

Stable isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species

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ABSTRACT: Stable isotope abundances of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in the bone of 13 species of marine mammals from the northwest coast of Africa were investigated to assess their positions in the local trophic web and their preferred habitats. Also, samples of primary producers and potential prey species from the study area were collected to characterise the local isotopic landscape. This characterisation indicated that $\delta^{13}\text{C}$ values increased from offshore to nearshore and that $\delta^{15}\text{N}$ was a good proxy for trophic level. Therefore, the most coastal species were *Monachus monachus* and *Sousa teuszii*, whereas the most pelagic were *Physeter macrocephalus* and *Balaenoptera acutorostrata*. $\delta^{15}\text{N}$ values indicated that marine mammals located at the lowest trophic level were *B. acutorostrata*, *Stenella coeruleoalba* and *Delphinus* sp., and those occupying the highest trophic level were *M. monachus* and *P. macrocephalus*. The trophic level of *Orcinus orca* was similar to that of *M. monachus*, suggesting that *O. orca* preys on fish. Conservation of coastal and threatened species (*M. monachus* and *S. teuszii*) off NW Africa should be a priority because these species, as the main apex predators, cannot be replaced by other marine mammals.

KEY WORDS: Marine mammals · Stable isotopes · Trophic ecology · Habitat use · NW Africa

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INTRODUCTION

Exploitation of marine ecosystems is causing a rapid depletion of top predators worldwide (Pauly et al. 1998a, Jackson & Sala 2001, Myers & Worm 2003) and, as a result, marine food webs are undergoing extraordinary changes in their structure and function (Jackson et al. 2001, Emslie & Patterson 2007). Fisheries are replacing apex predators in most marine food webs and exercise a formidable top-down control on these predators, but major differences in the behaviour of fisheries and that of marine apex predators (Trites et al. 2006) make intensely exploited ecosystems highly fluctuant (Anderson et al. 2008). An ecosystem-based management system has been advocated to avoid these problems, but this approach is often hindered by

a poor knowledge of the basic biological traits of most apex predators.

The waters of the NW coast of Africa are among the most productive in the world (Ferreira 1978, Feidi 1996). In these waters, 2 important currents meet—the cold Canary Current and the warm Guinea Current—generating a quasi-permanent upwelling zone that triggers a high biological productivity (Wells & Bleakley 1995, Longhurst 1998, Shumway 1999). Such productivity supports a highly diverse and abundant fauna of marine mammals, (Marchessaux & Campredon 1988, Robineau & Vely 1998, Nieri et al. 1999) which typically include, given the mix of waters, boreal species as well as tropical or subtropical species (Robineau & Vely 1998). Additionally, the region shelters the last remnant populations of some scarce or highly endangered spe-

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cies, such as the Mediterranean monk seal *Monachus monachus* (González et al. 1997), the Atlantic humpback dolphin *Sousa teuszii* (Van Waerebeek et al. 2004) and the African manatee *Trichechus senegalensis* (Padiá & Ibáñez 2005). Mauritania is one of the major African fishing nations and has developed, alongside traditional artisanal fishing, industrial fisheries, becoming one of the major fish exporting African countries (Ababouch 2000). Overfishing, overcapacity, habitat degradation and inequitable access agreements have contributed to the decline in catches throughout West Africa (Atta-Mills et al. 2004, ter Hofstede & Dickey-Collas 2006). Assessing the impact of fisheries on the local ecosystem is of great interest (Jouffre & Inejih 2005) but no studies have been conducted involving marine mammals.

Available information on the marine mammals of the region is limited to stranding and sighting reports in the case of cetaceans (Duguay 1976, Maigret 1980a,b, 1981, Marchessaux & Campredon 1988, Van Waerebeek et al. 1999), although a few demographic parameters are known for *Monachus monachus* (González et al. 1997, Gazo et al. 2000). Nevertheless, the trophic relationships among the marine apex predators of the region have never been investigated, and their possible interactions with the fisheries operating in the area are largely unknown.

The methods traditionally used in the study of the trophic ecology of marine mammals have been faecal or stomach-content analyses. These methods present limitations because they only show recently eaten prey, and results can be severely biased owing to differences in prey digestion (Hobson et al. 1996). Conversely, stable isotope analysis offers an integrated measure of all prey assimilated over a comparatively protracted period of time (Tieszen et al. 1983, Michener & Schell 1994, Hobson 1999). In marine mammals, stable isotopes of carbon and nitrogen have been extensively used to investigate the trophic ecology of populations (e.g. Hobson et al. 1997, Lesage et al. 2001, Drago et al. 2009). The relative abundance of heavy to light carbon isotopes ($\delta^{13}\text{C}$) has been used to discriminate between habitats where phytoplankton is the only source of organic carbon (pelagic and offshore habitats) and those where macrophytes are a relevant source of organic carbon (vegetated onshore benthic habitats) (Rubenstein & Hobson 2004, Fry 2006, Cardona et al. 2007). By contrast, the relative abundance of heavy to light nitrogen isotopes ($\delta^{15}\text{N}$) is commonly taken as an indicator of trophic level (Cabana & Rasmussen 1996) because this abundance increases from prey to predator owing to the preferential excretion of the light isotope (Caut et al. 2009).

In the present study, stable isotope profiles of carbon and nitrogen were used to investigate the habitat use

and trophic level of the marine mammals occurring in the waters off the northwest coast of Africa to determine their positions in the marine food web.

MATERIALS AND METHODS

Study site and sampling. The study was conducted in the Islamic Republic of Mauritania, located in the northwest region of Africa. Its coastline extends latitudinally more than 700 km from Cape Blanc to the Senegal River (Fig. 1). The northern part of the coast is composed of rocky cliffs with scattered small, tide-dependent and sandy beaches (Habitat 1, Fig. 1); the intermediate region consists of tidal mudflats inhabited by the seagrass *Halodule wrightii* and *Zostera noltii* and shallow waters that extend several kilometres offshore, supporting dense sublittoral meadows of the seagrass *Cymodocea nodosa* with scattered deep unvegetated water channels in between (Parc National du Banc d'Arguin, Habitat 2, Fig. 1); and the southern region is a nearly continuous sandy beach with scattered sublittoral patches of the seagrass *Cymodocea nodosa* (La Grand Plage, Habitat 3, Fig. 1). Despite this heterogeneity, there are no major differences among the 3 regions in the distribution of the potential prey for marine mammals, whose abundance depends mainly on the depth of the coastal waters and the variation in sea surface temperature related to upwelling (ter Hofstede & Dickey-Collas 2006).

