

RESIDENCIA, ESTRUCTURACIÓN SOCIAL, Y ESTRATEGIAS ALIMENTICIAS DE CALDERONES COMUNES EN EL ESTRECHO DE GIBRALTAR

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INTRODUCTION

The strait of Gibraltar is the only connection between the Mediterranean Sea and the Atlantic Ocean. Seven species of cetaceans occur regularly within the Strait (Cañadas *et al* 2005, Guinet *et al* 2007, De Stephanis *et al* (in press)). Among them a community of approximately 260 long-finned pilot whales is observed year-round in the strait of Gibraltar (Verborgh *et al* submitted, De Stephanis *et al* (submitted a)). Pilot whales have a hierarchical social system and individuals lives in stable social groups of related individuals (Ottensmeyer and Whitehead, 2003, Jankowski 2005, and De Stephanis *et al* (submitted b)). Pilot whale populations consist of several pods typically of 14 individuals, which form temporarily associated and interbreeding clans or grinds (Ottensmeyer and Whitehead, 2003, Jankowski 2005, and De Stephanis *et al* (submitted b)). Pods are stable social subunits which are likely to be matrilineal in structure (Amos 1993 *et al*, Fullard 2000, De Stephanis *et al* (submitted b))).

This species is sexually dimorphic with mature males being longer (mean: $552 \pm 1,7$ cm) and heavier (mean: 1694 ± 39 kg) than mature females ($432 \pm 0,8$ cm; 893 ± 10 kg) (Bloch *et al* 1993). Such large sexual dimorphism implies that mature males and females have different absolute metabolic requirements (Flinn *et al* 2002). Several studies have also revealed that in highly sexually dimorphic species, the two sexes could

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have different foraging ecology, e.g. sperm whales (*Physeter macrocephalus*) and Weddell Seals (*Leptonychotes weddellii*) (Flinn *et al* 2002, Evans and Hindell 2004, Zhao *et al* 2004).

The spatial distribution of the pilot whale community within the strait of Gibraltar highlighted a summer concentration over deep waters and steep bathymetric gradient in a restricted area, in the narrowest part of the strait (De Stephanis *et al* in press). During fall and winter this community of pilot whales dispersed more widely throughout the whole area of the strait of Gibraltar (De Stephanis *et al* (in press and submitted a)). This shift in distribution suggests either a change in the prey species targeted or a change in the distribution of the preferred preys between those two periods. So far this assumption is not supported by any evidences other than the observed change in the spatial distribution of pilot whales. The only existing knowledge about the diet of this community arise from the stomach content of 3 stomachs of pilot whales found stranded along the northern coast of the Strait during fall 2006. These contained squids beaks (cephalopod) and fish otoliths and bones but the species were not identified (unpublished data).

In other locations, stomach contents from stranded animals or drive fishery catch, consisted predominantly of squid and fish species (Desportes and Mouritsen 1993, Clarke and Goodall 1994, Abend and Smith 1995 and 1997, Gannon *et al* 1997, Bjørke and Gjørseter 1998, Clarke *et al* 1998, Aguiar dos Santos and Haimvici 2001, Santos *et al* 2001). However these data are subject to several limitations and biases. Animals that strand often have an empty stomach and can be sick and unable to prey efficiently on their usual prey, their stomach contents may therefore not be representative of the diet of healthy individuals. Furthermore stomach content analyses, often present a snap shot of the prey items consumed few days or hours preceding the death of the animal and it is difficult to assess possible seasonal or interannual shifts in diet.

Measurements of naturally occurring stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) can provide information to trace sources of primary productivity and relative trophic level of organisms in marine ecosystems (Michener and Schell, 1994). These methods are based on the principle that the composition of stable isotopes in an animal's diet will be reflected in its tissues (Klem 1935; Ackman and Eaton 1966; Rouvinen and Kiiskinen 1989; Hobson 1990; Wada *et al.* 1991; Iverson *et al.* 1995; Kirsch *et al.* 1998, 2000). Thus, compared with the short-term record of diet provided by stomach contents, interpretation of diet using these analyses is based on tissue samples that reflect the average composition of food resources that have been assimilated over periods of days to months, depending on tissue turnover (Tieszen 1978; Kirsch *et al.* 1998, 2000). Stable-carbon isotope values are found to vary between benthic or inshore food webs relative to pelagic food webs (Hobson and Welch, 1992; Hobson *et al.*, 1994). Furthermore in pelagic habitat, carbon isotope varies according to latitude (i.e. temperature) with impoverished high latitude waters relative to low latitude waters masses. There are little (i.e. approx. 1‰) or no change in the relative abundance of ^{13}C between trophic levels following the primary producer to primary consumer link (Hobson and Welch, 1992). For nitrogen, significant enrichment in ^{15}N occurs with trophic level, an effect that appears to be typically ranging between 1,7‰ and 4‰ with a mean value close to 3 ‰ (Michener and Schell, 1994, Abend and Smith 1997). The combined use of stable-carbon and stable-nitrogen isotope measurements of marine organisms, together with more conventional dietary approaches, can thus be used to provide important new information on trophic relationships and feeding ecology, including spatial use of

