



Fine-tuning the isotopic niche of a marine mammal community through a multi-element approach and variable spatial scales

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ABSTRACT

It is commonly assumed that the resolution of the isotopic niche of consumers can be improved with a larger number of chemical elements, but this is only true if steep environmental gradients exist at the appropriate spatial scale. Off Mauritania, the $\delta^{13}\text{C}$ value is a useful proxy to understand the distribution of marine mammals along the inshore-offshore gradient, and the $\delta^{15}\text{N}$ value to assess their trophic position. Here, the incorporation of $\delta^{18}\text{O}$ values as an independent habitat tracer largely improved the resolution of the isotopic niche, because the $\delta^{18}\text{O}$ gradients, mostly reflecting marked salinity gradients, spanned over broad spatial scales when compared to the home range of marine mammals. On the contrary, $\delta^{34}\text{S}$ values did not improve much the resolution of the isotopic niche at the species level, although it was useful to identify individuals relying on food webs associated with anoxic sediments, such as seagrass meadows. This is because the $\delta^{34}\text{S}$ gradient in the area develops over a small spatial scale, compared to the home range of the considered species. This study provides new insights into the use of a multi-element approach in isotopic ecology, and improves the understanding of habitat partitioning between the considered marine mammal species off North Western Africa.

1. Introduction

The precise characterization of a species' niche is critical in ecology as it provides a convenient approach to a variety of questions regarding resource availability, habitat use, and geographic distribution, both at the population and community levels (Newsome et al., 2010). However, marine mammals and other elusive species are difficult to study in the wild and their niches are often characterized through parameters such as stable isotope ratios, fatty acid profiles or contaminant levels (Newsome et al., 2010; Ramos and González-Solís, 2012). This is because these intrinsic tracers, stored in animal tissues through time, integrate information on diet composition and habitat use, although this information can only be interpreted if environmental gradients and their temporal and spatial scales are known.

Stable isotope ratios report the relative abundance of the heavy stable isotope of any chemical element in a sample, compared to that in a standard, and are usually reported in the so called δ notation (Bond and Hobson, 2012). The stable isotope ratios of carbon (C), nitrogen (N),

sulphur (S) and oxygen (O) are commonly used in ecology as intrinsic biogeochemical markers, as they inform about both the trophic and spatial components of the niche (Rubenstein and y Hobson, 2004; Newsome et al., 2010; Ramos and González-Solís, 2012). Accordingly, the isotopic niche of a species is defined as the area in the δ -space where the values of the population concentrate (Newsome et al., 2010) and is best characterized by the convex hull and standard ellipse areas in a given biplot (Syväranta et al., 2013).

Stable isotopes of C and N have been widely used to study the foraging ecology of marine mammal species worldwide, because they can be measured with a small sample of any tissue (Newsome et al., 2010; Ben-David and y Flaherty, 2012; Drago et al., 2021). The C stable isotope ratio ($^{13}\text{C}/^{12}\text{C}$; $\delta^{13}\text{C}$) in animal tissues directly reflects that of their diet and, in aquatic ecosystems, it discriminates accurately between benthic primary producers and phytoplankton (Post, 2002; Newsome et al., 2010). On the other hand, the N stable isotope ratio ($^{15}\text{N}/^{14}\text{N}$; $\delta^{15}\text{N}$) shows a considerable trophic enrichment due to the preferential excretion of the light isotope (^{14}N), and hence, allows

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inferring the trophic position of a species (Post, 2002; Rubenstein and y Hobson, 2004; Ramos and González-Solís, 2012). When combined, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are usually indicative of niche partitioning between species at a local spatial scale (Newsome et al., 2010; Ben-David and y Flaherty, 2012; Pinela et al., 2010; Graham et al., 2010; Botta et al., 2012; Costa et al., 2020; Drago et al., 2021). However, characterizing the isotopic niche of a species using only these two values may fail to capture all the dimensions that make up the isotopic space of an ecosystem (Ramos and González-Solís, 2012; Cani et al., 2023). For this reason, there is an increasing interest in using the stable isotope ratios of other chemical elements, such as S and O (Rossman et al., 2016; Drago et al., 2020; Cani et al., 2023).

The S stable isotope ratio ($^{34}\text{S}/^{32}\text{S}$; $\delta^{34}\text{S}$) reflects the sources of inorganic S available to primary producers (Peterson et al., 1985), and it is mostly applied in combination with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to improve the analysis on habitat use (Rossman et al., 2016; Borrell et al., 2021; García-Vernet et al., 2021). In general, marine phytoplankton is characterized by high $\delta^{34}\text{S}$ values, whereas seagrasses and mangroves, growing on hypoxic or anoxic sediments, are characterized by much lower $\delta^{34}\text{S}$ values because of the intense discrimination against the heavier isotope (^{34}S) during sulphate reduction (Peterson, 1999; Croisetière et al., 2009). Likewise, terrestrial particulate organic matter is also characterized by low $\delta^{34}\text{S}$ values (Peterson, 1999). On the other hand, the O stable isotope ratio ($^{18}\text{O}/^{16}\text{O}$; $\delta^{18}\text{O}$) is commonly used as a habitat tracer in terrestrial ecology, since its distribution can be predicted according to the hydrological cycle and the local geology (True-man et al., 2012). In the marine environment, there is a positive and linear correlation between the $\delta^{18}\text{O}$ values and the salinity of the water (Gat, 1996; Conroy et al., 2014), therefore being a useful descriptor of habitat use in areas with strong salinity gradients (Belem et al., 2019; Drago et al., 2020).

It should be noted that, in positive estuaries, where the salinity increases toward oceanic waters (Pritchard, 1952), the $\delta^{34}\text{S}$ and $\delta^{18}\text{O}$ gradients are usually generated by the same process, i.e., the freshwater run-off also transporting particulate organic matter from continental origin (Peterson, 1999; Belem et al., 2019). As a result, both $\delta^{34}\text{S}$ and $\delta^{18}\text{O}$ values vary similarly on a broad spatial scale, from tens to hundreds of kilometres (Cani et al., 2023). However, the $\delta^{34}\text{S}$ and $\delta^{18}\text{O}$ gradients may be uncoupled in negative estuaries, where intense evaporation exceeds the freshwater input nearshore (Pritchard, 1952) and, thus, generates a salinity gradient independent from the freshwater input. In this scenario, the primary source of $\delta^{34}\text{S}$ variation is the sulphate reduction in sediments, hence, the two gradients are generated by independent processes (Peterson, 1999; Belem et al., 2019).

The Parc National du Banc d'Arguin (PNBA), in Mauritania (Fig. 1A), offers a representative example of a negative estuary where the high temperatures and aridity of a desert climate, combined with limited water exchange with the adjoining Atlantic Ocean, create a strong offshore/inshore salinity and a $\delta^{18}\text{O}$ gradient year-round (Fig. 1B; Wolff et al., 1993). Conversely, no offshore/inshore $\delta^{34}\text{S}$ gradient is expected to exist in the PNBA as a result of the almost complete absence of freshwater run-off, and negligible wind-driven inputs of terrestrial particulate organic matter from the adjoining sparsely vegetated desert (Pottier et al., 2021). Here, the existence of patches of anoxic sediments covered by seagrasses (Pottier et al., 2021) is the only source of variability in $\delta^{34}\text{S}$ values of the fishes and sea turtles inhabiting the Parc (Cardona et al., 2009). However, nothing is known about the variation of these values in marine mammals.

Mauritanian waters support a diverse community of marine mammals that includes tropical, subtropical and boreal species (Robineau and Vely, 1998). This is not only because the Mauritanian coast represents a transition zone between the tropical and subtropical waters of the Northeastern Atlantic Ocean (Pelegri et al., 2017), but also because of the existence of two important upwelling areas, constantly enhancing coastal primary production and increasing habitat heterogeneity (Fig. 1A; Cropper et al., 2014).

In a previous study, Pinela et al. (2010) used $\delta^{13}\text{C}$ values to segregate several species of marine mammals along the offshore/inshore gradient off Mauritania, and $\delta^{15}\text{N}$ values to assess their trophic positions. Here, $\delta^{18}\text{O}$ values were incorporated to better discriminate between species using water masses of contrasting salinity, and $\delta^{34}\text{S}$ values to identify those species tightly linked to seagrass meadows.

2. Methods

2.1. Study area

The Islamic Republic of Mauritania is located at the Northwestern coast of Africa, between 16 and 22° N and 16–18° W (Fig. 1A). This is an area of hydrological complexity due to the strong winds and currents that create almost constant upwelling events throughout the year (Sevrin-Reyssac, 1993; Robineau and Vely, 1998).

On the northern parts of the Mauritanian coast, the salty, cold, and nutrient-rich waters of the Canary Current flow southward reaching the Cape Blanc Peninsula at around 21° N. According to Cropper et al. (2014), this area belongs to the “Permanent Annual Upwelling Zone” (Fig. 1A), where southward trade winds produce the offshore advection of surface waters, which are replaced by the colder and nutrient-rich subsurface waters, creating strong and permanent upwelling events along the coast. Consequently, part of these upwelled waters enters the PNBA, located south of Cape Blanc, and are transported southward across the tidal flats, eventually returning to the open ocean (Fig. 1B; Wolff and Smit, 1990). However, the influence of the upwelling decreases significantly towards the inner parts of the PNBA, where the shallow seas and the tidal changes decrease the intensity of the water circulation, thus increasing the transport time inside the bay (Wolff et al., 1993). Here, the influence of the Sahara winds creates conditions of particularly high salinities and temperatures, especially in the intertidal mudflats and channels covered by benthic primary producers, such as seagrasses and macroalgae (Fig. 1B; Wolff and Smit, 1990; Araujo and Campredon, 2016; Pottier et al., 2021).

From the south, the seasonal trade winds produce a series of upwelling events, especially during winter, in the “Mauritania-Senegalese Upwelling Zone” (Fig. 1A; Cropper et al., 2014). Here, the less salty, warmer, and nutrient-poorer Mauritanian Current (MC) flows northward along the Mauritanian coast bringing warmer surface waters up to about 20° N (Mittelstaedt, 1991; Fischer et al., 2016). Similarly, a sub-surface current noted as the Poleward Under-Current (PUC; Fig. 1A), almost indistinguishable from the Mauritanian Current, flows northward along the shelf break and reaches farther north than the surface waters, increasing in salinity as it mixes with the Canary Current off Cape Blanc (Fig. 1B; Peña-Izquierdo et al., 2012). The combination of these two northward currents creates the MC-PUC system (Fig. 1A).

West of the upwelling areas off the Mauritanian shelf, the Cape Verde Frontal Zone appears as a boundary between the Canary Current and the MC-PUC system (Fig. 1A; Zenk et al., 1991; Meunier et al., 2012). This boundary is not spatially fixed, but it is rather defined by the location of the 36 isohaline at the 150 m depth (Zenk et al., 1991). Hence, the interaction between the coastal upwelling and this frontal zone becomes complex and dynamic, especially as the two water masses may be upwelled and laterally mixed within this zone (Meunier et al., 2012). Furthermore, the variable contributions of salinity and temperature to the density create a weak and unstable density front with mesoscale variability; the destabilization of this front often results in the formation of mesoscale eddies off Cape Blanc (Meunier et al., 2012).