Bone samples from 13 species of marine mammals (243 individuals; Table 1) were collected opportunistically between 1990 and 2008 along the Mauritanian coastline. Except for *Monachus monachus*, for which all samples came from natural mortalities, we have no information on the cause of death of the marine mammals used in this study. Bone was selected because, owing to its low turnover rate, it is possible to elucidate several years of dietary history (Hobson & Clark 1992). The bone collected from each skull was a small fragment of turbinate bones from the nasal cavity because this fragment is easy to crush and its sampling did not damage the skull for subsequent studies. Furthermore, samples from 7 species of potential prey (fish and cephalopods), 1 species of sea turtle, 7 species of benthic macrophytes (benthic primary producers) and phytoplankton (pelagic primary producers) were also collected to characterise the isotopic landscape off the coast of Mauritania (Table 1).

The samples of leaf and thallus collected from seagrass and macroalgae, respectively, were dried with sodium chloride; and fish dorsal white muscle, cephalopod mantle and turtle muscle were stored in a freezer at -20°C until analysis. Samples of skull and other bone tissues were stored without preservatives at

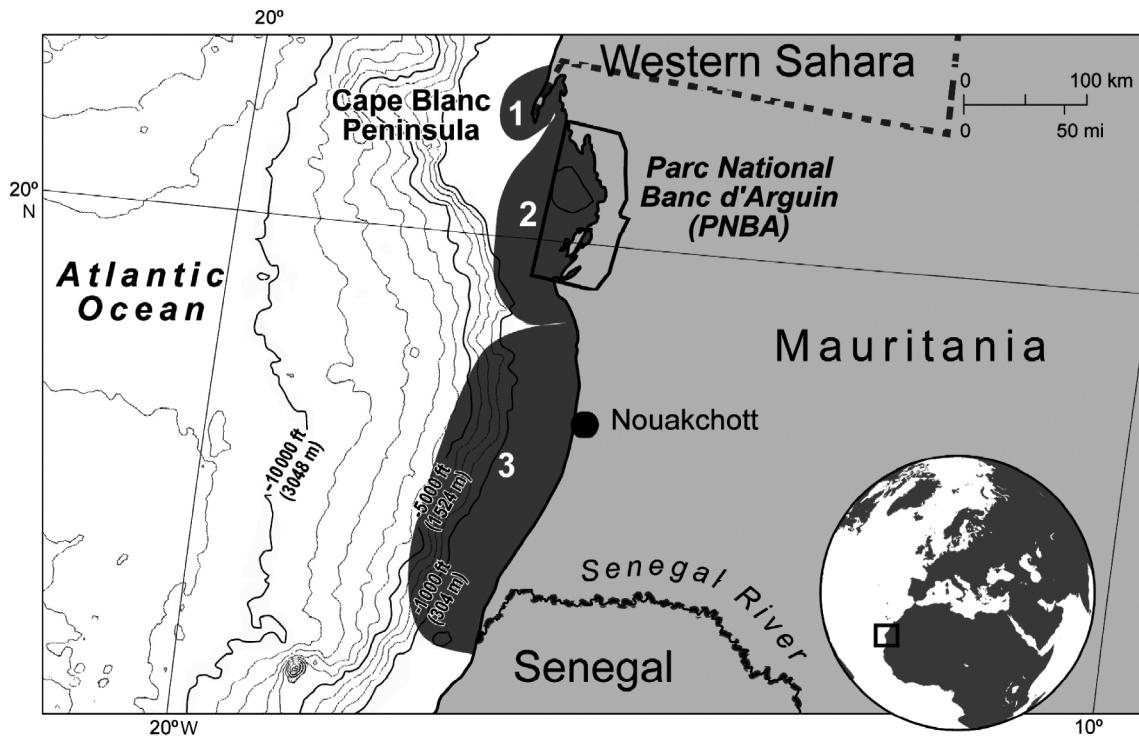


Fig. 1. Study area, with bathymetry, the overline of the continental shelf and the 3 main habitat types, indicated by dark grey areas with numbers (see 'Materials and methods' for habitat characterisation)

ambient temperature (15 to 25°C). Phytoplankton (whole organisms in collective samples) was refrigerated at 4°C, brought to the laboratory, filtered in a pre-combusted GF/C filter and processed for isotopic determination.

Stable isotope analyses. Stable isotope abundances (expressed as delta notation, δ), in which the relative variations of stable isotope ratios are expressed in per mille (‰) deviations from predefined international standards, were calculated as:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is the value of the heavy isotope of the sample (^{13}C or ^{15}N), R_{sample} is the ratio of the heavy to the light isotope of the sample ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) and R_{standard} is the ratio of the heavy to the light isotope in the reference standards, which were Vienna Pee Dee Belemnite calcium carbonate for carbon and atmospheric nitrogen (air) for nitrogen.

For the pre-treatment of the samples, ~1 g of tissue was rinsed with distilled water, dried for 3 d at 60°C and powdered with a mortar and pestle. Because lipids are depleted for ^{13}C compared with other molecules, and thus can mislead the analyses by decreasing the $\delta^{13}\text{C}$ signal (DeNiro & Epstein 1977), they were removed from the samples by rinsing the powdered tissue several times with a 2:1 chloroform:methanol solu-

tion (Bligh & Dyer 1959). When conducting stable isotope analysis in bone, several authors have carried out preventive demineralisation of the tissue by treating it with either a 0.5 or 1 M hydrochloric acid (HCl) solution (Bocherens et al. 1997, Newsome et al. 2006). However, a test using a subset of the samples ($n = 20$) revealed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ between demineralised and untreated samples, so this procedure was not followed. However, seagrass and macroalgae were treated with a 0.5 M HCl solution to eliminate inorganic carbonates that could bias the results (Ng et al. 2007). Phytoplankton was also treated with 0.05 M HCl to remove carbonates following the protocol of Ogawa & Ogura (1997). Some authors agree that it is possible that HCl treatment adversely affects the nitrogen isotopic signature (Bunn et al. 1995), thus primary producer samples (seagrass, macroalgae and collective phytoplankton samples) were separated into 2 subsamples used for carbon (after the HCl treatment) and for nitrogen (without the HCl treatment).