habitat (Hobson and Welch, 1992; Hobson *et al.*, 1994; Michener and Schell, 1994; Kelly, 2000; Lawson and Hobson, 2000).

The aims of this study were to analyse possible seasonal variation in diet of the long-finned pilot whales occurring in the strait of Gibraltar. Furthermore we wanted to assess possible inter-sexual and inter-group differences in diet. To our knowledge such comparisons have never been conducted for pilot whales, and the investigation of possible diet differences between stable social units belonging to the same community have not been investigated in any cetaceans.

MATERIAL AND METHODS

Study area and surveys

The study area is the strait of Gibraltar and contiguous waters, comprised between 5° and 6° of longitude west, covering all the area until the Moroccan waters. The strait of Gibraltar (Figure 1) is nearly 60 km long. Its western border is located between Cape Trafalgar (Europe) and Cape Espartel (Africa), 44 km apart. The Strait then narrows to the East to reach a minimum width of 14 km between Tarifa (Europe) and Punta Cires (Europe). Its eastern border is located between Gibraltar and Punta Almina (Africa) 23 km apart (Parrilla *et al.*, 1988). The bathymetry of the Strait is characterized by a west to east canyon, with shallower waters (200-300 m) found on the Atlantic side and deeper waters (800-1000 m) on the Mediterranean side (figure 1).

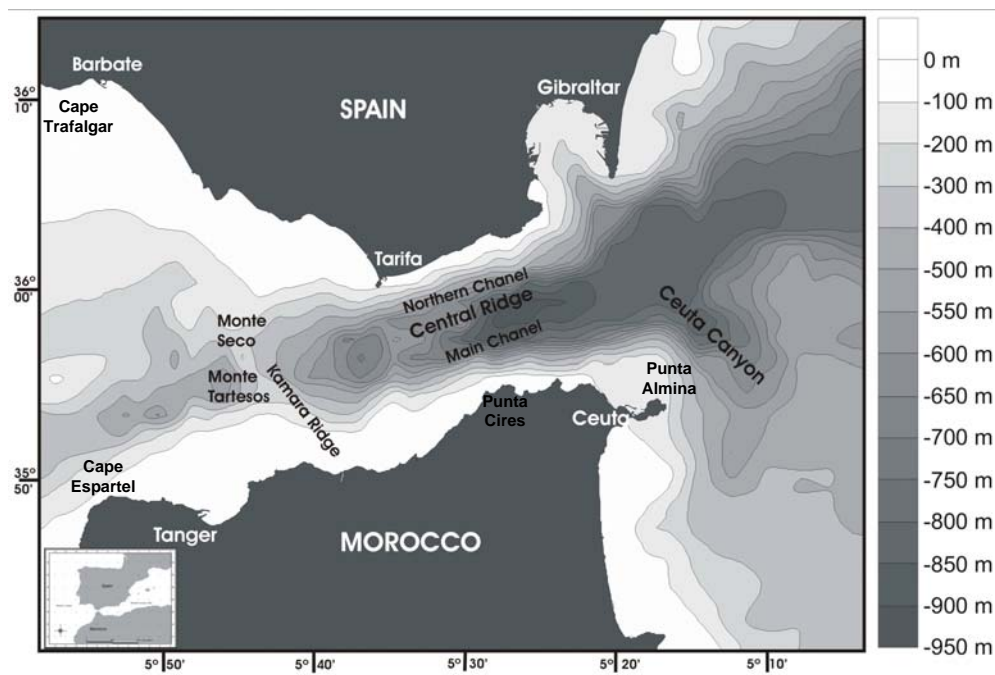


Figure 1.- Research area and bathymetry of the strait of Gibraltar (from Sanz *et al* 1988)