Different habitat types are found along the Mauritanian coast (Fig. 1A). The Cape Blanc Peninsula and the northern part of the PNBA, are mostly rocky cliffs with scattered, tide-dependent sandy beaches with patchy seagrass beds, mostly *Cymodocea nodosa*. The inshore regions of the PNBA constitute a unique ecosystem, with intertidal areas composed by shallow mudflats, crossed by channels covered with patches of seagrass beds, mostly dominated by *Zostera noltrii* and

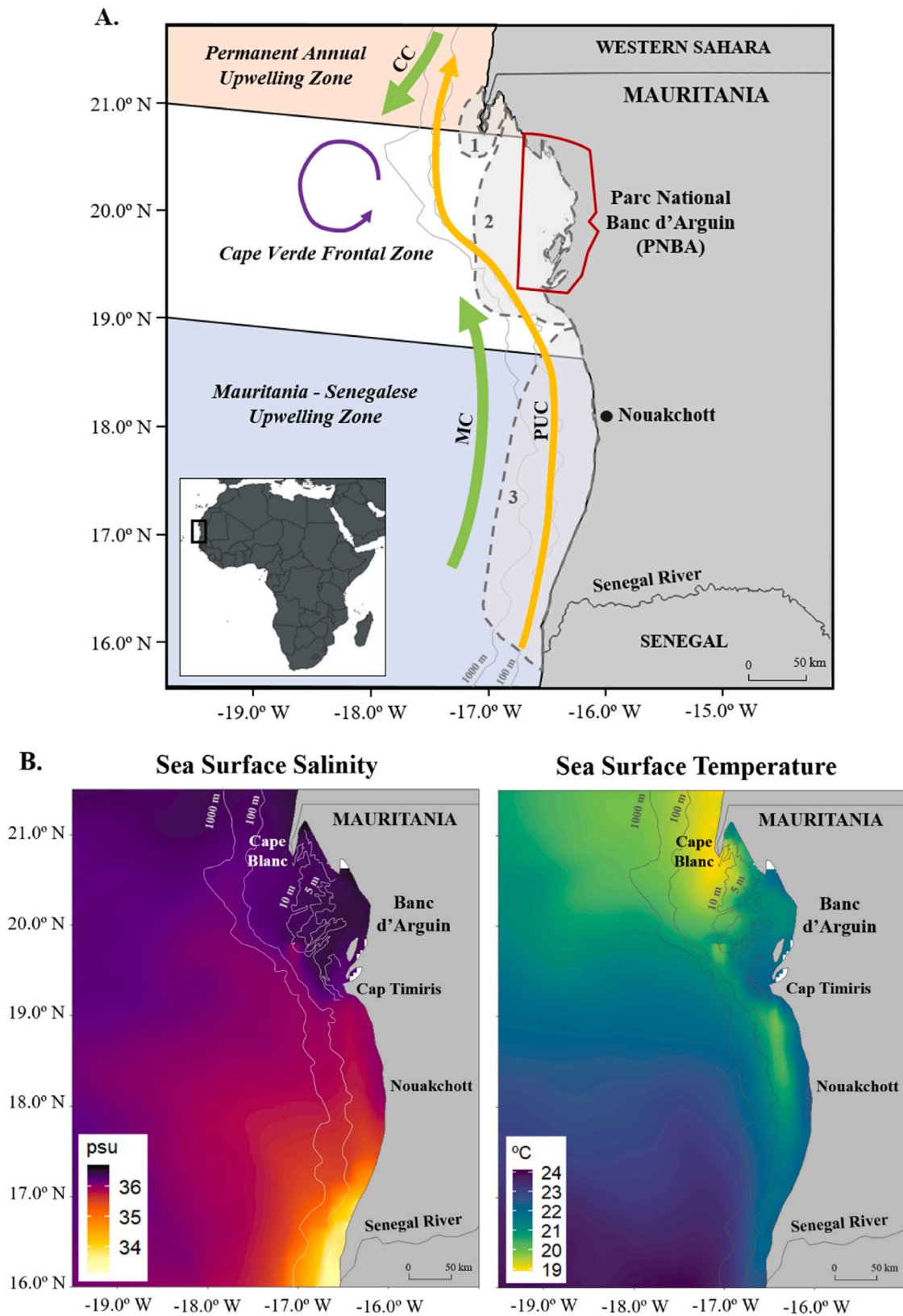


Fig. 1. A. Study area showing the upwelling zones (Cropper et al., 2014) and main habitat types (Legibre, 1991; Pottier et al., 2021) found along the Mauritanian coast: (1) Rocky cliffs and scattered, tide-dependent sandy beaches and patches of seagrass beds (*Cymodocea nodosa*). (2) Tidal mudflats, unvegetated in the northern region, and covered by seagrasses and mangroves in the southern region. (3) Sandy beach with scattered sublittoral seagrass patches, deltaic zones and ancient lagoons. The limits of the PNBA are denoted by the red contour. Green arrows indicate the general direction of the two major currents reaching the area: the Canary Current (CC) and the Mauritanian Current (MC). The yellow arrow represents the along-slope Poleward Under-Current (PUC), and the purple arrow represents the Cape Verde Frontal Zone. B. Annual mean sea surface salinity (practical salinity units, psu) and sea surface temperature (°C) off the Mauritanian coast in 1993, according to Copernicus. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Cymodocea nodosa, and mangrove forests in the southern parts. On the other hand, the coast of Nouakchott, known as the “Grande Plage”, is composed mainly of sandy beaches with scattered sublittoral seagrass patches (Lebigre, 1991; Pottier et al., 2021; Pinela et al., 2010).

The tidal flats inside the PNBA (Fig. 1A) are relatively isolated, producing differences in the underwater climate along the bay. For instance, the water temperature and salinity vary with season and location, and they can be several degrees higher on the eastern slope compared to the west, as well as on the north-south gradient (Fig. 1B; Sevrin-Reyssac, 1993). Hence, average temperature and salinity values of 16–20 °C and 35–36, respectively, can be found on the northern areas, where the cold ocean waters first enter the bay, and reach up to 25–29 °C and around 38–40, respectively, towards the southern parts due to the isolation of the coastal waters and the high evaporation rates (Fig. 1B; Wolff and Smit, 1990; Sevrin-Reyssac, 1993). However, temperature and salinity values higher than 35 °C and 38, respectively, have been recorded at the tidal flats and shallower pools during low tides (Wolff and Smit, 1990; Dedah, 1993; Sevrin-Reyssac, 1993). On the contrary, salinity on the southern coast is lower due to the influence of the MC and the Senegal River, with values lower than 20 at the estuary basin and reaching 35–36 around Nouakchott (Fig. 1B; Chevalier et al., 2014).

In this region, the marine mammal fauna is of particular interest. In the North, the Cape Blanc Peninsula holds the largest extant subpopulation of the endangered Mediterranean monk seal, *Monachus monachus*, whereas another critically endangered species, the Atlantic humpback dolphin, *Sousa teuszii*, inhabits the shallow areas and intertidal mudflats of the PNBA (Fig. 1A; Collins et al., 2017; Karamanlidis and Dendrinis, 2015). Other coastal species, such as the harbour porpoise, *Phocoena phocoena*, are often seen in the colder waters around Cape Blanc and in the northern fringe of the PNBA, while the most commonly reported species, the bottlenose dolphin *Tursiops truncatus*, can be found all over the Mauritanian coast and even in offshore areas (Fig. 1B; Robineau and Vely, 1998). Moreover, oceanic species such as the Atlantic spotted dolphin, *Stenella frontalis* are present offshore in the warmer tropical waters brought up by the Mauritanian Current (Fig. 1B; Robineau and Vely, 1998; Herzing and Perrin, 2018), whereas the long-finned pilot whale, *Globicephala melas* prefers the cold temperate waters of the Canary Current, and the common dolphin, *Delphinus delphis*, the second most commonly reported species in the area, is often found in deep waters offshore but is also seen in coastal areas (Fig. 1B; Robineau and Vely, 1998; Olson, 2018).

2.2. Sampling

Bone samples from 68 individuals, pertaining to seven marine mammal species, were collected along the coast of the Islamic Republic of Mauritania, from 1994 to 1997: Atlantic humpback dolphin *Sousa teuszii* (n = 3), bottlenose dolphin *Tursiops truncatus* (n = 15), harbour porpoise *Phocoena phocoena* (n = 15), long-finned pilot whale *Globicephala melas* (n = 3), Atlantic spotted dolphin *Stenella frontalis* (n = 5), common short-beak dolphin *Delphinus delphis* (n = 15), and Mediterranean monk seal *Monachus monachus* (n = 12). In all cases, samples were taken from the skull of dead stranded individuals and deposited at the scientific collection of the Faculty of Biology of the University of Barcelona (Spain). Only complete skulls found in good condition without evidence of weathering were selected to ensure no post-mortem alteration of the stable isotope ratios due to long-term exposure to the environmental conditions (Nelson et al., 1986). Additionally, the amount of carbonate in the samples was measured (Supp. Table 2) to assess the risk of precipitation of environmental carbonates (see below).

There is no information about the cause of death of these individuals, but it is assumed that in most cases was due to natural causes (Pinela et al., 2010), with a few cases of potential mortality caused by fishing interactions (Nieri et al., 1999). Although the age and standard length of the individuals were mostly unknown, the condylobasal length of each skull was measured and the degree of fusion of the premaxilla with the

maxilla was determined to ensure that only adult specimens were analysed (Mo et al., 2009). Small fragments of the skull were sampled from the auditory bulla in the case of the Mediterranean monk seals, and from the pterygoid in the case of cetaceans, to avoid damaging the skulls for subsequent studies. Furthermore, bone tissue has a relatively slow turnover rate, thus the values reported here integrate several years of information on the habitat use of each individual (Hobson et al., 2010; Schoeninger, 2010; Fahy et al., 2017).

2.3. Stable isotope analysis

Stable isotope ratios of C and N were compiled from Pinela et al. (2010) and Drago et al. (2021). Additional bone samples from the same specimens were collected for O and S stable isotope analysis. Bone samples were cleaned with distilled water, dried in a stove at 60 °C for 36 h, ground into a fine powder using a mortar and pestle, and split in two aliquots, one for $\delta^{18}\text{O}$ analysis and the other one for $\delta^{34}\text{S}$ analysis.

Prior to $\delta^{18}\text{O}$ analysis, the inorganic matrix of the bone was obtained by soaking the bone powder with 30% hydrogen peroxide (H_2O_2) for 48 h in partially covered vials at 4 °C, to remove any organic compounds and prevent the precipitation of secondary carbonate. The samples were then rinsed repeatedly with deionized (Milli-Q) water and treated with 1 M of calcium acetate–acetic acid buffer for another 24 h to remove any diagenetic carbonate. Finally, they were carefully rinsed again with Milli-Q water and dried for 24 h and left to dry in an oven at 50 °C for another 24 h (Koch et al., 1997). A Kiel III Carbonate Device preparation system (Thermo Electron-Dual Inlet, Thermo Fisher Scientific, Bremen, Germany) linked to a model MAT-25% gas source mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) was used for these analyses. Approximately 1.0 mg of each treated bone sample was weighed and dissolved in 100% phosphoric acid at 70 °C with concurrent cryogenic trapping of CO_2 and H_2O . The CO_2 was then admitted to the mass spectrometer for analysis. International isotope secondary standards distributed by the International Atomic Energy Agency (IAEA) of known $^{18}\text{O}/^{16}\text{O}$ ratios, in relation to the Vienna Pee Dee Belemnite (V-PDB) calcium carbonate were used. These consisted of the NBS-19 and NBS-18 calcite standard, with $\delta^{18}\text{O}$ values of -2.20‰ and -23.2‰ , respectively, relative to V-PDB. These two isotopic reference materials were employed once every six analysed samples in order to recalibrate the system and compensate for any measurement drift over time. The analytical precision of $\delta^{18}\text{O}$ values tested by replicate analyses was $\pm 0.05\text{‰}$ (standard deviation). Because $\delta^{18}\text{O}$ values in animal studies are more commonly presented relative to the Vienna Standard Mean Oceanic Water (V-SMOW) index, $\delta^{18}\text{O}$ values were converted from PDB to SMOW according to the following equation (Koch et al., 1997):

$$\delta^{18}\text{O}_{(\text{SMOW})} = [\delta^{18}\text{O}_{(\text{PDB})} \times 1.03086] + 30.86 \quad (1)$$

The integrity of the samples for the $\delta^{18}\text{O}$ analysis was assessed by estimating the percentage of carbonate (weight) of the samples (Suppl. Table 2), taking into account that the carbonate contents of well preserve mammalian bones, including those of cetaceans, ranges from 1.31 to 6.52 % (Sponheimer and Lee-Thorp, 1999; Nemliher et al., 2004; Munro et al., 2008).