Finally, ~1 mg of bone, 0.5 mg of white muscle from fish and of mantle from cephalopods, 4 mg of homogenised seagrass and of macroalgae and 12 mg of the homogenised phytoplankton with filter were weighed in tin capsules (3.3×5 mm), combusted at 900°C and analysed in a continuous flow isotope ratio mass spec-

Table 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of each species collected along the Mauritanian coast. Data are given as means \pm SD (‰), minimum and maximum isotope values, identification codes (ID code) and number of individuals per species (N). **Bold** values represent means \pm SD (‰), and minimum and maximum isotope values for each category

| Species | ID code | N | $\delta^{13}\text{C}$ | | | $\delta^{15}\text{N}$ (‰) | | |
|-------------------------------------|---------|----|-----------------------|-------|-------|---------------------------|------|------|
| | | | Mean \pm SD | Min. | Max. | Mean \pm SD | Min. | Max. |
| Pelagic primary producers | | | | | | | | |
| Phytoplankton | PHYTO | 3 | -24.4 \pm 3.5 | -26.9 | -20.3 | 8.9 \pm 0.3 | 8.6 | 9.2 |
| Benthic primary producers | | | | | | | | |
| Seagrass | | | | | | | | |
| <i>Cymodocea nodosa</i> | CNOD | 5 | -6.3 \pm 1.1 | -7.5 | -5.3 | 2.6 \pm 0.8 | 1.8 | 3.8 |
| <i>Halodule wrightii</i> | HWRI | 5 | -11.8 \pm 0.8 | -13.0 | -10.7 | 4.3 \pm 1.1 | 2.8 | 5.8 |
| <i>Zostera noltii</i> | ZNOL | 5 | -10.5 \pm 1.3 | -7.5 | -5.3 | 2.9 \pm 0.2 | 2.7 | 3.2 |
| Macroalgae | | | | | | | | |
| <i>Asparagopsis</i> sp. | ASPA | 2 | -19.7 \pm 0.4 | -19.9 | -19.4 | 3.7 \pm 0.5 | 3.3 | 4.1 |
| <i>Dictyota</i> sp. | DICT | 5 | -18.8 \pm 0.2 | -19.1 | -18.7 | 4.7 \pm 0.4 | 4.3 | 5.3 |
| <i>Padina</i> sp. | PADI | 2 | -16.1 \pm 1.3 | -17.0 | -15.2 | 3.4 \pm 0.9 | 2.7 | 4.0 |
| <i>Polysiphonia</i> sp. | POLY | 5 | -19.6 \pm 0.2 | -19.9 | -19.4 | 3.6 \pm 0.4 | 3.2 | 4.1 |
| <i>Sargassum</i> sp. | SARG | 5 | -17.7 \pm 0.2 | -17.9 | -17.5 | 5.1 \pm 0.4 | 4.4 | 5.4 |
| Fish | | | | | | | | |
| <i>Caranx rhonchus</i> | CRHO | 11 | -14.8 \pm 0.29 | -15.5 | -14.4 | 14.1 \pm 0.50 | 13.5 | 14.8 |
| <i>Mullus barbatus</i> | MBAR | 10 | -16.2 \pm 0.77 | -17.5 | -15.0 | 13.1 \pm 0.83 | 11.6 | 14.2 |
| <i>Pagellus bellotii</i> | PBEL | 9 | -15.7 \pm 1.25 | -18.0 | -14.2 | 14.3 \pm 1.07 | 13.0 | 16.0 |
| <i>Plectorhinchus mediterraneus</i> | PMED | 1 | -14.1 | | | 14.2 | | |
| <i>Sardinella aurita</i> | SAUR | 10 | -15.0 \pm 0.39 | -15.7 | -14.3 | 10.4 \pm 0.66 | 9.7 | 11.0 |
| <i>Scomberomorus tritor</i> | STRI | 2 | -15.7 \pm 0.21 | -15.8 | -15.5 | 14.1 \pm 0.32 | 14.0 | 14.4 |
| Cephalopods | | | | | | | | |
| <i>Loligo</i> sp. | LOLI | 1 | -15.1 | | | 14.4 | | |
| Marine turtles | | | | | | | | |
| <i>Chelonia mydas</i> | CMID | 4 | -9.3 \pm 2.2 | -11.6 | -6.8 | 7.8 \pm 1.2 | 6.0 | 8.6 |
| Marine mammals | | | | | | | | |
| <i>Balaenoptera acutorostrata</i> | BACU | 1 | -15.9 | | | 11.8 | | |
| <i>Delphinus</i> sp. | DDEL | 95 | -12.4 \pm 0.81 | -15.3 | -9.7 | 12.7 \pm 0.83 | 10.8 | 15.9 |
| <i>Globicephala macrorhynchus</i> | GMAC | 9 | -11.5 \pm 0.53 | -12.5 | -10.7 | 14.0 \pm 0.39 | 13.5 | 14.6 |
| <i>Globicephala melas</i> | GMEL | 2 | -11.1 \pm 0.42 | -11.4 | -10.8 | 14.1 \pm 0.27 | 13.9 | 14.3 |
| <i>Grampus griseus</i> | GGRI | 1 | -12.0 | | | 13.8 | | |
| <i>Monachus monachus</i> | MMON | 12 | -10.4 \pm 0.63 | -11.2 | -8.9 | 14.5 \pm 0.70 | 12.9 | 15.4 |
| <i>Orcinus orca</i> | ORCA | 3 | -11.9 \pm 1.39 | -13.2 | -10.4 | 14.5 \pm 0.52 | 14.0 | 15.0 |
| <i>Phocoena phocoena</i> | PPHO | 42 | -11.7 \pm 0.94 | -14.0 | -9.7 | 13.6 \pm 0.76 | 11.6 | 15.4 |
| <i>Physeter macrocephalus</i> | PMAC | 2 | -13.9 \pm 2.11 | -15.4 | -12.4 | 15.9 \pm 0.06 | 15.9 | 16.0 |
| <i>Sousa teuszii</i> | STEU | 11 | -9.7 \pm 0.93 | -11.5 | -8.1 | 13.3 \pm 1.33 | 11.7 | 15.3 |
| <i>Stenella coeruleoalba</i> | SCOE | 1 | -12.0 | | | 11.9 | | |
| <i>Stenella frontalis</i> | SFRO | 4 | -12.1 \pm 0.30 | -12.4 | -11.8 | 13.2 \pm 1.02 | 12.3 | 14.6 |
| <i>Tursiops truncatus</i> | TTRU | 60 | -11.1 \pm 1.23 | -15.4 | -8.3 | 13.9 \pm 1.30 | 11.4 | 17.1 |

trometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan, Bremen, Germany). Atropine was used as a standard to check the elemental composition for carbon and nitrogen. International isotope secondary standards of known $^{13}\text{C}/^{12}\text{C}$ ratios, as given by the IAEA (International Atomic Energy Agency)—namely, polyethylene (IAEA CH7, $\delta^{13}\text{C} = -31.8\text{‰}$), graphite (USGS24, $\delta^{13}\text{C} = -16.1\text{‰}$) and sucrose (IAEA CH6, $\delta^{13}\text{C} = -10.4\text{‰}$)—were used for calibration at a precision of 0.2‰. For nitrogen, international isotope secondary standards of known $^{15}\text{N}/^{14}\text{N}$ ratios—namely, $(\text{NH}_4)_2\text{SO}_4$ (IAEA N1, $\delta^{15}\text{N} = +0.4\text{‰}$ and IAEA N2, $\delta^{15}\text{N} = +20.3\text{‰}$) and KNO_3 (IAEA NO₃, $\delta^{15}\text{N} = +4.7\text{‰}$)—were used for calibration at a precision of 0.3‰.

Data analyses. The assumption of normality in the distributions of the sample groups was checked with the Kolmogorov-Smirnov test. The assumption of homogeneity of variances between sample groups was checked with Levene's test.

Differences in mean bivariate isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) among marine mammal species were assessed using a multivariate analysis of variance (MANOVA) because they displayed a normal distribution. Univariate ANOVA was conducted separately for both isotopes. If a statistical significant interaction was found between marine mammal species for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using an ANOVA, additional pairwise comparisons were made using a generalised linear model because it admits data that do not meet the assumption

of homogeneity of variance. Post hoc analyses were made by means of least significant differences (LSD) tests based on estimated marginal means. As a method of estimation, the maximum likelihood (ML) was used in all cases. Normality distributions and identity as a link function were always used (for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), because data followed a normal distribution. Goodness of fit values (Akaike's information criterion, AIC) were used to compare different models. The confidence interval level was set at 95% for all comparisons. The post hoc pairwise comparison by generalised linear model is a more flexible and less conservative statistical tool than the post hoc pairwise comparison by general linear model because several types of distribution and models can be chosen to fit the data. The post hoc test was conducted for the species represented by more than one sample (*Stenella coeruleoalba*, *Grampus griseus* and *Balaenoptera acutorostrata* were excluded from the analysis).

Unless otherwise stated, data are presented as means \pm standard deviation (SD) throughout the man-

uscript, except when a species is represented by a single individual. All the statistical analyses were conducted using the SPSS ver.15.

RESULTS

The isotopic landscape

Macroalgae presented lower $\delta^{13}\text{C}$ values in comparison with seagrass but presented higher $\delta^{13}\text{C}$ values in comparison with phytoplankton (Fig. 2, Table 1). The $\delta^{13}\text{C}$ value of green turtles was close to that of the seagrass that they consume (Cardona et al. 2009), whereas the $\delta^{13}\text{C}$ of fish and cephalopods were between those of phytoplankton and benthic primary producers. As expected, coastal fish (*Plectorhinchus mediterraneus*, *Caranx rhonchus* and *Sardinella aurita*) displayed higher $\delta^{13}\text{C}$ values than did more offshore species (*Pagellus bellotii*, *Scomberomorus tritor* and *Mullus barbatus*), but none of the sampled species

