.5 ± 0.1 at station 4 *vs* 0.2 ± 0.0 at station 1, Supplementary 3).

3.3 Spatial and seasonal variations of $\delta^{15}N$ and $\delta^{13}C$ values

Muscle $\delta^{15}N$ and $\delta^{13}C$ values of *S. senilis* varied significantly according to the interaction of the season and the station and to the station (Tabs. 4 and 5). The isotopic values of organisms seemed to converge during the monsoon (ellipses moving closer together, 3) and presented less inter-individual variability (ellipses tighter together, 3) compared with the dry season. The $\delta^{15}N$ values increase following a geographical gradient from upstream to downstream. Individuals from the stations closest to the mouth of the estuary were on average more ^{15}N enriched than those further upstream. This was observed both during the monsoon where there is a 2‰ difference between the downstream stations and the upstream stations (8.6 ± 0.5‰ at stations 3 and 4, *vs* 6.5 ± 0.4‰ at stations 1 and 2), and the dry season where there is a 3.4‰ difference between the stations (9.2 ± 0.4‰ at station 4 *vs* 5.8 ± 0.3‰ at station 1) (Fig. 3, Tab. 4).

Regarding the $\delta^{13}C$ values, they followed a decreasing gradient from upstream to downstream during the monsoon. The $\delta^{13}C$ values were, on average, 1‰ more enriched between each successive station downstream (−19.6 ± 0.8‰ at the station 1; −20.4 ± 0.3‰ at the station 2; and −20.8 ± 0.3‰ at the station 3). However, this gradient was not observed at the furthest station downstream. Individuals at station 4 were more ^{13}C enriched than at stations further upstream both during the monsoon (−19.2 ± 0.2‰ at station 4 *vs.* −20.3 ± 0.5‰ at stations 1 to 3), and the dry season (−18.8 ± 0.2‰ at station 4 *vs.* −20.2 ± 0.2‰ at station 1) (Fig. 3, Tab. 4).

3.4 Changes in food diversity

In terms of diversity in food sources, the fatty acid and sterol compositions differ between seasons at each respective station, i.e., stations 1 and 4 both show lower resources diversity in April than in October (both $p < 0.05$) (Fig. 4A). Conversely, the diversity derived from stable isotope compositions differs between stations but not between seasons for the same station (Fig. 4B). Thus, in October, the diversity of

Table 4. Results of PERMANOVAs testing the relative importance of season, station and their interaction on FA and sterol profiles of S. senilis and the Scheirer-Ray-Hare test, testing the correlation of data as a function of season, station and their interaction on $\delta^{13}C$ and $\delta^{15}N$ values. Significance is indicated by stars: * if p<0.05; ** if p<0.01 and *** if p<0.001; and NS for not significant.

	FA composition			Sterol composition			$\delta^{13}C$			$\delta^{15}N$		
	df	F	*p*-value<	df	F	*p*-value<	df	H	*p*-value<	df	H	*p*-value<
Station	1	48.9	***	1	99.5	***	3	120.0	***	3	142.1	***
Season	1	41.2	***	1	171.0	***	1	0.1	NS	1	0.0	NS
Station:Season	1	21.6	***	1	18.0	***	1	12.6	***	1	11.7	***
Residuals	169			169			169			169		

sources is highlighted at station 2, followed by stations 1 and 3, then station 4 (all $p < 0.05$). However, the diversity remains unchanged between April and October at stations 1 and 4, respectively.

4 Discussion

By combining isotope and lipid analysis, the present study revealed a spatio-temporal structuration in the potential diet sources used by *S. senilis* along the Sine Saloum estuary. Bivalves along the estuary consume dinoflagellates, while these in the upper part of the estuary might also consume bacteria and zooplankton.

4.1 Microalgae as dietary sources at all stations

Our results suggest that *S. senilis* diet depends on phytoplankton. During the dry season, the highest proportions of dinoflagellates biomarkers 22:6n-3 and 18:4n-3 were found in the digestive glands of *S. senilis*, both in the upstream and downstream parts of the estuary (Tab. 3 suggesting the importance of the dinoflagellates in the diet of *S. senilis*, as observed in other bivalve species (*Pecten maximus* by Nerot et al. (2015); *Spondylus crassisquama* by Mathieu-Resuge et al. (2019b); *Crassostrea gigas*, *Arca boucardi*, *Mytilus caruscus*, *Saxidomus purpurata*, *Mya japonica*, *Prothothaca jadoensis*, and *Prothothaca euglypta* by Kharlamenko and Kiyashko (2018)). As pointed out by taxonomic identification in the seawater, Dinoflagellates were present throughout the estuary, all year long, but in greater quantity during the dry season. This predominance of dinoflagellates over diatoms in *S. senilis* diet is further supported by the 20:5n-3 / 22:6n-3 ratio, which remains below 1 across all stations and both seasons, suggesting a higher assimilation of dinoflagellates compare to diatoms (Kelly and Scheibling, 2012).