No pre-treatment was applied to the crushed bone prior to $\delta^{34}\text{S}$ analysis, to avoid removing amino acids that contain this element (Nehlich, 2015). Approximately 10 mg of each sample was weighed into a tin capsule and a catalyst (vanadium pentoxide V_2O_5) was added to accelerate the combustion and reduce variability (Nehlich and Richards, 2009). Samples were loaded and combusted at 1030 °C and analysed with an Elemental Analyzer (Carlo Erba 1108) coupled to a Delta Plus XP mass spectrometer through a ConFlow III interface (both from ThermoFisher). International isotope secondary standards distributed by the International Atomic Energy Agency (IAEA) of known $^{34}\text{S}/^{32}\text{S}$ ratios, in relation to the Vienna- Canyon Diablo Troilite (VCDT) were used. These consisted in barium sulphate (NBS-127: $\delta^{34}\text{S} = +21.2\text{‰}$, IAEA SO-5:

$\delta^{34}\text{S} = +0.5\text{‰}$ and IAEA SO-6: $\delta^{34}\text{S} = -34.1\text{‰}$) and YCEM ($\delta^{34}\text{S} = +12.8$), and they were employed once every 12 samples. Analytical precision for repeat measurements of the reference material, run in parallel with the bone samples, was 0.1 ‰.

Stable isotope abundances are expressed in delta (δ) notation, with the relative variations of stable isotope ratios expressed in per mil (‰) deviations from predefined international standards, and they were calculated as:

$$\delta^i\text{X} = \left[\left(\frac{i\text{X}}{j\text{X}} \right)_{\text{sample}} \right] / \left[\left(\frac{i\text{X}}{j\text{X}} \right)_{\text{standard}} \right] - 1 \quad (2)$$

where $j\text{X}$ is the heavier isotope (^{13}C , ^{15}N , ^{18}O or ^{34}S), and $i\text{X}$ is the lighter isotope (^{12}C , ^{14}N , ^{16}O or ^{32}S) in the analytical sample and international measurement standard (Bond and Hobson, 2012).

All the stable isotope analyses were performed at the Centres Científics i Tecnològics (CCiT-UB) of the University of Barcelona, Spain.

2.4. Data analysis

Normality was tested by means of the Shapiro-Wilk test, and homoscedasticity by means of the Levene test. As the distribution of the stable isotope ratios often departed from normality, and variances were often heteroscedastic, the non-parametric Kruskal-Wallis test, followed by Dunn's post-hoc test with the Holm correction for multiple comparisons, were used for further analysis (Chen et al., 2017).

In order to estimate the isotopic niche width and niche overlap between the considered marine mammal species, the standard ellipse area in two-dimensional plots ($\delta^{18}\text{O}$ - $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ - $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$) were calculated using the package "SIBER" (Stable Isotope Bayesian Ellipses; Jackson et al., 2011). Partitioning among $\delta^{34}\text{S}$ values was not considered here because differences between species were not statistically significant. Two complementary approaches were used to estimate the isotopic niche width (Jackson et al., 2011). The standard ellipse areas corrected for small sample size (SEAc) were used to plot the isotopic niche of each species within the isotopic space (isospace) and to calculate the overlap among species, and the Bayesian standard ellipse areas (SEAB) were used to obtain an unbiased estimate of the isotopic niche width with 95% credibility intervals (Supp. Table 1).

Spatiotemporal trends in SST ($^{\circ}\text{C}$) and SSS (practical salinity) used in Fig. 1B were sourced from the Global Ocean Physics and Biogeochemistry Reanalyses (GLOBAL_MULTIYEAR_PHY_001_030) of the EU Copernicus Marine Environment Monitoring Service (<https://marine.copernicus.eu/>).

All statistical analyses and plots were carried out using R Statistical Software v 4.1.2 (R Core Team, 2021).

Finally, in order to confirm the results obtained in the present study, the inferences on the geographic distribution of each marine mammal species, derived from their isotopic niche, were compared with that derived from a variety of sources: sighting and stranding reports from ship-based surveys (Fig. 5; Fraser, 1973; Duguy, 1975; Maigret et al., 1976; Maigret, 1980a; Maigret, 1980b; Maigret, 1981; Smeenk et al., 1992; Vely et al., 1995; Robineau and Vely, 1998; Nieri et al., 1999; Tulp and Leopold, 2004; Gazo and Aguilar, 2005; Camphuysen et al., 2013; Weir and Collins, 2015; Russell et al., 2018; Camphuysen, 2021; Camphuysen et al., 2022; Samba Bilal et al., 2023), sightings from shore (González et al., 1997), sightings from fishing vessels (University of Barcelona database), and electronic tracking of individuals (Gazo and Aguilar, 2005). This was done by combining the location of the sightings and strandings with the salinity and temperature maps built for the area (Fig. 1B), as well as the distribution of the main benthic primary producers (Pottier et al., 2021).

3. Results

The carbonate contents of all the samples analysed in this study fell within the range reported for well-preserved mammalian bone

(1.31–6.52 %), except for one sample belonging to a bottlenose dolphin, which had a slightly lower carbonate percentage (1.00; Suppl. Table 2). It should be noted that bottlenose dolphins presented the widest range of carbonate percentage (1.00–5.28 %), but the $\delta^{18}\text{O}$ values of the individuals at both extremes of this range were similar (Suppl. Table 2), thus suggesting the absence of influence of the amount of carbonate on the $\delta^{18}\text{O}$ values and ruling out the presence of environmental carbonates in the samples with the highest carbonate contents.

Statistically significant differences existed between the considered marine mammal species for $\delta^{18}\text{O}$ values ($X^2 = 32.37$, $p < 0.001$), $\delta^{13}\text{C}$ ($X^2 = 39.63$, $p < 0.001$), and $\delta^{15}\text{N}$ ($X^2 = 33.77$, $p < 0.001$), but not for $\delta^{34}\text{S}$ values ($X^2 = 57.23$, $p = 0.455$). Nevertheless, a remarkable individual variability in $\delta^{34}\text{S}$ values was observed in all species, especially in bottlenose dolphins, harbour porpoises, Mediterranean monk seals, and Atlantic humpback dolphins. Furthermore, several individuals of each of the aforementioned species had $\delta^{34}\text{S}$ values lower than 15 ‰ (Fig. 2), whereas all individuals of common dolphins, spotted Atlantic dolphins and long-finned pilot whales stayed above this threshold (Fig. 2).

According to the $\delta^{18}\text{O}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, distinct isotopic niches can be found between the considered species. On one side, Atlantic spotted dolphins and Mediterranean monk seals presented the lowest mean $\delta^{18}\text{O}$ values, whereas common dolphins and Atlantic humpback dolphins showed the highest values (Fig. 3). On the other hand, Atlantic humpback dolphins, Mediterranean monk seals, bottlenose dolphins and harbour porpoises showed the highest mean $\delta^{13}\text{C}$ values, while common dolphins had the lowest values (Fig. 3). Additionally, common dolphins and Atlantic spotted dolphins showed the lowest mean $\delta^{15}\text{N}$ values, and Mediterranean monk seals had the highest values (Fig. 3).

The above-mentioned differences suggest that Atlantic humpback dolphins, Mediterranean monk seals, Atlantic spotted dolphins, and common dolphins had unique, distinct isotopic niches (Fig. 4; Table 1). On the contrary, bottlenose dolphins had an extremely broad isotopic niche, encompassing those of harbour porpoises and long-finned pilot whales in the three considered dimensions ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Fig. 4; Table 1). The latter two species also showed similar isotopic niches on the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ axes, but long-finned pilot whales had higher $\delta^{15}\text{N}$ values. Moreover, the distribution of the species according to the boat-based sighting reports agrees with this interpretation, as Atlantic humpback dolphins were restricted to the PNBA, Mediterranean monk seals, harbour porpoises and long-finned pilot whales occurred mostly off Cape Blanc, Atlantic spotted dolphins and common dolphins inhabited mostly the continental slope and oceanic waters, and bottlenose dolphins occurred everywhere, from the innermost areas of the PNBA to oceanic waters beyond the continental shelf (Fig. 5).

4. Discussion

It is commonly assumed that the resolution of the isotopic niche of consumers improves when considering a larger number of chemical elements. This has elicited a progressively increasing interest in multi-element approaches in isotopic ecology (Rossman et al., 2016; Borrell et al., 2021; García-Vernet et al., 2021; Cani et al., 2023). Nevertheless, resolution is expected to improve only if steep environmental gradients exist at the appropriate spatial scale, as highlighted by the present study. Here, incorporating $\delta^{18}\text{O}$ values certainly improved our understanding on niche partitioning between the marine mammals occurring off Northwestern Africa (Fig. 3; Fig. 4), but the $\delta^{34}\text{S}$ values were not as useful to distinguish between species (Fig. 2). It should be noted, however, that individual variability in $\delta^{34}\text{S}$ values was high, which suggested a heterogeneous environment, but in this case, the intraspecific variability was as large as the interspecific variability. This is because the process generating a heterogeneous distribution of $\delta^{34}\text{S}$ values in prey species operates at a much smaller spatial scale than the home range of the considered species.

Conversely, major salinity gradients exist at a geographical scale compatible with that of the home ranges of the considered marine

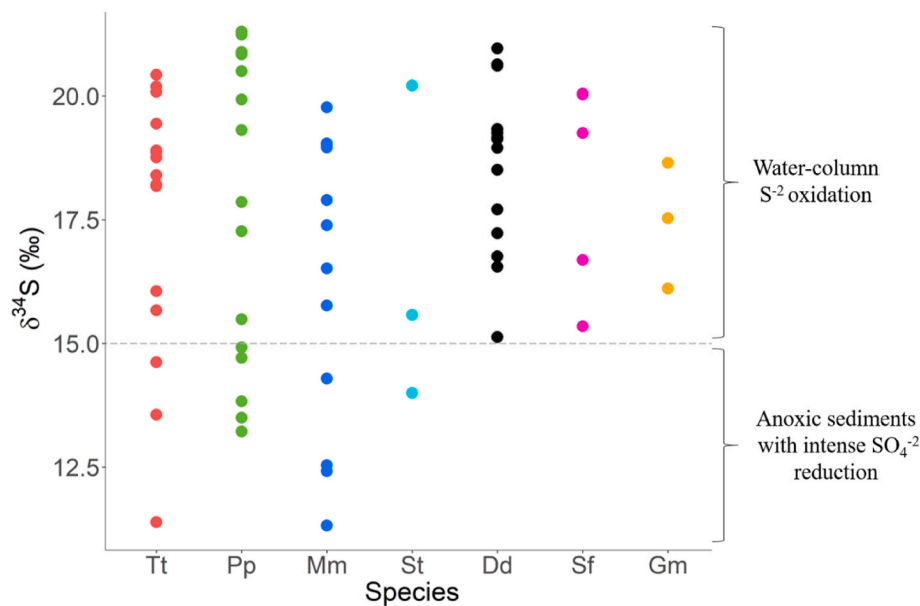


Fig. 2. Scatterplot of the sulphur stable isotope ratios ($\delta^{34}\text{S}$) for the considered marine mammal species from Mauritania. The dotted grey line indicates the approximate transition between the two environmental conditions described on the right. Species: common dolphin (Dd; $n = 15$), bottlenose dolphin (Tt; $n = 15$), harbour porpoise (Pp; $n = 15$), Mediterranean monk seal (Mm; $n = 12$), Atlantic humpback dolphin (St; $n = 3$), Atlantic spotted dolphin (Sf; $n = 5$) and long-finned pilot whale (Gm; $n = 3$).

mammal species (Fig. 5; Wolff and Smit, 1990; Klenz et al., 2018). The region is characterized by the existence of several water masses with very distinct physical and chemical properties (Peña-Izquierdo et al., 2012). To the best of our knowledge, *in situ* measurements of the $\delta^{18}\text{O}$ values of sea water in the study region are missing, but using the $\delta^{18}\text{O}$ /Salinity relationship reported by Schmidt (1999) for the upper ocean layer (<250 m) and the salinity values reported for each area within the study region, it was possible to estimate the $\delta^{18}\text{O}$ values of each water mass. It should be noted that both the temperature and the balance between evaporation and precipitation can affect the $\delta^{18}\text{O}$ values of surface waters, but the latter is often the main driver of their distribution (Conroy et al., 2014). Hence, the positive and linear correlation existing between the $\delta^{18}\text{O}$ values and the salinity of the water (Conroy et al., 2014; Belem et al., 2019) facilitates the isotopic distinction between water masses.