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Survey transects were conducted between 1999 and 2006 from the CIRCE (Conservation, Information and Research on Cetaceans) research motorboat *Elsa* (11 metres) sampling the study area. The observers were placed on an observation platform, 4 meters above the sea level. Two trained observers occupied the observation lookout post in one hour shifts during daylight with visibility over 3 nm (5,6 km), assisted with 8x50 binoculars, covering 180° ahead of the vessel. When a group of pilot whales was seen, the location of the ship, the distance and bearing of the group were recorded, to be able to localise them when approaching. The location of the animals was also recorded when they were approached by the vessel to photo-identify individuals and perform skin biopsies of known individuals (i.e. those individuals indexed in the strait of Gibraltar pilot whales photo-identification catalogue (De Stephanis *et al* (submitted a, b) and Verborgh *et al* (submitted)).

Pilot whales sampling strategy

The skin biopsies were performed using a 67 kg draw crossbow (Barnett Wildcat XL) at distances ranging from 5 to 15 m from the animal, and the dart was fired from at the midlateral region near the dorsal fin of the whale. A stop collar attached to the tip of the bolt prevented penetration deeper than the biopsy tip and caused the bolt to rebound upon impact with the whale. The darts were designed to float and were collected using a dip net. The skin biopsies collected included epidermis and dermis layers with biopsy arrows with 1,5 cm long and 0,6 cm in internal diameter. Both the tips and the arrows were designed and fabricated by Finn Larsen of the Danish Institute for Fisheries Research, Charlottenlund, Denmark. Samples were obtained under a permit issued by the Spanish Ministry of Environment.

Prior to sampling, animals were identified using the natural marking of their dorsal fin (Auger-Méthé and Whitehead 2007, De Stephanis *et al* (submitted a), Verborgh *et al* (submitted)) to avoid double sampling and to allow samples to be analysed according to individual identity and the social units to which they belong.

Immediately after collection, the skin samples were preserved in two different ways. One part was immediately put in a 2 ml tube containing a solution of 20% dimethylsulphoxide (DMSO) in saturated salt (NaCl) (Amos and Hoelzel 1991) and frozen at -20°C. This part of the sample was used to perform genetic sexing of individuals. The second part was frozen to -20°C without any treatment, and was used to assay $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values.

Samples were collected during two sampling periods. 5 individuals from 3 distinctive social units (de Stephanis *et al*. submitted c) were sampled during fall 2005 (25–27 October 2005). 51 individuals belonging to different social units were sampled during mid-summer 2006 (25 July- 1 August).

Sex determination

The sex of 56 individuals was assessed genetically by PCR (Polymerase Chain Reaction) of introns within the *Zfx* and *Zfy* genes (Shaw *et al*. 2003). To double check the results obtained with the *Zfx/Zfy* specific primers and avoid false positives, we reamplified the same samples with primers specific for males only,

targeting the *SRY* gene (Rosel, 2003). DNA was extracted and purified from a 20-mg aliquot of skin with the Qiagen "DNeasy Blood and Tissue Kit". PCR was performed on 30 ng of purified DNA in a 20- μ l reaction volume otherwise containing: 2 μ l of 10x *Taq* polymerase reaction buffer (supplied by the manufacturer), 1,5 mM MgCl₂, 0,2 mM dNTPs, 0,1 mg/ml BSA, 1 U of *Taq* polymerase (Invitrogen), and either 0,2 μ M of primers LGL331-forward and LGL335-reverse (for *Zfx/Zfy* amplification), or 0,2 μ M of primer *SRY*-forward and 0,04 μ M of primer *SRY*-reverse (for *SRY* amplification). The PCR reactions were performed as follows: 1 cycle at 94°C for 3 min, then 35 cycles of denaturation for 30 sec at 94°C, annealing for 30 sec at 52°C (for *Zfx/Zfy* primers) or 56°C (for *SRY* primers), and amplification at 72°C for 45 sec. Then each sample was loaded on a 1% agarose gel and the fragments were separated by electrophoresis. *Zfx/Zfy* specific primers allowed for the differentiation between males (2 bands, ~930 bp for the X-specific band and ~1000 bp for the Y-specific fragment) and females (1 band). A confirmation of the results was obtained with the primers specific for the *SRY* gene which is positive for males (1 band, ~350 bp) and negative for females (no band). The sequences of the primers are presented in table 1.