However, 20:5n-3 / 22:6n-3 ratio was consistently higher downstream, particularly during the monsoon season, suggesting a potential larger contribution of diatoms to *S. senilis* diet in this part of the estuary. These contrasts support a higher contribution of diatoms downstream, more pronounced during the monsoon. During monsoon events, nutrient-rich runoffs could significantly impact the phytoplankton communities, and diatoms could bloom with ease due to their greater tolerance to variation in salinity and temperature (Huang et al., 2004; Logan and Taffs, 2013), replacing the less tolerant dinoflagellates (Madhu et al., 2007; Menzel et al., 1963). The diatoms, which may bloom following the supply of nutrients or be resuspended from sediments during the monsoon, could be of benthic or pelagic origin (Patil and Anil, 2008). In a previous study carried out by Faye et al. (2011) in another part of the Sine Saloum, the $\delta^{13}C$ values of *S. senilis* were similar to those we observed at station 2 and intermediate to those of benthic microalgae (−17.3 ± 1.3‰) and sedimentary organic matter (SOM, −24.6 ‰), suggesting that the diet of *S. senilis* was made up of these two benthic compartments. Therefore, the diatom biomarkers detected in greater abundance in *S. senilis* during the monsoon could be of benthic origin. As our values of $\delta^{13}C$ for *S. senilis* were also intermediate to these values, this suggests that like other bivalve species (*Crassostrea gigas* and *Ruditapes philippinarum*, in Kasim and Mukai (2006); *Tellina capsoides*, *T. piratical* and *T. sp*, in Compton et al. (2008); *Cerastoderma edule*, in Kang et al. (1999); *Diplodonta semiasperoides* in Kharlamenko and Kiyashko (2018)), *S. senilis* might consumed preferentially benthic diatoms.

The higher SEAb derived from lipid profiles *S. senilis* (Fig. 4A) suggest a higher taxonomic diversity of food resources used during the monsoon. This interpretation is supported by lipid biomarkers profiles (Figs. 2A and 2B), which indicate a potential combined assimilation of benthic diatoms (resuspended and/or blooming) and of other microorganisms (also likely stimulated by runoff). But despite these seasonal changes, the SEAb derived from the isotopic composition of *S. senilis* (Fig. 4B) remain relatively stable within each station across seasons, indicating little local variability of the carbon and nitrogen sources. However, the SEAb show some spatial contrasts: station 4 exhibits narrow SEAb during both seasons, consistent with a possible trophic reliance on homogeneous sources, likely of marine origin. In contrast, station 2 displays widest SEAb during the monsoon, suggesting that they may exploit a broader and more heterogeneous trophic resources.

4.2 Organic matter from plants and bacteria, especially during the monsoon season

In a mangrove ecosystem, the particulate organic matter (POM) and the SOM are mainly made up of terrestrial plant debris, mangrove litter, phytoplankton and coastal marine debris (Bouillon et al., 2002; Meziane et al., 2007; Muzuka and Shunula, 2006; Prasad et al., 2017). Within the Sine Saloum, mangroves and seagrass can both potentially represent a

Table 5. Results of post hoc tests, testing for difference in FA and sterol profiles of *S. senilis* among stations (1 to 4) and seasons (April and October). Within the same column, different letters indicate significantly different values ($p<0.05$) between groups.

Station	Season	FA profile		Sterol profile		$\delta^{13}C$		$\delta^{15}N$	
		Season comparison	Station comparison	Season comparison	Station comparison	Season comparison	Station comparison	Season comparison	Station comparison
1	Dry	a	a	a	a	a	a	a	a
	Monsoon	b		b		b		a	
2	Dry	b	b	b	b	b	b	a	b
3	Monsoon	b	c	b	c	b	c	a	c
4	Dry	a	d	a	d	a	d	a	d
	Monsoon	b		b		b		a	