From the North, the Canary Current flows southward bringing salty, cold, and nutrient-rich waters with a high phytoplankton growth rate (Peña-Izquierdo et al., 2012; Cropper et al., 2014; Pelegrí et al., 2017). Usual salinity values for this current are between 35 and 37 (Wolff and Smit, 1990), which corresponds to estimated $\delta^{18}\text{O}$ values of 0.3–1.3 ‰, according to the Schmidt (1999) equation. Nevertheless, when reaching the shallow waters of Banc d'Arguin, salinity values increase up to 38–40 (Wolff and Smit, 1990), corresponding to $\delta^{18}\text{O}$ values of 1.8–2.8 ‰, according to the Schmidt (1999) equation. From the South, two currents flow northward, one as the less salty, warmer, and oligotrophic Mauritanian Current (MC) on the surface, and another as the along-slope subsurface Poleward Undercurrent (PUC), forming the MC-PUC system (Fig. 1A). Both of these currents share similar properties, but the PUC reaches farther North, beyond Cape Blanc, and shows a slight salinity increase as it mixes with the Canary Current (Peña-Izquierdo et al., 2012). In this case, due to the influence of the Senegal River at the southernmost coast of Mauritania, surface water salinity values can be lower than 30 inside the estuary (Chevalier et al., 2014), which corresponds to $\delta^{18}\text{O}$ values lower than -2.2 ‰ according to the Schmidt (1999) equation. On the other hand, at the coast of Nouakchott and all along the “Grande Plage”, salinity oscillate between 33 and 36 (Chevalier et al., 2014) corresponding to $\delta^{18}\text{O}$ values between -0.7 and 0.8 ‰, according to the Schmidt (1999) equation. Moreover, between

19° N and 21° N, the highly dynamic Cape Verde Frontal Zone represents the mixing area between the Canary Current and the MC-PUC system (Fig. 1A), with a marked thermohaline indicating the limit between the two water masses (Zenk et al., 1991; Peña-Izquierdo et al., 2012).

In general, a difference in $\delta^{18}\text{O}$ values of at least 4.0 ‰ seems to exist between areas such as Banc d'Arguin and the Senegal River estuary, whereas the averaged difference between the Canary Current and the Mauritanian Current is 0.8 ‰, and between the Banc d'Arguin and the two currents is 1.5 and 2.3 ‰, respectively. The largest difference found for the $\delta^{18}\text{O}$ values in the bone of the marine mammals analysed here was 3.3 ‰, between an Atlantic humpback dolphin and a harbour porpoise, but several species had mean differences of more than 0.8 ‰, such as the common dolphin compared to the Mediterranean monk seal and the Atlantic spotted dolphin, and the Atlantic humpback dolphin with the rest of the considered species. Hence, considering that the $\delta^{18}\text{O}$ composition of the biogenic apatite of marine mammal bones is strongly correlated with that of body water (Barrick et al., 1992; Newsome et al., 2010), the above reported differences likely indicate the use of distinct water masses by the different species, which is further discussed in the latter section.

It is worth mentioning, however, that Clementz and Koch (2001) reported a near 2.0 ‰ ^{18}O -enrichment in cetaceans compared to pinnipeds that were assumed to use identical water masses, although they were unable to provide an explanation for that offset. Furthermore, in this study the stable isotope ratios of monk seals were analysed in the tympanic bulla while those of cetaceans were analysed in the pterygoid bone, which might introduce an additional confounding factor when comparing the stable isotope values from the two sample sets. Previous research has shown homogeneous $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across the skull bones of pinnipeds (Riofrío-Lazo and Aurióles-Gamboa, 2013; Clark et al., 2017), while finding significant differences between bones from the skull, the axial and the appendicular skeletons of marine mammals due to differences in turnover rates (Clark et al., 2017; Bas et al., 2019). No comparable studies are available on the variability of $\delta^{18}\text{O}$ values across skeletal elements, but the periosteal bone has a much lower water content than other bones in cetaceans (Honda et al., 1984) and it is likely to have a lower turnover rate. Hence, the $\delta^{18}\text{O}$ values of the auditory bulla of pinnipeds and the pterygoid of cetaceans might integrate dietary

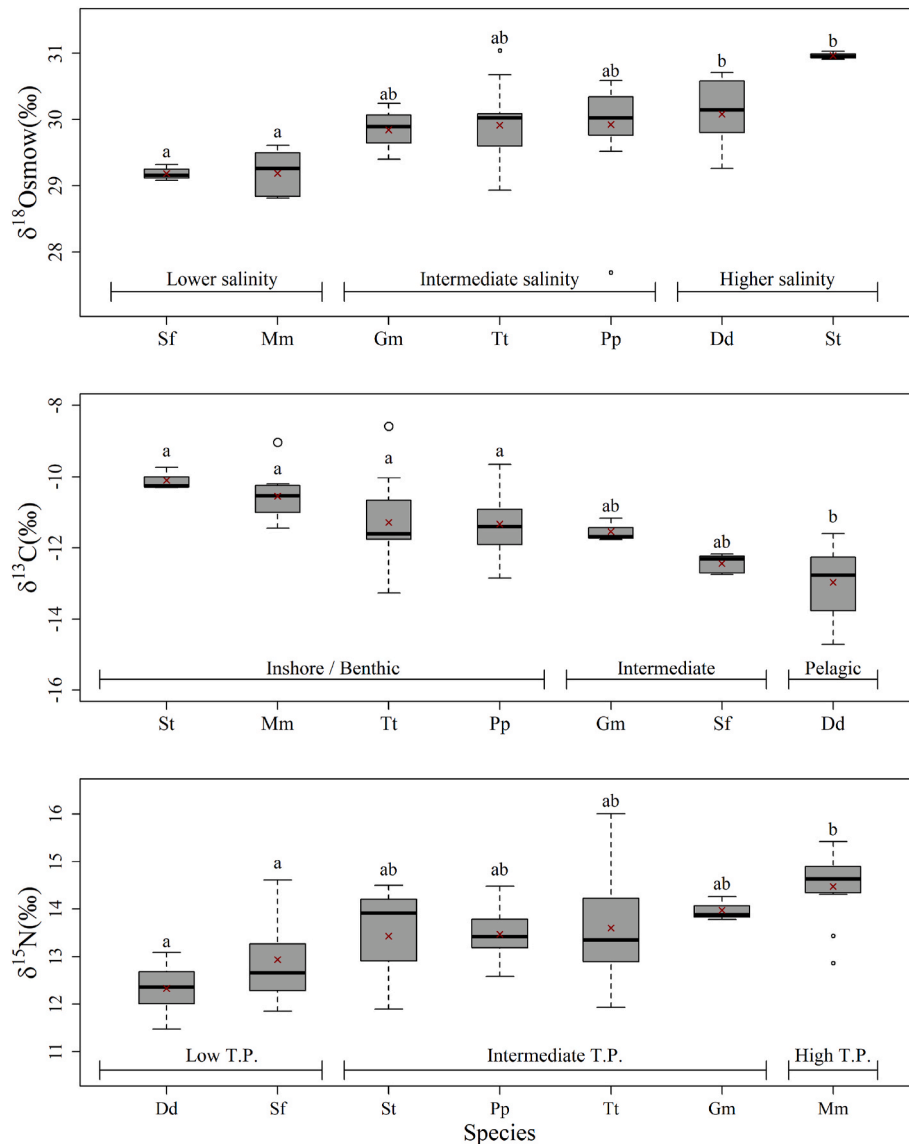


Fig. 3. Boxplots of the stable isotope ratios ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) for the considered marine mammal species from Mauritania. Species with different superscript letters are statistically different in their mean values, according to the Dunn's test of multiple comparisons and Kruskal-Wallis rank sums test with Holm's method for the correction for multiple comparisons. Boxes represent the first and third quartile, lines the median, "x" the mean, and whiskers the 95% confidence interval. Species: common dolphin (Dd; $n = 15$), bottlenose dolphin (Tt; $n = 15$), harbour porpoise (Pp; $n = 15$), Mediterranean monk seal (Mm; $n = 12$), Atlantic humpback dolphin (St; $n = 3$), Atlantic spotted dolphin (Sf; $n = 5$) and long-finned pilot whale (Gm; $n = 3$).

information over different time windows and hence, caution is necessary when comparing the stable isotope ratios reported here for monk seals and those of cetaceans.

In any case, when combining the $\delta^{18}\text{O}$ gradient reported above with the $\delta^{13}\text{C}$ gradient caused by on-shore/off-shore differences in the type of primary producers, further differentiations come to light. In Mauritania, coastal primary producers, such as seagrasses and macroalgae, have higher $\delta^{13}\text{C}$ values than phytoplankton (Cardona et al., 2009; Carlier et al., 2015). The same is also true for coastal and offshore consumers, with the highest $\delta^{13}\text{C}$ values found in the inhabitants of seagrass meadows (Cardona et al., 2009; Pinela et al., 2010). Moreover, $\delta^{13}\text{C}$ values can also assist in recognizing the influence of the upwelling in the system, since phytoplankton originated from these oceanographic phenomena and the resulting nutrient increase in surface waters tend to have higher $\delta^{13}\text{C}$ values than the oceanic phytoplankton, but still lower than benthic primary producers (Carlier et al., 2015).

Overall, high $\delta^{18}\text{O}$ values are associated with the influence of the Canary Current, as well as areas with high evaporation rates such as the

PNBA (Fig. 1), whereas the $\delta^{13}\text{C}$ values depend mostly on the primary source of C (Belem et al., 2019; Carlier et al., 2015; Drago et al., 2021). Likewise, $\delta^{15}\text{N}$ values seem to be a good proxy to determine the trophic position in this ecosystem, with consumers generally showing higher $\delta^{15}\text{N}$ values than their respective prey (Cardona et al., 2009; Pinela et al., 2010).

On the other hand, the variation of $\delta^{34}\text{S}$ values in marine waters depends mostly on the source of inorganic S and the oxidative state of the environment (Peterson et al., 1985). For instance, coastal primary producers often use ^{34}S -depleted sulphides (S^{-2}) produced in anoxic sediments, which results in low $\delta^{34}\text{S}$ values similar to those found in terrestrial organic matter (Peterson et al., 1985; Peterson, 1999). However, inputs of terrestrial particulate organic matter are negligible in desert regions and, hence, the sulphate (SO_4^{2-}) reduction in anoxic sediments is the only process generating a drop in $\delta^{34}\text{S}$ values in the area (Peterson, 1999). This is particularly true at the PNBA, where some of the main benthic primary producers are often associated with low $\delta^{34}\text{S}$ values. This is the case of the seagrass *Cymodocea nodosa* (Cardona et al.,