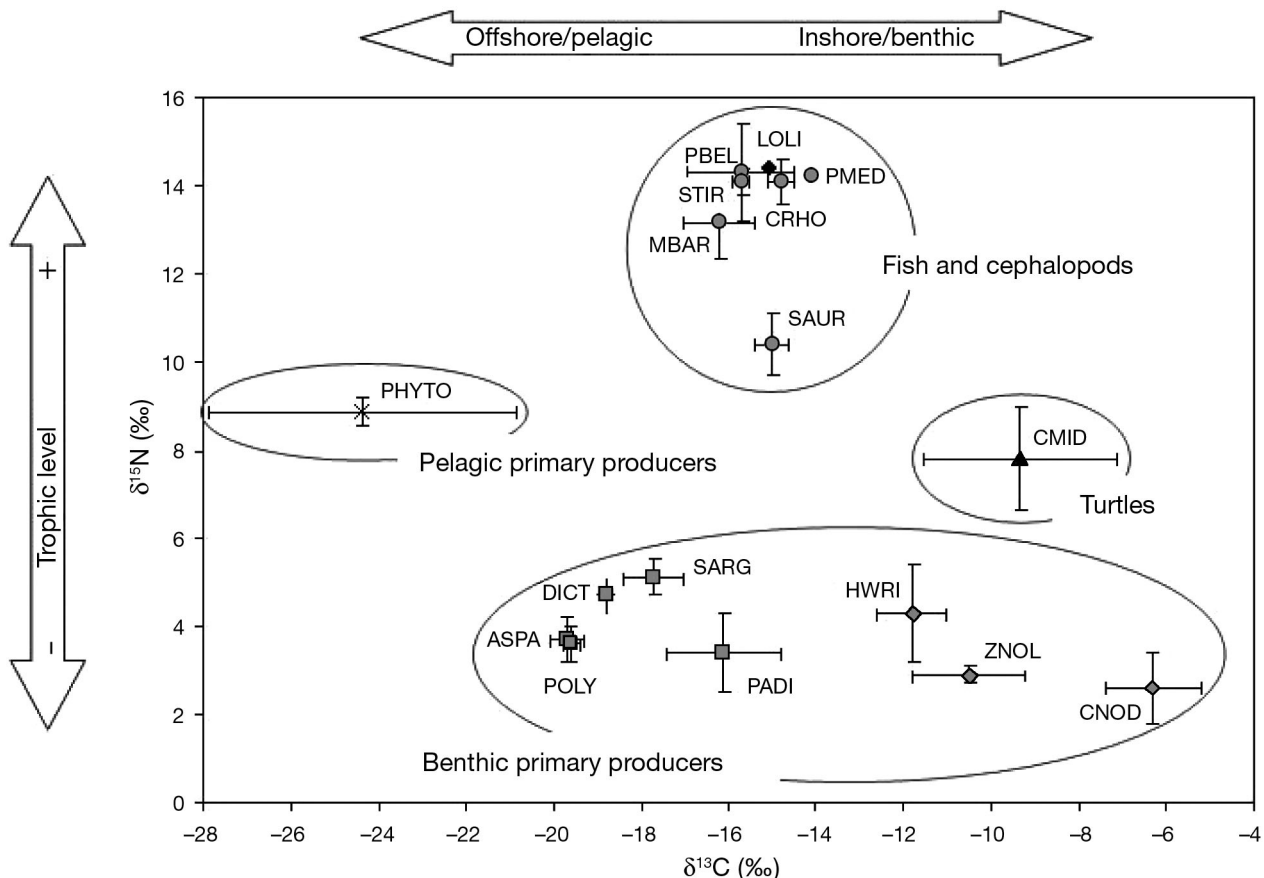


Fig. 2. Mean (\pm SD, ‰) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values for all trophic groups considered, except marine mammals: phytoplankton (\times), seagrass (\blacklozenge), macroalgae (\blacksquare), fish (\bullet), cephalopods (\blacklozenge) and sea turtle (\blacktriangle). The identification codes and number of individuals for each species are presented in Table 1; ellipses enclose groups listed in Table 1

was truly oceanic. The $\delta^{15}\text{N}$ of macrophytes was highly variable and ranged from 2.6‰ (the seagrass *Cymodocea nodosa*) to 5.4‰ (the macroalgae *Sargassum* sp.). Phytoplankton displayed higher $\delta^{15}\text{N}$ values than did any benthic macrophyte. As expected, green turtles were more enriched for $\delta^{15}\text{N}$ than were benthic primary producers, and the zooplanktophagous fish *S. aurita* was more enriched for $\delta^{15}\text{N}$ than was phytoplankton. Likewise, fish including only small invertebrates in their diets (*M. barbatus* and *S. aurita*) presented lower $\delta^{15}\text{N}$ values when compared with fish consuming large invertebrates and fish (*C. rhonchus*, *S. tritor* and *P. mediterraneus*). Such an isotopic landscape indicates that the bone of oceanic marine mammals should present lower $\delta^{13}\text{C}$ values than that of coastal marine mammals, especially those inhabiting seagrass meadows. Furthermore, $\delta^{15}\text{N}$ is a good proxy for trophic level in the considered system, although species inhabiting seagrass meadows might present lower $\delta^{15}\text{N}$ values in comparison with oceanic species at the same trophic level.

Stable isotopic composition of marine mammals

Statistically significant differences exist among the bivariate isotopic signals of the considered species of marine mammals (MANOVA test, Wilk's lambda = 0.413, $F = 14.131$, $p < 0.001$). ANOVA indicated that both nitrogen and carbon were involved in these differences ($\delta^{13}\text{C}$: $F = 16.982$, $p < 0.001$; $\delta^{15}\text{N}$: $F = 11.256$, $p < 0.001$; Table 2). The results of the post hoc test for pairwise comparisons between species for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are illustrated in Table 3.

As revealed by the $\delta^{13}\text{C}$ values, 4 major groups of marine mammals exist as delineated by their distribution along the coastal–oceanic axis (Fig. 3). Carbon isotope values together with the results of the post hoc pairwise comparisons allowed us to group species according to the similarity of their $\delta^{13}\text{C}$ values. The most coastal group, characterised by values of the $\delta^{13}\text{C}$ close to those of seagrass, included *Monachus monachus* ($\delta^{13}\text{C} = -10.4\text{‰}$) and *Sousa teuszii* ($\delta^{13}\text{C} = -9.7\text{‰}$). The most oceanic group, characterised by highly negative $\delta^{13}\text{C}$ values, included *Physeter macrocephalus* ($\delta^{13}\text{C} = -13.9\text{‰}$). *Balaenoptera acutorostrata* ($\delta^{13}\text{C} = -15.9\text{‰}$) probably belonged to this group, although only one individual was sampled. The remaining 9 species had $\delta^{13}\text{C}$ values between these 2 groups, with *Delphinus* sp., *Globicephala macrorhynchus*, *Phocoena phocoena*, *Stenella frontalis* and *Orcinus orca* presenting lower $\delta^{13}\text{C}$ values than *Globicephala melas* and *Tursiops truncatus* (Table 1, Fig. 3).

Regarding the $\delta^{15}\text{N}$ values, significant differences were observed between the most $\delta^{15}\text{N}$ -enriched spe-

Table 2. Summary of the results of the ANOVA to test for differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the marine mammal species investigated in the study area

| Factor | SS | df | MS | F | p | r ² |
|---------------------------|-----------|-----|-----------|-----------|--------|----------------|
| $\delta^{13}\text{C}$ (‰) | | | | | | |
| Model | 140.791 | 9 | 15.643 | 16.982 | <0.001 | 0.399 |
| Intercept | 7009.343 | 1 | 7009.343 | 7608.979 | <0.001 | |
| Species | 140.791 | 9 | 15.643 | 16.982 | <0.001 | |
| Error | 211.875 | 230 | 0.921 | | | |
| Total | 33183.103 | 240 | | | | |
| $\delta^{15}\text{N}$ (‰) | | | | | | |
| Model | 94.977 | 9 | 10.553 | 11.256 | <0.001 | 0.306 |
| Intercept | 10178.900 | 1 | 10178.900 | 10857.200 | <0.001 | |
| Species | 94.977 | 9 | 10.553 | 11.256 | <0.001 | |
| Error | 215.631 | 230 | 0.938 | | | |
| Total | 43505.029 | 240 | | | | |