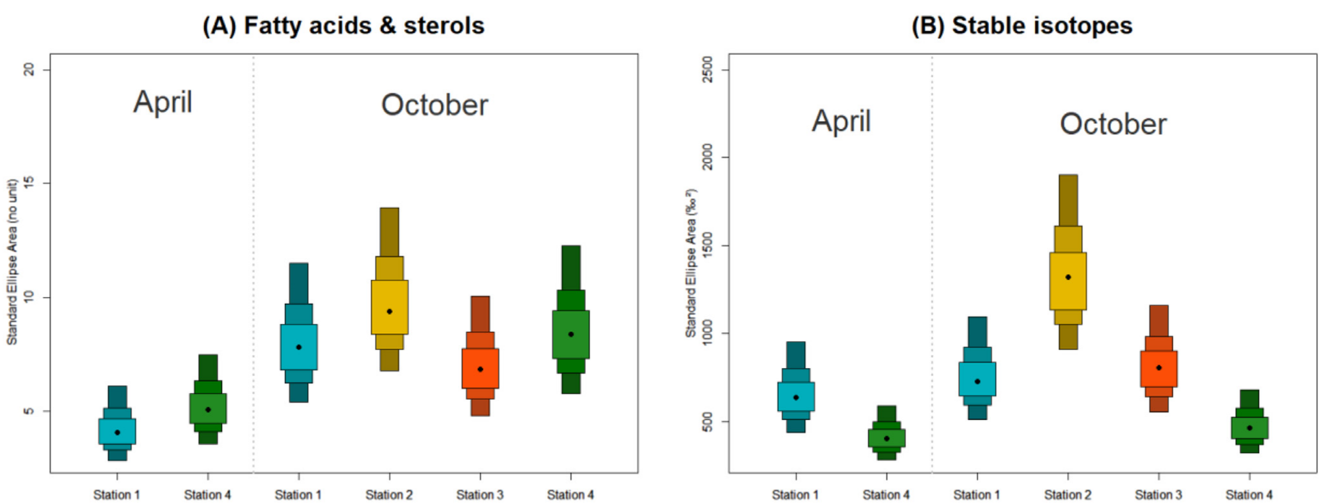

Fig. 4. Diversity of food resources of *Senilia senilis* at each station and season estimated with Bayesian standard ellipse areas (SEAb) obtained from (A) PCA coordinates (see Fig. 2) for both fatty acids and sterols and (B) $\delta^{13}C$ and $\delta^{15}N$ values (see Fig. 3). Boxes represent the credible interval (95%, 75%, and 50%) for the Bayesian standard ellipse areas and dots are median values.

resource of organic matter (SOM and POM). Mangrove are particularly dense at downstream stations. While extensive seagrass beds are distributed along the coast of the Sine Saloum delta, near station 4 and even further south; these seagrass beds are composed of several fully submerged species such as *Zostera* noltei, *Halodule* wrightii and *Cymodocea nodosa* (Sidi Cheikh et al., 2022). Organic matter derived from the decomposition of mangrove and seagrass vegetation may be available to *S. senilis* either directly or indirectly though the microbial loop, as observed in another study on trophic links within mangrove ecosystems (Bouillon et al., 2008). However, the contribution of terrestrial plants in the Sine Saloum was likely low, as only the increased presence of campesterol downstream supports this trend. In contrast, the contribution of bacteria to the diet of *S. senilis* was probably higher upstream, especially after the monsoon, as indicated by the higher proportions of bacterial biomarkers such as 17:0, anteiso 17:0, and 15:0. Within a mangrove estuary, $\delta^{13}C$ values of the POM differ between downstream and upstream due to dilution by freshwater inflow and dissolved inorganic carbon inputs from remineralization (Bouillon et al., 2008, 2000) which reduce the values of $\delta^{13}C$ close to −30‰ (Bouillon et al., 2008; Gning et al., 2010). Therefore, at the station closer to the marine environment (i.e., station 4), the $\delta^{13}C$ values were higher than upstream and close to those of the marine phytoplankton (−18‰ to −22‰, Bouillon et al., 2000). The diversity of stable isotopes profiles indicates station-specific differences suggesting spatial diversity in carbon and nitrogen sources. The SEAb values remained relatively constant across seasons for each station, indicating that while the diversity of trophic inputs may vary with hydrological changes, their overall origin remains stable in a given location.

4.3 Zooplankton: potential food sources upstream

Common calanoid zooplankton FAs biomarkers like 22:1n-11 and 20:1n-11 (Bode et al., 2015; Teuber et al., 2014) were observed in higher proportions upstream of the river suggesting a contribution of this compartment to the diet of *S. senilis*. Zooplankton consumption by filter feeder bivalves has previously been demonstrated by using different methods. Stomach content analysis of the cockle *Arca noae* and various other bivalves species showed that these species could ingest a large variety of zooplankton organisms