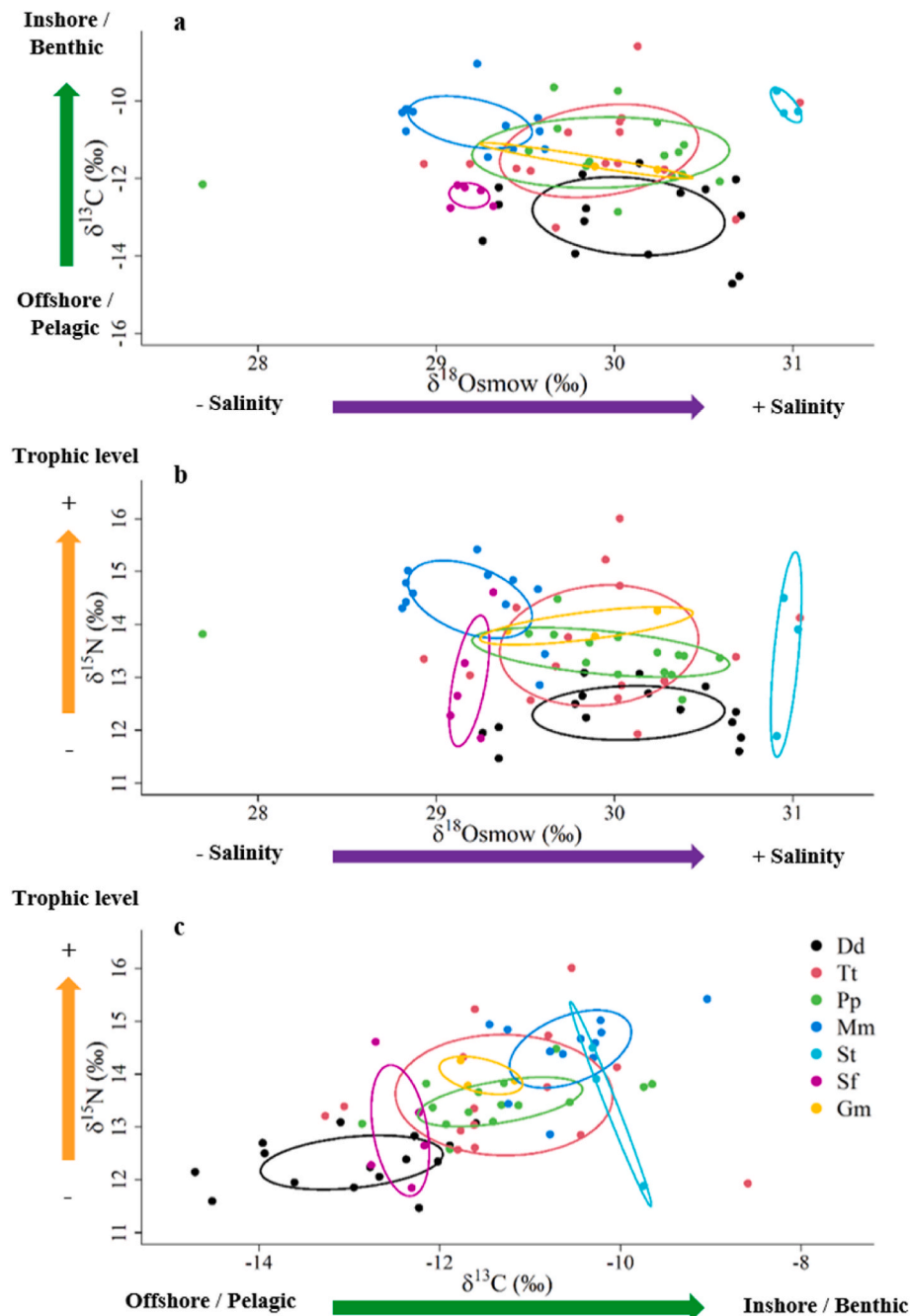


Fig. 4. Standard ellipses corrected for small sample size (SEAc) in the isospace ($\delta^{18}\text{O}_{\text{SMOW}}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the marine mammal species from Mauritania. The colored arrows indicate the general interpretation of the respective isotopic values for each element, where green corresponds to carbon ($\delta^{13}\text{C}$), purple to oxygen ($\delta^{18}\text{O}$) and orange to nitrogen ($\delta^{15}\text{N}$). Species: common dolphin (Dd; $n = 15$), bottlenose dolphin (Tt; $n = 15$), harbour porpoise (Pp; $n = 15$), Mediterranean monk seal (Mm; $n = 12$), Atlantic humpback dolphin (St; $n = 3$), Atlantic spotted dolphin (Sf; $n = 5$) and long-finned pilot whale (Gm; $n = 3$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2009), the saltmarshes *Spartina* sp. (Peterson et al., 1985) and mangroves (Velasquez-Vacca et al., 2023). Nevertheless, the limited distribution of these benthic primary producers along the Mauritanian coast (Lebigre, 1991; Pottier et al., 2021) suggests a mismatch between the spatial scale of $\delta^{34}\text{S}$ gradients (few kilometers) and the range of marine mammal movements (tens to hundreds of kilometers). Outside the PNBA, the intense bio-turbation and sediment resuspension induced by the upwelling events along the coast generate more oxidizing conditions in deeper sediment layers, and thus resulting in coastal $\delta^{34}\text{S}$ values resembling those of oxidative marine waters (Zopfi et al., 2008; Diaz et al., 2012). Hence, the presence of scattered seagrass patches (Pottier

et al., 2021) likely explains why some individuals of the four species inhabiting coastal areas (Mediterranean monk seals, harbour porpoises, bottlenose dolphins and Atlantic humpback dolphins) had $\delta^{34}\text{S}$ values lower than 15 ‰, an indicative of foraging in areas with intense SO_4^{2-} reduction (Fig. 2; Peterson et al., 1985), even though the average values of their populations did not differ from those of oceanic species (common dolphins, Atlantic spotted dolphins and long-finned pilot whales). In this scenario, $\delta^{34}\text{S}$ values do not allow to discriminate between species, but are useful to identify individuals foraging consistently on ^{34}S -depleted prey and hence linked to anoxic sediments (i.e. seagrass meadows).

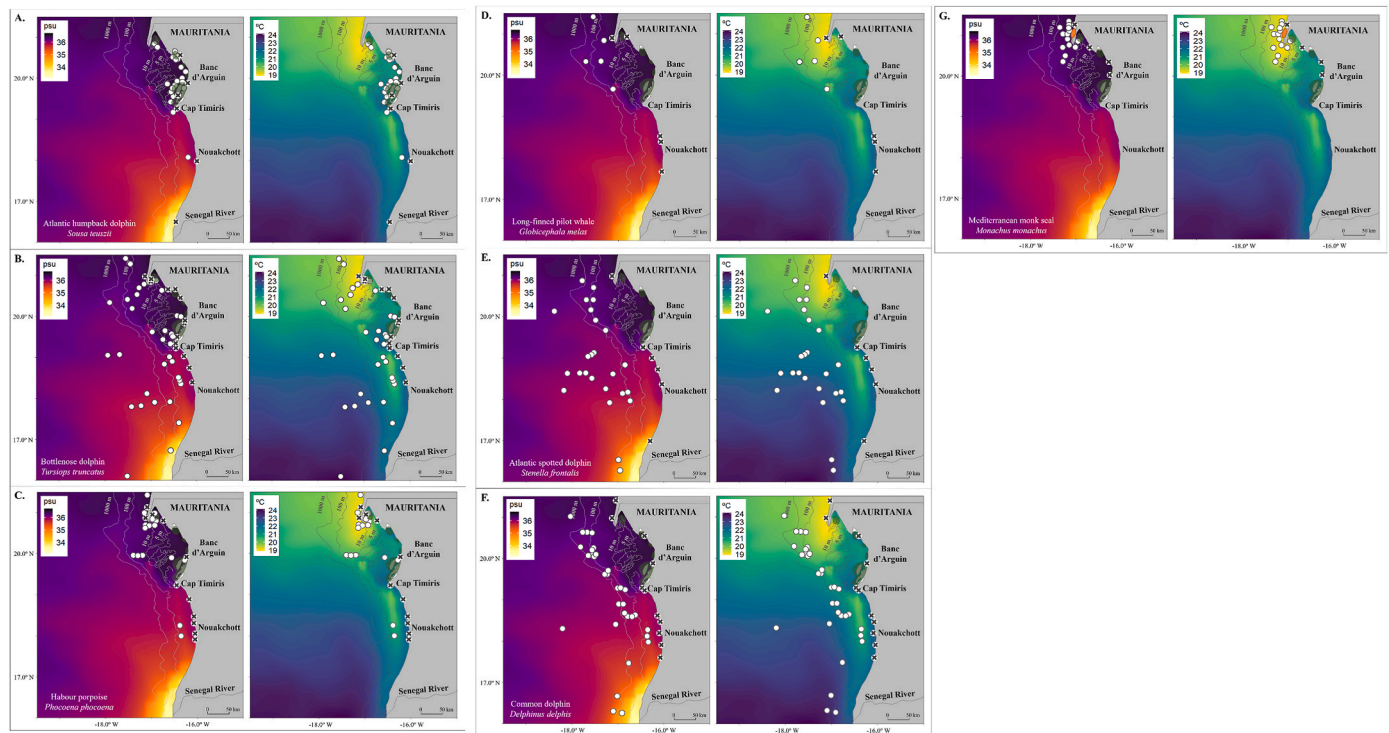


Fig. 5. Sighting and stranding reports for the considered marine mammal species along the Mauritanian coast (Fraser, 1973; Duguy, 1975; Maigret et al., 1976; Maigret, 1980a, 1980b, 1981; Smeenk et al., 1992; Vely et al., 1995; Robineau and Vely, 1998; Nieri et al., 1999; Tulp and Leopold, 2004; Gazo and Aguilar, 2005; Camphuysen et al., 2013, 2022; Weir and Collins, 2015; Russell et al., 2018; Camphuysen, 2021; Samba Bilal et al., 2023), placed over the annual mean sea surface salinity (left) and temperature (right) in the area. In each case, the species name is written in the bottom-left corner of the salinity map, each white point corresponds to at least one sighting, the white points with a dark “X” show the stranding locations, and the green oval shades represent the location of the main benthic primary producers inside the Parc National du Banc d’Arguin (Pottier et al., 2021). The orange region shown in subfigure G. represents the position of “Las Cuevecillas”, the location of the main haul-out caves for Mediterranean monk seals. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4.1. Habitat preferences of marine mammals

The Atlantic humpback dolphin is an endemic species to the shallow areas of the western African coast, from Western Sahara to Angola, with limited exchange between populations (Weir and Collins, 2015). The IUCN Red List of Threatened Species (International Union for Conservation of Nature) catalogues the species as “Critically Endangered”, with a decreasing trend in population size (Collins et al., 2017). In Mauritania, most sightings are clustered inside the PNBA, especially around the islands, and only occasional records of the species exist southward along the coast of Nouakchott (Fig. 5, A; Collins, 2015; Weir and Collins, 2015). Even with a small sample size, the consistency of the isotopic values of this species agrees with the almost exclusive use of the inner PNBA as feeding grounds, although a larger sample size would be advised to confirm these results more robustly.

On the other hand, bottlenose dolphins are described as the most common cetacean species in Mauritanian waters, since they are broadly distributed along the coast, both in nearshore and offshore areas, as well as inside the PNBA (Fig. 5, B; Robineau and Vely, 1998; Tulp and Leopold, 2004; Camphuysen et al., 2013; Russell et al., 2018; Camphuysen et al., 2022). Their wide range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values previously led Pinela et al. (2010) to suggest the possible existence of two ecotypes in the area, one with coastal and one with oceanic habits. The same was suggested by Van Waerebeek et al. (2016) based on several reports of bottlenose dolphins in association with short-finned pilot whales in pelagic habitats, and the year-round presence of the species in coastal areas of less than 14 m depth. This ecotype differentiation is further supported in the present study by the large intraspecific variation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (Fig. 3; Fig. 4). For instance, out of the analysed marine mammal species, only the three Atlantic Humpback dolphins

and one bottlenose dolphin seemed to consistently use the saltiest areas of the PNBA as foraging grounds, presenting the highest $\delta^{18}\text{O}$ values of the study with also high $\delta^{13}\text{C}$ values (Fig. 4). By contrast, other individuals of the bottlenose dolphin showed intermediate $\delta^{18}\text{O}$ values with a wide range of $\delta^{13}\text{C}$ values, which can encompass the coastal areas off Cape Blanc, as well as the Cape Verde Frontal Zone off the PNBA, with the influence of both coastal primary producers and phytoplankton. In addition, a few individuals had some of the lowest $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (Fig. 4), indicating the constant use of low salinity areas with high influence of oceanic phytoplankton, such as the MC-PUC system off the coast of Nouakchott (Fig. 4; Fig. 5, B). Furthermore, the variability of $\delta^{34}\text{S}$ values amongst this population agrees with the presence of scattered seagrass meadows and other benthic primary producers along the Mauritanian coast. This intraspecific variation found here for the bottlenose dolphin suggests not only the presence of two ecotypes, one coastal and one offshore, but also that within the coastal ecotype, some individuals likely remain inside the PNBA for extended periods of time.