Table 3. Results of the post hoc test for multiple comparisons between the marine mammal species collected along the Mauritanian coast (see Table 1 for codes). Carbon isotope ($\delta^{13}\text{C}$) p-values are reported below the diagonal and those for nitrogen isotopes ($\delta^{15}\text{N}$) are reported above the diagonal. Significant p-values (<0.05) are highlighted in **bold**

| | DDEL | GMAC | MMON | PPHO | STEU | TTRU | SFRO | GMEL | ORCA | PMAC |
|------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| DDEL | | 0.000 | 0.000 | 0.000 | 0.052 | 0.000 | 0.334 | 0.049 | 0.002 | 0.000 |
| GMAC | 0.008 | | 0.271 | 0.259 | 0.104 | 0.778 | 0.154 | 0.940 | 0.458 | 0.009 |
| MMON | 0.000 | 0.008 | | 0.006 | 0.004 | 0.064 | 0.020 | 0.577 | 0.988 | 0.042 |
| PPHO | 0.000 | 0.523 | 0.000 | | 0.351 | 0.118 | 0.399 | 0.513 | 0.128 | 0.001 |
| STEU | 0.000 | 0.000 | 0.076 | 0.000 | | 0.055 | 0.829 | 0.305 | 0.060 | 0.000 |
| TTRU | 0.000 | 0.199 | 0.026 | 0.001 | 0.000 | | 0.143 | 0.825 | 0.314 | 0.003 |
| SFRO | 0.585 | 0.284 | 0.002 | 0.435 | 0.000 | 0.033 | | 0.291 | 0.077 | 0.001 |
| GMEL | 0.060 | 0.588 | 0.332 | 0.363 | 0.054 | 0.960 | 0.218 | | 0.633 | 0.048 |
| ORCA | 0.357 | 0.567 | 0.017 | 0.805 | 0.000 | 0.155 | 0.732 | 0.378 | | 0.091 |
| PMAC | 0.024 | 0.001 | 0.000 | 0.001 | 0.000 | 0.000 | 0.029 | 0.003 | 0.018 | |

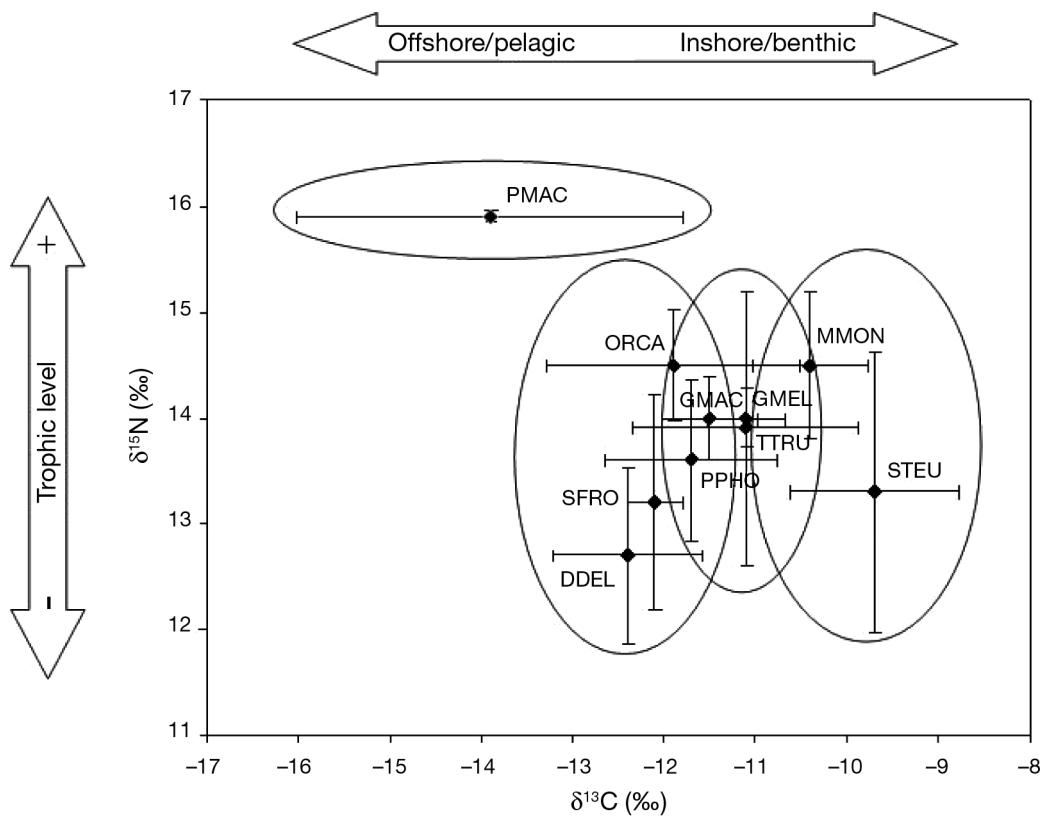


Fig. 3. Mean (\pm SD, ‰) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of the marine mammal species collected in Mauritania. The identification codes and number of individuals for each species are presented in Table 1; ellipses group the species that did not display significant differences in $\delta^{13}\text{C}$ values ($p > 0.05$)

cies (*Physeter macrocephalus*) and those species less enriched (e.g. *Delphinus* sp. and *Sousa teuszii*; Tables 1 & 3, Fig. 3). The only specimens of *Balaenoptera acutorostrata* and *Stenella coeruleoalba* analysed were also highly depleted for $\delta^{15}\text{N}$ —11.8 and 11.9‰, respectively. Differences in $\delta^{15}\text{N}$ values among species revealed differences in trophic level: species with higher $\delta^{15}\text{N}$ values were at a higher trophic level than species with lower $\delta^{15}\text{N}$ values. However, as previously stated, coastal species might present lower $\delta^{15}\text{N}$ values in comparison with oceanic species at the same trophic level. Accordingly, *P. macrocephalus* was the species with the highest trophic level, while *B. acutorostrata* and *S. coeruleoalba* were the species with the lowest trophic levels. It is important to notice that the mean trophic level of *Orcinus orca* ($\delta^{15}\text{N} = 14.5\text{‰}$) was equal to that of *Monachus monachus* ($\delta^{15}\text{N} = 14.5\text{‰}$) and lower than that of *P. macrocephalus* ($\delta^{15}\text{N} = 15.9\text{‰}$). However, direct comparisons between species may be slightly biased owing to the fact that *M. monachus* is a much more coastal species than *O. orca*.