Primers	Sequence
LGL331-forward	5'-CAAATCATGCAAGGATAGAC-3'
LGL335-reverse	5'-AGACCTGATTCCAGACAGTACCA-3'
<i>SRY</i> -forward	5'-ACCGGCTTTCCATTCGTGAACG-3'
<i>SRY</i> -reverse	5'-CATTGTGTGGTCTCGTGATC-3'

Table 1.-The sequence of the primers

Isotopic relationship determination

Skin samples were dried at 60°C during 48 hours and were then pulverized. High lipid concentration can mask a large part of the isotopic signature preventing comparison (Sotiropoulos *et al.* 2004; Hobson; *et al.* 1997; Hobson, *et al.* 1996), to avoid this problem samples (0,2 g) were rinsed several times with a 2:1 chloroform:methanol solution to remove lipids following the protocol recommended by Morin and Lesage 2003.

In the laboratory of Isotopic Mass Relationship Spectrometry of the Autonomous University of Madrid, each sample was reduced to a purified gas (CO₂, N₂, SO₂, SH₆ y H₂) that was analysed by a mass spectrometer. The spectrometer used was a Micromass Cf-Isochrom of magnetic sector that analyses the isotopic relationship of ¹³C/¹²C and ¹⁵N/¹⁴N in CO₂ and N₂ were determined through continuous flow elemental analyser Carlo Erba 1108-Chns. The analytic precision was 0,1 ‰ and 0,2‰ for C and N respectively. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = \left(\frac{R_{SAMPLE}}{R_{STANDARD}} - 1 \right) \times 1000$$

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Where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The R_{standard} values were based on the PeeDee Belemnite (PDB) for ^{13}C and atmospheric N_2 (AIR) for ^{15}N . The levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are given as mean \pm SD.

Photo-identification and groups

The methodology used to organise the photo-identification catalogue, obtain the degree of association between each pair of individuals, and to define social units followed the methodology used by Ottensmeyer and Whitehead (2003), Jankowski (2005) and De Stephanis *et al.* (submitted b). The strength of the behavioural relationships between dyads of individuals was represented using one index of the frequency of co-occurrence, the half-weight association index (Ginsberg and Young 1992, Ottensmeyer and Whitehead, 2003) that gave a Matrix of Association between each pair of individuals (MAI). The eight long lasting social units previously identified (De Stephanis *et al.* submitted b) were used in this study.

Comparing the social structure and the diet.

To compare the social structure and the diet, two approaches were used. First, three matrices of Euclidean distances (MED_1) were built, to assess the distances in the levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between individuals. The first matrix took into consideration both the levels of carbon and nitrogen, and their distance between each pair of individuals A and B according to the formula:

$$\text{Dist}(A, B) = \sqrt{(\delta^{13}\text{C}_A - \delta^{13}\text{C}_B)^2 + (\delta^{15}\text{N}_A - \delta^{15}\text{N}_B)^2}$$

Two other matrices were constructed using the differences in levels of $\delta^{13}\text{C}$ (MED_2) and $\delta^{15}\text{N}$ (MED_3), respectively between each pair of individuals. Only the samples collected during mid-summer 2006 were used for this analysis. The matrix of association index rates (MAI) was compared with the three matrices of Euclidean distances using a Mantel Test.

Second, the results obtained using the first approach were verified by comparing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of individuals between social units defined in De Stephanis *et al.* (submitted b).

RESULTS

Isotopic relationship determination with sex and season

Among the 56 pilot whales sexed genetically, 23 were females and 33 were males. No statistical differences in either $\delta^{15}\text{N}$ nor $\delta^{13}\text{C}$ was found according to the sex of individuals: ($\delta^{15}\text{N}$ females: $11,51 \pm 0,15$ ‰, males: $11,38 \pm 0,09$ ‰: Mann-Whitney U-test = 351, $Z = -0,356$ $p = 0,72$; $\delta^{13}\text{C}$: females: $-16,37 \pm 0,09$ ‰, males: $-16,45 \pm 0,09$ ‰, $U = 296$, $Z = -1,290$, $p = 0,20$). When comparing the results by season, significant