Likewise, the isotopic niche of harbour porpoises and long-finned pilot whales seem to fit the isotopic landscape described for consumers foraging near and offshore the Cape Blanc Peninsula, respectively (Fig. 5C and D). Most harbour porpoises analysed here had high $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, indicating an extensive use of coastal areas with high salinity, such as the northern coast of Mauritania, which agrees with the local sightings of the species and their reported coastal habits and preference for cold temperate waters (Fig. 5, C; Bjørge and Tolley, 2018). There are also several sightings of the species offshore the PNBA and within the neritic zone, and only a few detections inside the Parc, which explains the large intraspecific variation of $\delta^{34}\text{S}$, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (Fig. 2; Fig. 3; Robineau and Vely, 1998; Camphuysen, 2021; Camphuysen et al., 2022). Furthermore, the lowest $\delta^{18}\text{O}$ value found in

Table 1

Percentage of overlapped area between each pair of marine mammal species for the different combinations of stable isotope values (isospaces) shown in Fig. 3, calculated with the R package “SIBER”. In each case, the “% Overlap 1” indicates the percentage of the isotopic niche area of “Species 1” overlapped with the isotopic niche area of “Species 2” for a given pair of species and isospace, and vice versa for “% Overlap 2”. Only the species pairs that showed constant overlap in all analysed dimensions were considered to use a similar isospace in Mauritanian waters. Species: common dolphin (Dd; n = 15), bottlenose dolphin (Tt; n = 15), harbour porpoise (Pp; n = 15), Mediterranean monk seal (Mm; n = 12), Atlantic humpback dolphin (St; n = 3), Atlantic spotted dolphin (Sf; n = 5) and long-finned pilot whale (Gm; n = 3).

Species (1 vs 2)	$\delta^{18}\text{O}$ vs $\delta^{13}\text{C}$ (% Overlap)		$\delta^{18}\text{O}$ vs $\delta^{15}\text{N}$ (% Overlap)		$\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ (% Overlap)	
	1	2	1	2	1	2
Dd vs Tt	12.76	10.51	17.10	7.42	0.00	0.00
Dd vs Pp	6.49	5.31	0.00	0.00	0.00	0.00
Dd vs Mm	0.00	0.00	0.00	0.00	0.00	0.00
Dd vs St	0.00	0.00	0.00	0.00	0.00	0.00
Dd vs Sf	0.00	0.00	0.00	0.00	26.55	34.66
Dd vs Gm	0.00	0.00	0.00	0.00	0.00	0.00
Tt vs Pp	82.32	81.76	39.26	84.10	26.46	99.93
Tt vs Mm	1.90	5.70	2.35	6.43	15.69	48.29
Tt vs St	0.00	0.00	0.00	0.00	2.44	25.00
Tt vs Sf	0.00	0.00	0.00	0.00	5.41	19.78
Tt vs Gm	11.15	88.06	22.98	93.26	10.82	99.93
Pp vs Mm	5.40	16.31	3.66	4.68	8.36	6.81
Pp vs St	0.00	0.00	0.00	0.00	0.00	0.00
Pp vs Sf	0.00	0.00	2.83	7.19	1.36	1.32
Pp vs Gm	12.46	99.10	19.81	37.54	10.46	25.58
Mm vs St	0.00	0.00	0.00	0.00	8.54	28.47
Mm vs Sf	0.00	0.00	5.04	10.03	0.00	0.00
Mm vs Gm	2.62	6.90	6.07	8.99	0.97	2.90
St vs Sf	0.00	0.00	0.00	0.00	0.00	0.00
St vs Gm	0.00	0.00	0.00	0.00	0.00	0.00
Sf vs Gm	0.00	0.00	1.99	1.48	0.00	0.00

this study belonged to a harbour porpoise, and even though it was an isolated individual, it agrees with the use of low salinity areas in the southern parts of the Mauritanian coast (Fig. 1B). This might be an indication of an overlap between the Mauritanian population and the individuals observed further south in Senegalese waters (Ridgway et al., 1998; Fontaine et al., 2014).

Moreover, long-finned pilot whales showed a partial overlap with harbour porpoises in all the considered isospaces, especially for the $\delta^{18}\text{O}$ values (Fig. 4; Table 1), suggesting the use of similar water masses (i.e., the Canary Current). Regardless, the lower mean $\delta^{13}\text{C}$ value of the former indicates a more offshore/pelagic feeding, consistent with the local sighting reports and their preference for cold-temperate waters (Fig. 3; Fig. 5, D). However, a larger sample size is needed to confirm these results. It is believed that Mauritania marks the southernmost limit of the species' distribution in the northeastern Atlantic, but since they are easy to confuse with the more common short-finned pilot whales, there are only few confirmed sightings of the species in the area (Robineau and Vely, 1998; Olson, 2018).

The last two cetacean species considered here, the Atlantic spotted dolphin, and the common dolphin, presented the lowest mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and the highest mean $\delta^{34}\text{S}$ values (Fig. 2; Fig. 3), typical from offshore/pelagic species. In fact, all sightings of these two species occurred either close or offshore the 100 m isobath (Fig. 5E and F), but the large differentiation in $\delta^{18}\text{O}$ values between them suggests the preferential use of different water masses as their main foraging grounds (Fig. 3; Fig. 4). On one side, the low $\delta^{18}\text{O}$ values of the Atlantic spotted dolphins indicate the use of lower salinity areas from the South Atlantic Central Water, here as the Mauritanian Current, which is consistent with their known preference for warm tropical waters (Fig. 5, E; Herzog and Perrin, 2018). In contrast, the higher $\delta^{18}\text{O}$ values and the wider range of $\delta^{13}\text{C}$ values found for common dolphins suggest the use of higher

salinity areas influenced by the Canary Current, either with upwelling-derived or oceanic phytoplankton (Fig. 5, F). However, the lower $\delta^{18}\text{O}$ values of some of these individuals indicate an overlap with the isotopic niche of the Atlantic spotted dolphins, something that is also evident in the reported sightings (Fig. 5E and F). In general, both species tend to inhabit deep waters close to the continental shelf break, but common dolphins often venture into coastal areas and do not seem to be bothered as much by changes in water temperature (Aguilar, personal observation; Robineau and Vely, 1998; Camphuysen et al., 2022).

Lastly, the Cape Blanc Peninsula (Fig. 1) shelters one of the two remaining large aggregations of the Mediterranean monk seal worldwide (Littnan et al., 2018), with the species currently listed as “Vulnerable” in the IUCN Red List of Threatened Species (Karamanlidis et al., 2023). Unlike cetaceans, the area used by Mediterranean monk seals is mainly linked to the location of their haul-out caves (Fig. 5, G). Thus, their distribution along the coast extends from Tarf el Guerguerat in Western Sahara (21° 11' N, 17° 01' W) to the tip of Cape Blanc (González et al., 1997) with scattered sightings further south and along the eastern coast of the Peninsula, such as at the tip of Cansado (20° 51' N, 17° 00' W) (Maigret, 1981; Camphuysen et al., 2013, 2022). However, a large part of this population concentrates in “Las Cuevecillas”, an area located about 35 km north of the tip of Cape Blanc and where the main haul-out caves are placed (Fig. 5, G; González et al., 1997). All samples here analysed were collected along this latter segment of coastline.

Little is known about the diet and offshore behaviour of Mediterranean monk seals in Mauritanian waters. The species is generally described as opportunistic coastal feeder (Karamanlidis et al., 2016), but the determination of its feeding habitat is complex due to a large intrapopulation variation. Juveniles and some reproductive males maintaining aquatic territories in front of the haul-out sites used by the females (Pastor et al., 2011) remain near the coast and feed in close neighboring waters, whilst adult females and some adult males periodically engage in foraging trips to a distance of at least 40 km offshore (Gazo and Aguilar, 2005). However, despite the distance travelled, such foraging trips rarely exceed 40–50 m depth (Gazo and Aguilar, 2005) because in this region the topography of the seafloor is quite flat and the continental slope is located far from shore (Fig. 1; Krastel et al., 2006; Karamanlidis et al., 2016). In fact, the high $\delta^{13}\text{C}$ values found for this species (Fig. 3) is consistent with a benthic feeding, and the presence of individuals with $\delta^{34}\text{S}$ values lower than the 15 ‰ threshold (Fig. 2) indicates that at least part of the population is using a foraging ground associated with seagrass meadows. This could be the Lévrier Bay, although sightings in this location are sparse (Fig. 5, G; Maigret, 1981; González et al., 1997). Alternatively, there might be some seagrass patches or another unknown source of low $\delta^{34}\text{S}$ values in the benthic areas along the continental slope off Cape Blanc. Given that the maximum diving depth recorded in the area (100 m for an adult male, and 78 m for a lactating female) (Gazo and Aguilar, 2005), is considerably lower than those recorded in the Mediterranean Sea (Karamanlidis et al., 2016), it is possible that the species is using most of the upper continental shelf as foraging grounds. In addition, the high $\delta^{15}\text{N}$ values indicate that they are feeding at higher trophic levels than the rest of the considered species (Fig. 3; Fig. 4; Pinela et al., 2010). On the other hand, the low $\delta^{18}\text{O}$ values of monk seals compared to those of cetaceans are odd, considering that the main water mass reaching their known foraging grounds is the salty Canary Current (Fig. 1; Gazo and Aguilar, 2005; Peña-Izquierdo et al., 2012). A possible explanation is the 2.0 ‰ offset between $\delta^{18}\text{O}$ values in pinnipeds and cetaceans reported by Clementz and Koch (2001). If this was true, monk seals would not be using less salty waters than cetaceans, but would overlap in distribution with most of them, except with Atlantic spotted dolphins. This confounding factor should be considered in future studies comparing $\delta^{18}\text{O}$ values between these two groups of marine mammals.

5. Conclusions

Overall, the addition of $\delta^{18}\text{O}$ values to the Mauritanian isotopic landscape in the present study allowed to distinguish between marine mammal species according to their use of the different water masses reaching the area. This is because the spatial scale of distribution of the salinity gradient is appropriate in this case, and thus, $\delta^{18}\text{O}$ values worked effectively as a complementary habitat tracer for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, improving the resolution of the isotopic niches. Meanwhile, the $\delta^{34}\text{S}$ values were more useful to identify individuals associated with anoxic sediments, since the scale of variation of the $\delta^{34}\text{S}$ gradient in the area was smaller and did not encompass the whole scale of movements of marine mammals. This study provides new insights into the use of multi-element approach in isotopic ecology, and improves the understanding of habitat partitioning between the considered marine mammal species in the eastern North Atlantic Ocean.

CRedit authorship contribution statement

Alessandra Cani: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luis Cardona:** Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Formal analysis, Conceptualization. **Álex Aguilar:** Writing – review & editing, Visualization, Methodology, Investigation, Funding acquisition. **Asunción Borrell:** Writing – review & editing, Visualization, Methodology, Investigation. **Massimiliano Drago:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2024.108641>.