DISCUSSION

Although the use of stable isotopes as diet tracers is a powerful technique, interpretation of the results is not always straightforward because the method is more reliable when large differences exist between the isotopic signals of the considered sources. Many researchers do not assess the variability in $\delta^{15}\text{N}$ among primary producers because it is assumed that they have similar $\delta^{15}\text{N}$ values. Although this is true in some ecosystems and regions, exceptions are common (Drago et al. 2009). The present study reveals a high variability in $\delta^{15}\text{N}$ among macrophyte species from the same region and also between macrophytes and phytoplankton, with differences often larger than the average increase expected per trophic level (Minagawa & Wada 1984, Caut et al. 2009). As a consequence, variability in the $\delta^{15}\text{N}$ of marine mammal bone may reflect not only differences in trophic level but also shifts among foraging grounds with primary producers that differ in $\delta^{15}\text{N}$ values. In the Mauritanian ecosystem, coastal marine mammals are expected to

have lower $\delta^{15}\text{N}$ values than their oceanic counterparts because macrophytes display lower $\delta^{15}\text{N}$ values than particulate organic matter. In species feeding on a variety of prey species with different nitrogen baselines, diet composition is difficult to establish simply through stable isotope analysis of nitrogen. Fortunately, the $\delta^{13}\text{C}$ of primary producers from Mauritania varied more consistently among groups, with phytoplankton less enriched in ^{13}C than macroalgae, and macroalgae less enriched in ^{13}C than seagrass. This allowed us to interpret the enrichment in ^{13}C of the bone of marine mammals as evidence of more-coastal foraging habitats.

Therefore, *Sousa teuszii* and *Monachus monachus* appear to be the most coastal species, a result consistent with published information about the distribution of these species off Mauritania. The main area of occurrence of *S. teuszii* is the Banc d'Arguin, a large system of shallow waters and channels extending along the northern coast of the country (Maigret et al. 1976, Maigret 1980a, Van Waerebeek et al. 2004). *M. monachus* is found off the Cape Blanc Peninsula, although it has also been observed to travel several miles offshore to obtain its prey (Gazo & Aguilar 2005). Despite the similarity in the $\delta^{13}\text{C}$ values of *M. monachus* and *S. teuszii*, the former was far more enriched for $\delta^{15}\text{N}$. This result is also consistent with stomach-content analysis, as *S. teuszii* consumes primarily detritivorous and zooplanktophagous fish that are abundant nearshore (Cadenat & Paraíso 1957, Van Waerebeek et al. 2004), whereas *M. monachus* principally eats lobsters, octopus and benthic, carnivorous fish (Marchesaux 1989). However, increasing fish landings have resulted in stocks, especially those of demersal fish and invertebrates (crustaceans and cephalopods), being overexploited or severely depleted (Christensen et al. 2004, Jouffre & Inejih 2005), most likely affecting the feeding behaviour of *M. monachus* and *S. teuszii*.

Also, the $\delta^{13}\text{C}$ values suggest that *Balaenoptera acutorostrata* and *Physeter macrocephalus* are the most oceanic species in the region; *B. acutorostrata* has been observed both in coastal and offshore waters off of the Western Sahara (Van Waerebeek et al. 1999). Distribution data for *P. macrocephalus* off Mauritania are limited (Maigret 1980b), although the species is oceanic over most of its range worldwide (Rendell et al. 2004). The diet of these species off NW Africa is unknown, but elsewhere *P. macrocephalus* preys mostly on large, oceanic squid with a high trophic level (Clarke et al. 1976, Pauly et al. 1998b, Ostrom et al. 1993, González et al. 1994), which is consistent with its high $\delta^{15}\text{N}$ in the study area. By contrast, *B. acutorostrata* primarily consumes schooling fish (Das et al. 2003, Hassani et al. 1997, Pauly et al. 1998b, MacLeod et al. 2007). This kind of prey could explain its semblance with *S. coerulea*

with respect to $\delta^{15}\text{N}$ values, although only one specimen of the latter was analysed.

The remaining species lie between the former 2 groups, spaced along a continuous gradient. *Tursiops truncatus* is found in both coastal and offshore habitats along the Mauritanian coastline (Robineau & Vely 1998). This probably explains the large intraspecific variability in the $\delta^{13}\text{C}$ values and suggests the occurrence of persistent individual differences in foraging habits or even the existence of coastal versus offshore populations and/or ecotypes in the area, as has been found elsewhere (Segura et al. 2006).

Nevertheless, the mean $\delta^{13}\text{C}$ value of *Tursiops truncatus* was close to that of *Globicephala melas*, a typical deepwater species in the North Atlantic (MacLeod et al. 2007) that is also known to occur over the continental shelf off Banc d'Arguin and off the Grande Plage (Maigret et al. 1976, Robineau & Vely 1998). *G. melas* displayed a slightly higher $\delta^{13}\text{C}$ value than *Globicephala macrorhynchus*, a species usually inhabiting deeper water over the upper slope in the North Atlantic (Davis et al. 2002), although nothing is known about its distribution off Mauritania. Finally, these 3 species presented lower $\delta^{13}\text{C}$ values than those of *Sousa teuszii* and *Monachus monachus* and higher values than those of typical oceanic species, such as *Delphinus* sp. and *Physeter macrocephalus* (Robineau & Vely 1998, Rendell et al. 2004). However, *T. truncatus*, *G. melas* and *G. macrorhynchus* also showed similar $\delta^{15}\text{N}$ values, suggesting that they possibly forage for similar prey. Published dietary data, only available for *T. truncatus* off Mauritania, identified the detritivorous grey mullet *Mugil cephalus* as their main prey item (Robineau & Vely 1998). This observation does not seem to correlate with the typical prey of the 2 species of *Globicephala* (Overholtz & Waring 1991). It is possible, however, that only a fraction of the population of *T. truncatus* regularly consumes grey mullet, while most of the population has a diet similar to that of *Globicephala* spp. This scenario has been reported, for instance for northern Spain, where *G. melas* and *T. truncatus* feed mainly on neritic cephalopods (González et al. 1994). Likewise, in the Gulf of California, the coastal ecotype of *T. truncatus* displayed values of the $\delta^{13}\text{C}$ similar to those of coastal prey items such as the mullet *M. cephalus*, whereas the offshore ecotype of *T. truncatus* displayed values of the $\delta^{13}\text{C}$ more similar to those of pelagic fish and medium-sized squid (Segura et al. 2006).