(Davenport et al., 2011, 2000; Ezgeta-Balić et al., 2012; Lehane and Davenport, 2002; Peharda et al., 2012; Zeldis et al., 2004). Prey ranged from tintinnids to crustaceans nauplii and metanauplii, cladocerans, lamellibranch larvae, copepods nauplii and metanauplii but also to adult copepods and copepodites in lesser number. In addition to the stomach content analysis, FAs were also used to detect zooplankton consumption by *Glauconome chinensis* and *Sinovacula constricta* by Wang et al. (2015). As in the present study, they found FAs markers of zooplankton (20:1 and 22:1) in the organisms, without however pointing to a species-specific selection. In the current study, we observed these same FAs biomarkers in the SPOM and surface sediment (Supplementary 2), pointing to an intake of these FAs *via* the diet (not biosynthesis). The proportions of zooplankton biomarkers FAs were higher in the upstream stations of the Sine Saloum, and during the monsoon season. This period coincided with lower abundances of phytoplankton (except for Cyanophyceae, Tab. 1); the zooplankton could therefore play a crucial role in providing energy to *S. senilis* at this time of the year when the phytoplankton compartment is less available.

These findings are reinforced by the higher prey taxa diversity observed through lipids profiles during the monsoon across the estuary.

4.4 Fatty acids as indicator of physiological response to environmental variations

The increase proportions of the non-methylated interrupted (NMI) fatty acids 22:2i and 22:2j in *S. senilis* collected upstream of the river suggests the possibility of a physiological response to environmental stress. It was been suggested that these fatty acids are synthesized by bivalves to mitigate oxidative damage, as the chemical structure of NMI impedes the oxidative chain reaction (Kraffe et al., 2004; Le Grand et al., 2011, 2013). This could indicate that the upstream environment of the Sine Saloum is more stressful than the downstream environment, which could have physiological consequences for *S. senilis* populations in the area. Indeed, a previous study (Sané, 2024) determined that growth rates of *S. senilis* in the upstream area were lower than those of individuals further downstream. This could also be a proxy of physiological stress that indicate the limit of distribution of the organisms inside the estuary; during sampling, no cockles were found higher up the estuary. Experiments were carried out to determine optimums of temperature (25 °C to 30 °C) and salinity (12 to 62 PSU) of *S. senilis*. Upstream, conditions are likely exceeding these optimums (Bousso, 2000), and the presence of NMI in their membranes may be required to ensure their wellbeing in this more stressful environment.

4.5 Perspectives

This study provides new insights into the feeding ecology of *S. senilis* along the Sine Saloum estuary, highlighting spatial and seasonal variations in its food sources. While our results support diet flexibility, they also indicate the need for systematic sampling of potential food sources both spatially and temporally, to better capture the integration times of lipid and isotopic markers and detect small-scale spatial heterogeneity in food source use. Future research could take a more quantitative approach, particularly through experimental studies aimed at calculating the integration time of different food sources and specifying *S. senilis* dietary preferences more precisely. This would enhance our understanding of their feeding strategies and the ecological processes involved. Additionally, comparing the diverse ecosystems of the Sine Saloum through life history traits (such as growth rates and reproduction) and potential climatic trajectories could provide valuable insights into how *S. senilis* may respond to future environmental changes.

Acknowledgments

We would like to thank Beatriz Becker for phytoplankton identification, Gallas for help with the sampling and the Lipidocean core facility for analytical support. This work was supported by the French National Research Agency within the framework of the IROCWA project (ANR-19-CE32-0003-01 grant). BS benefited from an ARTS grant from IRD.

Data availability statement

The data and related documentations that support the findings of this study are openly available in DataSuds repository (IRD, France) at https://doi.org/10.23708/QFPCCR. Data reuse is granted under CC-BY license.

Supplementary material

Supplementary 1. FAs and sterols mean compositions (mean ± standard deviation), in % of total FAs and % of total sterols, respectively, in the digestive gland of S. senilis and stable isotopes (in ‰) in the abductor muscle of S. senilis at 4 stations and 2 seasons in the Sine Saloum estuary, Senegal.

Supplementary 2. Stable isotopes, FAs, and sterols mean compositions of the suspended particulate organic matter (SPOM) and surface sediment (SS) at 4 stations and 2 seasons in the Sine Saloum estuary, Senegal.

Supplementary 3. Ratio of the 20:5n-3 and 22:6n-3 fatty acids (EPA/DHA) in the digestive glands of *S. senilis* at 4 stations and 2 seasons in the Sine Saloum estuary, Senegal.

The Supplementary Material is available at https://www.alr-journal.org/10.1051/alr/2025017/olm.

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Cite this article as: Janowski E, Sané B, Sardenne F, Mathieu-Resuge M, Buscaglia M, Harrault L, Munaron J-M, Diouf M, Thomas Y. 2025. Seasonal changes in the diet of the bloody cockle (*Senilia senilis*) along the Sine Saloum inverse estuary. *Aquat. Living Resour.* 38: 20, https://doi.org/10.1051/alr/2025017