References

- Araujo, A., Campredon, P., 2016. Banc d'Arguin (Mauritania). *The Wetland Book: II: Distribution, Description, and Conservation*, pp. 1319–1332.
- Barrick, R.E., Fischer, A.G., Kolodny, Y., Luz, B., Bohaska, D., 1992. Cetacean bone oxygen isotopes as proxies for Miocene ocean composition and glaciation. *Palaios* 7 (5), 521–531. <https://doi.org/10.2307/3514849>.
- Bas, M., García, N.A., Crespo, E.A., Cardona, L., 2019. Intrasekeletal variability in stable isotope ratios of C and N among pinnipeds and cetaceans. *Mar. Mamm. Sci.* 36 (1), 375–385. <https://doi.org/10.1111/mms.12644>.
- Belem, A.L., Caricchio, C., Albuquerque, A.L.S., Venancio, I.M., Zucchi, M., Santos, T.H.R., Alvarez, Y.G., 2019. Salinity and stable oxygen isotope relationship in the Southwestern Atlantic: constraints to paleoclimate reconstructions. *An Acad. Bras Ciências* 91.
- Ben-David, M., Flaherty, E.A., 2012. Stable isotopes in mammalian research: a beginner's guide. *J. Mammal.* 93 (2), 312–328. <https://doi.org/10.1644/11-MAMM-S-166.1>.
- Björge, A., Tolley, K.A., 2018. Habor porpoise. In: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), *Encyclopedia of Marine Mammals*, third ed. Academic Press, San Diego, pp. 448–451.
- Bond, A.L., Hobson, K.A., 2012. Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. *Waterbirds* 35 (2), 324–331.
- Borrell, A., Gazo, M., Aguilar, A., Raga, J.A., Degollada, E., Gozalbes, P. y, García-Vernet, R., 2021. Niche partitioning amongst northwestern Mediterranean cetaceans using stable isotopes. *Prog. Oceanogr.* 193, 102559. ISSN 0079-6611.
- Botta, S., Hohn, A.A., Macko, S.A., Secchi, E.R., 2012. Isotopic variation in delphinids from the subtropical western South Atlantic. *J. Mar. Biol. Assoc. U. K.* 92 (8), 1689–1698.
- Camphuysen, C.J., van Spanje, T.M., Verdaat, J.P., 2013. Ship-based Seabird and Marine Mammal Surveys off Mauritania, Nov-Dec 2012: Cruise Report, vol. 72. NIOZ.
- Camphuysen, C.J., 2021. Vulnerable Wildlife Concentrations at the Mauritanian Shelf. A Preliminary Atlas of Vulnerability to Surface Pollutants. Royal Netherlands Institute for Sea Research (NIOZ), The Netherlands, p. 45.
- Camphuysen, C.J., Schreurs, T.A.W., Bilal, A.S., 2022. Ship-based Seabird and Marine Mammal Surveys off Mauritania, 17 February–1 March 2022, p. 73. Royal Netherlands Institute for Sea Research (NIOZ), Den Burg, Texel and the Institut Mauritanien de Recherche Océanographique et des Pêche (IMROP), Nouadhibou.
- Cani, A., Cardona, L., Valdivia, M., González, E.M., Drago, M., 2023. Niche partitioning among marine mammals inhabiting a large estuary as revealed by stable isotopes of C, N, S, and O. *Estuar. Coast* 46 (4), 1083–1097. <https://doi.org/10.1007/s12237-023-01193-y>.
- Cardona, L., Revelles, M., Parga, M.L., Tomás, J., Aguilar, A., Alegre, F., Raga, A., Ferrer, X., 2009. Habitat use by loggerhead sea turtles *Caretta caretta* off the coast of eastern Spain results in a high vulnerability to neritic fishing gear. *Mar. Biol.* 156, 2621–2630. <https://doi.org/10.1007/s00227-009-1288-9>.
- Carlier, A., Chauvaud, L., van Der Geest, M., Le Loc'h, F., Le Duff, M., Vernet, M., Raffray, J., Diakhaté, D., Labrosse, P., Wagué, A., Le Goff, C., 2015. Trophic connectivity between offshore upwelling and the inshore food web of Banc d'Arguin (Mauritania): new insights from isotopic analysis. *Estuar. Coast Shelf Sci.* 165, 149–158. <https://doi.org/10.1016/j.ecss.2015.05.001>.
- Chen, S.Y., Feng, Z., Yi, X., 2017. A general introduction to adjustment for multiple comparisons. *J. Thorac. Dis.* 9 (6), 1725–1729. <https://doi.org/10.21037/jtd.2017.05.34>.
- Chevalier, C., Pagano, M., Corbin, D., Arfi, R., 2014. The salinity responses of tropical estuaries to changes in freshwater discharge, tidal mixing and geomorphology: case study of the man-affected Senegal River Estuary (West Africa). *Mar. Freshw. Res.* 65 (11), 987–1002. <https://doi.org/10.1071/MF13169>.
- Clark, C.T., Horstmann, L., Misarti, N., 2017. Quantifying variability in stable carbon and nitrogen isotope ratios within the skeletons of marine mammals of the suborder Caniformia. *J. Archaeol. Sci.: Report* 15, 393–400. <https://doi.org/10.1016/j.jasrep.2017.09.007>.
- Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia* 129, 461–472. <https://doi.org/10.1007/s004420100745>.
- Collins, T., 2015. Re-Assessment of the conservation status of the atlantic humpback dolphin, *Sousa teuszii* (Kükenthal, 1892), using the IUCN red list criteria. In: *Advances in Marine Biology*, vol. 72. Academic Press, pp. 47–77.
- Collins, T., Braulik, G.T., Perrin, W., 2017. *The IUCN Red List of Threatened Species* 2017: e.T20425A123792572. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T20425A50372734.en>. *Sousa teuszii* (errata version published in 2018). (Accessed 15 December 2023).
- Conroy, J.L., Cobb, K.M., Lynch-Stieglitz, J., Polissar, P.J., 2014. Constraints on the salinity–oxygen isotope relationship in the central tropical Pacific Ocean. *Mar. Chem.* 161, 26–33.
- Costa, A.F., Botta, S., Siciliano, S., Giarrizzo, T., 2020. Resource partitioning among stranded aquatic mammals from Amazon and Northeastern coast of Brazil revealed through Carbon and Nitrogen Stable Isotopes. *Sci. Rep.* 10 (1), 1–13.
- Croisietière, L., Hare, L., Tessier, A., Cabana, G., 2009. Sulphur stable isotopes can distinguish trophic dependence on sediments and plankton in boreal lakes. *Freshw. Biol.* 54 (5), 1006–1015.
- Cropper, T.E., Hanna, E., Bigg, G.R., 2014. Spatial and temporal seasonal trends in coastal upwelling off Northwest Africa, 1981–2012. *Deep Sea Res. Oceanogr. Res.* Pap. 86, 94–111. <https://doi.org/10.1016/j.dsr.2014.01.007>.
- Dedah, S.O., 1993. Wind, surface water temperature, surface salinity and pollution in the area of the Banc d'Arguin, Mauritania, 86. In: Wolff, W.J., van der Land, J., Nienhuis, P.H., de Wilde, P.A.W.J. (Eds.), *Ecological Studies in the Coastal Waters of Mauritania*, Developments in Hydrobiology, vol. 86, pp. 9–19. https://doi.org/10.1007/978-94-011-1986-3_2. Springer, Dordrecht.
- Diaz, R., Moreira, M., Mendoza, U., Machado, W., Böttcher, M.E., Santos, H., Belém, A., Capilla, R., Escher, P., Albuquerque, A.L., 2012. Early diagenesis of sulfur in a tropical upwelling system, Cabo Frio, southeastern Brazil. *Geology* 40 (10), 879–882.
- Drago, M., Valdivia, M., Bragg, D., González, E.M., Aguilar, A., y Cardona, L., 2020. Stable oxygen isotopes reveal habitat use by marine mammals in the Río de la Plata estuary and adjoining Atlantic Ocean. *Estuar. Coast Shelf Sci.* 238, 106708 <https://doi.org/10.1016/j.ecss.2020.106708>. ISSN 0272-7714.
- Drago, M., Signaroli, M., Valdivia, M., González, E.M., Borrell, A., Aguilar, A., Cardona, L., 2021. The isotopic niche of Atlantic, biting marine mammals and its relationship to skull morphology and body size. *Sci. Rep.* 11 (1), 1–14.