The species below the previous 3 in decreasing order of $\delta^{13}\text{C}$ are *Phocoena phocoena*, *Orcinus orca*, and *Grampus griseus*. *P. phocoena* inhabits cold-temperate and subpolar regions in the North Atlantic, generally showing affinity for shelf waters (Skov et al. 1995). Mauritania is the southern limit of the distribution range of

the species probably because of the coastal upwelling, which produces relatively cold waters (Smeenk et al. 1992). Sightings suggest that *P. phocoena* lives close to the coast in the non-upwelling season and moves offshore in the onset of the upwelling season (Marchesaux & Campredon 1988, Smeenk et al. 1992, Robineau & Vely 1998). The diet of *P. phocoena* off NW Africa is unknown, but mean $\delta^{15}\text{N}$ values are similar to those of *Tursiops truncatus*, which is consistent with a fish-based diet (Fontaine et al. 1994). *Orcinus orca* has been reported in both coastal and oceanic areas off Mauritania, except in the very shallow waters of the Parc National du Banc d'Arguin (Duguay 1976, Maigret 1981). However, its $\delta^{13}\text{C}$ values reveal a preference for the deeper parts of the continental shelf and the shelf break, as they are close to the values for *Delphinus* sp. The Mauritanian population of *O. orca* appears to be the 'offshore' ecotype, which is an ecotype thought to eat fish (Ford et al. 2000, Saulitis et al. 2000). This is in agreement with visual observations that suggested that *O. orca* avoided other marine mammals, including the monk seal *M. monachus* (A. Aguilar unpubl. data). The mean $\delta^{15}\text{N}$ of this species suggests a diet based on carnivorous fish, as reported for southern Spain (De Stephanis et al. 2008). *Grampus griseus* is poorly reported in NW Africa (Robineau & Vely 1998), but isotopic values revealed an oceanic habitat preference that occurs seaward of the continental slope and is concentrated along the upper continental slope (Baumgartner 1997, Davis et al. 2002).

Delphinus sp. is seldom observed onshore in Mauritania (Robineau & Vely 1998) and displays a typical oceanic behaviour. *Stenella frontalis* also typically inhabits the shelf break (Nieri et al. 1999) because the quasi-permanent upwelling may act as a thermal barrier and prevent it from approaching the inshore coastal zone (Robineau & Vely 1998). Likewise, *Stenella coeruleoalba* is oceanic over most of its range (Aguilar 2000, Davis et al. 2002). Accordingly, these 3 species are more depleted for $\delta^{13}\text{C}$ than *Monachus monachus*, *Sousa teuszii* and *Tursiops truncatus*. *Delphinus* sp. and *S. coeruleoalba* presented some of the lowest $\delta^{15}\text{N}$ values of all marine mammals, which is similar to what has been observed for other marine trophic webs (Das et al. 2003, Walker and Macko 1999). The discrepancies in $\delta^{15}\text{N}$ values of these species compared with that of other pelagic marine mammals possibly reflects the higher proportion of low-trophic-level prey, such as *Sardinella aurita*, in the diet of these species off the coast of Mauritania. Additionally, dolphins are opportunistic feeders and thus take advantage of the local abundance of prey (Hassani et al. 1997).

The results obtained in the present study suggest that the outer continental shelf and the upper slope are the areas with greater marine mammal species diver-

sity. However, coastal areas are home to the most vulnerable and endangered species in the Mauritanian marine ecosystems. In the outer continental shelf and upper slope, there could be a certain redundancy between species because their isotopic signals are very similar, indicating that they occupy a very similar ecological niche. By contrast, the reduced number of species and the greater difference in isotopic signals indicate less redundancy in the coastal areas. From this point of view, conservation of coastal species (*Monachus monachus* and *Sousa teuszii*) in Mauritania should be a priority because, if these species were to disappear, they could not be replaced in the trophic web by other marine mammals. In the case of *M. monachus*, it is likely that this species is already extinct from the ecological point of view, given the small number of individuals of this population (Forcada et al. 1999). Artisanal fisheries could have an impact on *M. monachus* and *S. teuszii*, although industrial fishing operating in the deepest parts of the continental shelf are the only sources of incidental bycatch recorded to date in the region and *Phocoena phocoena* and *Stenella frontalis* are the only species known to be affected (Nieri et al. 1999). Nevertheless, overfishing of the local demersal species by the intensive bottom trawling fishing in Mauritania (Jouffre & Inejih 2005) may have limited the prey availability for *M. monachus*, which might explain, in part, the reproductive problems of this species (Pastor 2010). Therefore, the highest priority of conservation efforts should be to reduce the impact of artisanal and industrial bottom trawling fishing on the less abundant and most vulnerable species. Nonetheless, it will also be important to regularly estimate and control the populations and catches of fishes in the whole study area because this region shelters a great diversity of marine mammals. There are inevitable consequences of fishing down the food web: increased ecosystem instability, unsustainable fisheries and an inability for the ecosystem to support healthy, abundant populations of apex predators (Trites et al. 2006). Excessive catches of one species may lead to the collapse of an important predator or prey in the system, which may cause changes in the growth and survival patterns of other species in the food web (Walters & Kitchell 2001). Some groups of apex predators, such as marine mammals, may be affected by fisheries even when the distributions of prey and predators do not overlap, driving species at the end of the food chain to the brink of extinction (Trites et al. 2006). Conservation efforts should be made locally to protect these species because this area suffers a high fishing pressure (ter Hofstede & Dickey-Collas 2006, Christensen et al. 2004) and animals are constantly exposed to threats such as intensive fishing (Kenety 2001, Christensen et al. 2004), prey stock depletion (ter Hofstede & Dickey-

Collas 2006, Christensen et al. 2004), pollution and human disturbance (Colman et al. 2005). Conservation efforts should be unequivocally related to the local fishing policies, such as effective monitoring, control and surveillance of fisheries in the region (Atta-Mills et al. 2004); strengthening political interest to implement sustainable fisheries in NW Africa, because African leaders appear to be disregarding overfishing as a priority issue that needs to be addressed (NEPAD 2001); and lobbying the European Union and Asian countries, such as Japan and China, for policy reforms to minimize the impacts of European and Asian fishing fleets on NW African coastal marine resources.

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