- Duguy, R., 1975. Contribution à l'étude des mammifères marins de la côte nord-ouest Afrique. *Rev. Trav. Inst. Pêches Marit.* 39 (3), 321–332.
- Fahy, G.E., Deter, C., Pitfield, R., Miszkiewicz, J.J., Mahoney, P., 2017. Bone deep: variation in stable isotope ratios and histomorphometric measurements of bone remodelling within adult humans. *J. Archaeol. Sci.* 87, 10–16.
- Fischer, G., Romero, O., Merkel, U., Donner, B., Iversen, M., Nowald, N., Ratmeyer, V., Ruhland, G., Klann, M., Wefer, G., 2016. Deep ocean mass fluxes in the coastal upwelling off Mauritania from 1988 to 2012: variability on seasonal to decadal timescales. *Biogeosciences* 13 (10), 3071–3090. <https://doi.org/10.5194/bg-13-3071-2016>.
- Fontaine, M.C., Roland, K., Calves, I., Austerlitz, F., Palstra, F.P., Tolley, K.A., Ryan, S., Ferreira, M., Jauniaux, T., Llavona, A., Öztürk, B., 2014. Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. *Mol. Ecol.* 23 (13), 3306–3321.
- Fraser, F.C., 1973. Record of a dolphin (*Sousa teuszii*) from the coast of Mauritania. *Trans. N. Y. Acad. Sci.* 35 (2), 132–135.
- García-Vernet, R., Borrell, A., Víkingsson, G., Halldórsson, S.D., Aguilar, A., 2021. Ecological niche partitioning between baleen whales inhabiting Icelandic waters. *Prog. Oceanogr.* 199, 102690 <https://doi.org/10.1016/j.pocean.2021.102690>.
- Gat, J.R., 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. *Annu. Rev. Earth Planet Sci.* 24 (1), 225–262.
- Gazo, M., Aguilar, A., 2005. Maternal attendance and diving behavior of a lactating Mediterranean monk seal. *Mar. Mamm. Sci.* 21 (2), 340–345.
- González, L.M., Aguilar, A., López-Jurado, L.F., Grau, E., 1997. Status and distribution of the Mediterranean monk seal *Monachus monachus* on the Cabo Blanco Peninsula (Western Sahara-Mauritania) in 1993–1994. *Biol. Conserv.* 80, 225–233.
- Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Auriolles, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*, pp. 299–318.
- Herzing, D.L., Perrin, W.F., 2018. Atlantic spotted dolphin. In: Würsig, B., Thewissen, J. G.M., Kovacs, K.M. (Eds.), *Encyclopedia of Marine Mammals*, third ed. Academic Press, San Diego, pp. 40–42.
- Hobson, K.A., Barnett-Johnson, R., Cerling, T., 2010. Chapter 13: using isoscapes to Track animal Migration. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*. Springer Science & Business Media, Dordrecht, pp. 273–298.
- Honda, K., Fujise, Y., Itano, K., Tatsukawa, R., 1984. Composition of chemical components in bone of striped dolphin, *Stenella coeruleoalba*: distribution characteristics of heavy metals in various bones. *Agric. Biol. Chem.* 48 (3), 677–683. <https://doi.org/10.1080/00021369.1984.10866203>.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80 (3), 595–602.
- Karamanlidis, A., Dendrinos, P., 2015. *The IUCN Red List of Threatened Species* 2015: e.T13653A117647375. <https://doi.org/10.2305/IUCN.UK.2015.4.RLTS.T13653A45227543.en>. *Monachus monachus* (errata version published in 2017). (Accessed 27 March 2023).
- Karamanlidis, A.A., Dendrinos, P., De Larrinoa, P.F., Gücü, A.C., Johnson, W.M., Kiraç, C. O., Pires, R., 2016. The Mediterranean monk seal *Monachus monachus*: status, biology, threats, and conservation priorities. *Mamm. Rev.* 46 (2), 92–105.
- Karamanlidis, A.A., Dendrinos, P., Fernandez de Larrinoa, P., Kiraç, C.O., Nicolaou, H., Pires, R., 2023. In: *Monachus monachus*. The IUCN Red List of Threatened Species 2023: e.T13653A238637039. (Accessed 15 December 2023).
- Klenz, T., Dengler, M., Brandt, P., 2018. Seasonal variability of the Mauritania Current and hydrography at 18 N. *J. Geophys. Res.: Oceans* 123 (11), 8122–8137.
- Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxyapatite. *J. Archaeol. Sci.* 24 (5), 417–429.
- Krastel, S., Wynn, R.B., Hanebuth, T.J., Henrich, R., Holz, C., Meggers, H., Kuhlmann, H., Georgiopolou, A., Schulz, H.D., 2006. Mapping of seabed morphology and shallow sediment structure of the Mauritania continental margin, Northwest Africa: some implications for geohazard potential. *Norw. J. Geol.* 86 (3), 163–176.
- Lebigne, J.M., 1991. Les marais maritimes de Mauritanie: protection et valorisation. *Les. Cah. d'Outre-Mer* 44 (176), 379–400. <https://doi.org/10.3406/caoum.1991.3413>.
- Littman, C., Karamanlidis, A., Dendrinos, P., 2018. Monk seals. In: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), *Encyclopedia of Marine Mammals*, third ed. Academic Press, San Diego, pp. 618–622.
- Maigret, J., 1980a. Données nouvelles sur l'écologie du *Sousa teuszii* (Cetacea, Delphinidae) de la côte ouest africaine. *Bull. Inst. Fr. Afr. Noire* 42A (3), 619–633.
- Maigret, J., 1980b. Les mammifères marins des côtes de Mauritanie. Etat des observations en 1980. *Bulletin du Centre National de Recherches Océanographiques et des Pêches, Nouadhibou* 9 (1), 130–152.
- Maigret, J., 1981. Les mammifères marins des côtes de Mauritanie. 2^e Rapport annuel des observations signalées en 1981. *Bulletin du Centre National de Recherches Océanographiques et des Pêches, Nouadhibou* 10 (1), 81–85.
- Maigret, J., Trotignon, J., Duguy, R., 1976. Observations de Cétacés sur les Côtes de Mauritanie (1971–1975). ICES, Comité des Mammifères Marins CM (4), 7.
- Meunier, T., Barton, E.D., Barreiro, B., Torres, R., 2012. Upwelling filaments off Cap Blanc: interaction of the NW African upwelling current and the Cape Verde frontal zone eddy field? *J. Geophys. Res.* 117, C08031 <https://doi.org/10.1029/2012JC007905>.
- Mittelstaedt, E., 1991. The ocean boundary along the northwest African coast: circulation and oceanographic properties at the sea surface. *Prog. Oceanogr.* 26 (4), 307–355.
- Mo, G., Zotti, A., Agnesi, S., Finoia, M.G., Bernardini, D., Cozzi, B., 2009. Age classes and sex differences in the skull of the Mediterranean monk seal, *Monachus monachus* (Hermann, 1779). A study based on bone shape and density. *Anat. Rec.: Advan. Integr. Anat. Evolution. Biol.* 292 (4), 544–556.
- Munro, L.E., Longstaffe, F.J., White, C.D., 2008. Effects of heating on the carbon and oxygen-isotope compositions of structural carbonate in bioapatite from modern deer bone. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266 (3–4), 142–150. <https://doi.org/10.1016/j.palaeo.2008.03.026>.
- Nehlich, O., Richards, M.P., 2009. Establishing collagen quality criteria for sulphur isotope analysis of archaeological bone collagen. *Archaeol. Anthropol. Sci.* 1 (1), 59–75.
- Nehlich, O., 2015. The application of sulphur isotope analyses in archaeological research: a review. *Earth Sci. Rev.* 142, 1–17.
- Nelson, B.K., DeNiro, M.J., Schoeninger, M.J., De Paolo, D.J., Hare, P.E., 1986. Effects of diagenesis on strontium, carbon, nitrogen and oxygen concentration and isotopic composition of bone. *Geochim. Cosmochim. Acta* 50 (9), 1941–1949.
- Nemliher, J.G., Baturin, G.N., Kallaste, T.E., Murdmaa, I.O., 2004. Transformation of hydroxyapatite of bone phosphate from the ocean bottom during fossilization. *Lithol. Miner. Resour.* 39, 468–479. <https://doi.org/10.1023/B:LIML.0000040736.62014.2d>.
- Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci.* 26, 509–572. <https://doi.org/10.1111/j.1748-7692.2009.00354.x>.
- Nieri, M., Grau, E., Lamarche, B., Aguilar, A., 1999. Mass mortality of Atlantic spotted dolphins (*Stenella frontalis*) caused by a fishing interaction in Mauritania. *Mar. Mamm. Sci.* 15 (3), 847–854.
- Olson, P.A., 2018. Pilot whales. In: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), *Encyclopedia of Marine Mammals*, third ed. Academic Press, San Diego, pp. 701–705.
- Pastor, T., Cappozzo, H.L., Grau, E., Amos, W., Aguilar, A., 2011. The mating system of the Mediterranean monk seal in the Western Sahara. *Mar. Mamm. Sci.* 27 (4), E302–E320.
- Pelegri, J.L., Peña-Izquierdo, J., Machín, F., Meiners, C., Presas-Navarro, C., 2017. Oceanography of the Cape Verde basin and Mauritanian slope waters. Deep-sea Ecosystems off Mauritania: Research of Marine Biodiversity and Habitats in the Northwest African Margin, pp. 119–153.
- Peña-Izquierdo, J., Pelegri, J.L., Pastor, M.V., Castellanos, P., Emelianov, M., Gasser, M., Salvador, J., Vázquez-Domínguez, E., 2012. The continental slope current system between Cape Verde and the Canary Islands. *Sci. Mar.* 76, 65–78.
- Peterson, B.J., Howarth, R.W., Garritt, R.H., 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227 (4692), 1361–1363. <https://doi.org/10.1126/science.227.4692.1361>.
- Peterson, B.J., 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. *Acta Oecol.* 20 (4), 479–487.
- Pinela, A., Borrell, A., Cardona, L. y, Aguilar, A., 2010. Stable isotopes reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. *Mar. Ecol.: Prog. Ser.* 416, 295–306. <https://doi.org/10.3354/meps08790>.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83 (3), 703–718.
- Pottier, A., Catry, T., Trégarot, E., Maréchal, J.P., Fayad, V., David, G., Cheikh, M.S., Failler, P., 2021. Mapping coastal marine ecosystems of the National Park of Banc d'Arguin (PNBA) in Mauritania using Sentinel-2 imagery. *Int. J. Appl. Earth Obs. Geoinf.* 102, 102419 <https://doi.org/10.1016/j.jag.2021.102419>.
- Pritchard, D.W., 1952. Estuarine hydrography. In: *Advances in Geophysics*, vol. 1. Elsevier, pp. 243–280.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>. (Accessed 13 June 2022).
- Ramos, R. y, González-Solís, J., 2012. Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. *Front. Ecol. Environ.* 10, 258–266. <https://doi.org/10.1890/110140>.
- Ridgway, S.H., Harrison, R., Harrison, R.J., 1998. In: *Handbook of Marine Mammals: the Second Book of Dolphins and the Porpoises*, p. 486. Elsevier.
- Riofrío-Lazo, M., Auriolles-Gamboa, D., 2013. Timing of isotopic integration in marine mammal skull: comparative study between calcified tissues. *Rapid Commun. Mass Spectrom.* 27 (9), 1076–1082. <https://doi.org/10.1002/rcm.6556>.
- Robineau, D., Vely, M., 1998. Les cétacés des côtes de Mauritanie (Afrique du Nord-ouest). Particularités et variations spatio-temporelles de répartition: Rôle des facteurs océanographiques. *Revue d'Ecologie, Terre et Vie, Société nationale de protection de la nature* 53 (2), 123–152 hal-03529162.
- Rossmann, S., Ostrom, P.H., Gordon, F., Zipkin, E.F., 2016. Beyond carbon and nitrogen: guidelines for estimating three-dimensional isotopic niche space. *Ecol. Evol.* 6 (8), 2405–2413. <https://doi.org/10.1002/ece3.2013>.
- Rubenstein, D.R., y Hobson, K.A., 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends Ecol. Evol.* 19 (5) <https://doi.org/10.1016/j.tree.2004.03.017>.
- Russell, G., Sánchez-Cabanes, A., Nimak-Wood, M., 2018. The autumn occurrence and spatial distribution of cetaceans in the waters of Mauritania during a geophysical survey in 2012. *Afr. J. Mar. Sci.* 40 (4), 371–381.
- Samba Bilal, A., Wagne, M.M., Wagué, A., Dia, A., Van Waerebeek, K., 2023. The Cetaceans of Mauritania, West Africa: a concise zoogeographical review with two new species records. *J. Animal Diversit.* 5 (1), 1–35.
- Schmidt, G.A., 1999. Error analysis of paleosalinity calculations. *Paleoceanography* 14 (3), 422–429. <https://doi.org/10.1029/1999PA000008>.

- Schoeninger, M.J., 2010. Chapter 15: toward a $\delta^{13}\text{C}$ isoscape for primates. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*. Springer Science & Business Media, Dordrecht, pp. 319–333. https://doi.org/10.1007/978-90-481-3354-3_15.
- Sevrin-Reyssac, J., 1993. Hydrology and underwater climate of the Banc d'Arguin, Mauritania: a review. In: *Ecological Studies in the Coastal Waters of Mauritania: Proceedings of a Symposium Held at Leiden, The Netherlands 25–27 March 1991*. Springer, Netherlands, pp. 1–8.
- Smeenk, C., Leopold, M.F., Addink, M.J., 1992. Note on the harbour porpoise *Phocoena phocoena* in Mauritania, west Africa. *Lutra* (35), 98–104.
- Sponheimer, M., Lee-Thorp, J.A., 1999. Alteration of enamel carbonate environments during fossilization. *J. Archaeol. Sci.* 26 (2), 143–150. <https://doi.org/10.1006/jasc.1998.0293>.
- Syväranta, J., Lensu, A., Marjomäki, T.J., Oksanen, S., Jones, R.I., 2013. An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. *PLoS One* 8 (2), e56094. <https://doi.org/10.1371/journal.pone.0056094>.
- Tulp, I., Leopold, M.F., 2004. Marine Mammals and Seabirds in Mauritanian Waters: Pilot Study April 2004, No. 04.020, vol. 42. RIVO Biologie en Ecologie.
- Trueman, C.N., MacKenzie, K.M., Palmer, M.R., 2012. Identifying migrations in marine fishes through stable-isotope analysis. *J. Fish. Biol.* 81 (2), 826–847. <https://doi.org/10.1111/j.1095-8649.2012.03361.x>.
- Van Waerebeek, K., Ofori-Danson, P.K., Debrah, J., Collins, T., Djiba, A., Samba Ould Bilal, A., 2016. On the Status of the Common Bottlenose Dolphin *Tursiops truncatus* in Western Africa, with Emphasis on Fisheries Interactions, 1947–2015. *Document SC/66b/SM19 Presented to the Scientific Committee Of the International Whaling Commission*, vol. 20. Bled, Slovenia.
- Velasquez-Vacca, A., Seminoff, J.A., Jones, T.T., Balazs, G.H., Cardona, L., 2023. Isotopic ecology of Hawaiian green sea turtles (*Chelonia mydas*) and reliability of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ analyses of unprocessed bone samples for dietary studies. *Mar. Biol.* 170 (7), 81. <https://doi.org/10.1007/s00227-023-04232-1>.
- Vely, M., Dia, A.T., N'diaye, R., 1995. Premières données concernant l'inventaire des mammifères marins du Parc National du Banc d'Arguin. Rapport CIRAD-EMVT N° 015. Union Européenne et CIRAD-EMVT.
- Weir, C.R., Collins, T., 2015. A review of the geographical distribution and habitat of the Atlantic humpback dolphin (*Sousa teuszii*). *Adv. Mar. Biol.* 72, 79–117.
- Wolff, W.J., Smit, C.J., 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea* 78 (1), 17–38.
- Wolff, W.J., Van der Land, J., Nienhuis, P.H., De Wilde, P.A.W.J., 1993. The functioning of the ecosystem of the Banc d'Arguin, Mauritania: a review. *Hydrobiologia* 258, 211–222.
- Zenk, W., Klein, B., Schroder, M., 1991. Cape Verde frontal zone. *Deep-Sea Res., Part A* 38, S505–S530.
- Zopfi, J., Böttcher, M.E., Jørgensen, B.B., 2008. Biogeochemistry of sulfur and iron in Thioploca-colonized surface sediments in the upwelling area off central Chile. *Geochem. Cosmochim. Acta* 72 (3), 827–843.