differences were found in the levels of $\delta^{15}\text{N}$ (summer $11,27 \pm 0,38\%$, Fall $12,70 \pm 0,72 \%$, Mann-Whitney U-tests, Nitrogen: $U= 1$, $Z= -3,616$ $p < 0,005$) but not in $\delta^{13}\text{C}$ (summer $:16,37 \pm 0,40\%$, Fall $-16,20 \pm 0,22 \%$, $U= 92,50$, $Z= -0,78$ $p= 0,44$; Fig. 2). Furthermore the range of $\delta^{15}\text{N}$ was larger in fall ($10,12\%$ to $12,05\%$) compared to summer (12% to $13,85\%$). In summer $\delta^{13}\text{C}$ ranged from $-17,26\%$ to $-15,25\%$.

Comparing the social structure and the diet.

Biopsies were obtained from 4 stable social units (A (4 individuals out of the 8 individuals photo-identified and belonging to unit A), D (3/3), F (3/9), H (2/7), see De Stephanis *et al.* submitted, b.) to allow comparison of the N and C stable isotopic signature between social units. The $\delta^{13}\text{C}$ values were significantly different between social units (Kruskal-Wallis chi-squared = 8,51, $df = 3$, $p\text{-value} < 0,05$), while no differences were found in $\delta^{15}\text{N}$ values (Kruskal-Wallis chi-squared = 3,95, $df = 3$, $p\text{-value} = 0,27$) (figure 3). When comparing the matrix MED_1 and MAI, the social structure and the stable isotope signature were marginally correlated (Mantel r-statistic=0,13, $p=0,07$, (10000 permutations)). When comparing the levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ independently with the association index rates matrix (MAI), the matrices were significantly related for $\delta^{13}\text{C}$ values (MED_2) (Mantel statistic $r= 0,17$, $p < 0,05$ (10000 permutations)), but not for $\delta^{15}\text{N}$ values (MED_3) (Mantel statistic $r= -0,07$, $P=0,79$ (10000 permutations)).

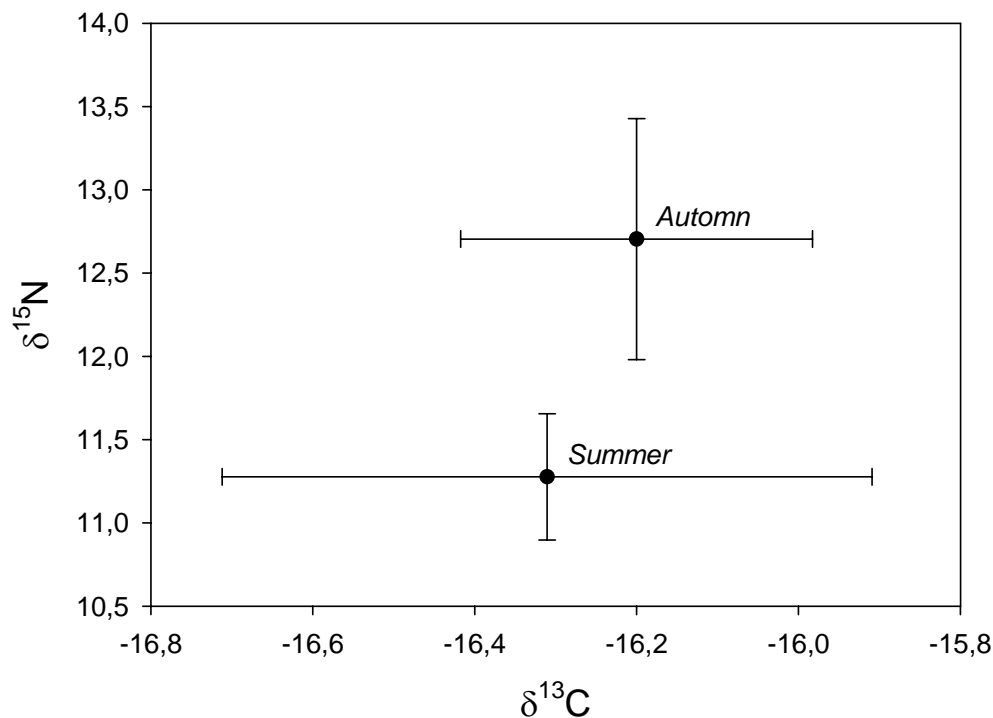


Figure 2.- $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with SD for pilot whales species in the strait of Gibraltar during the summer and the autumn.

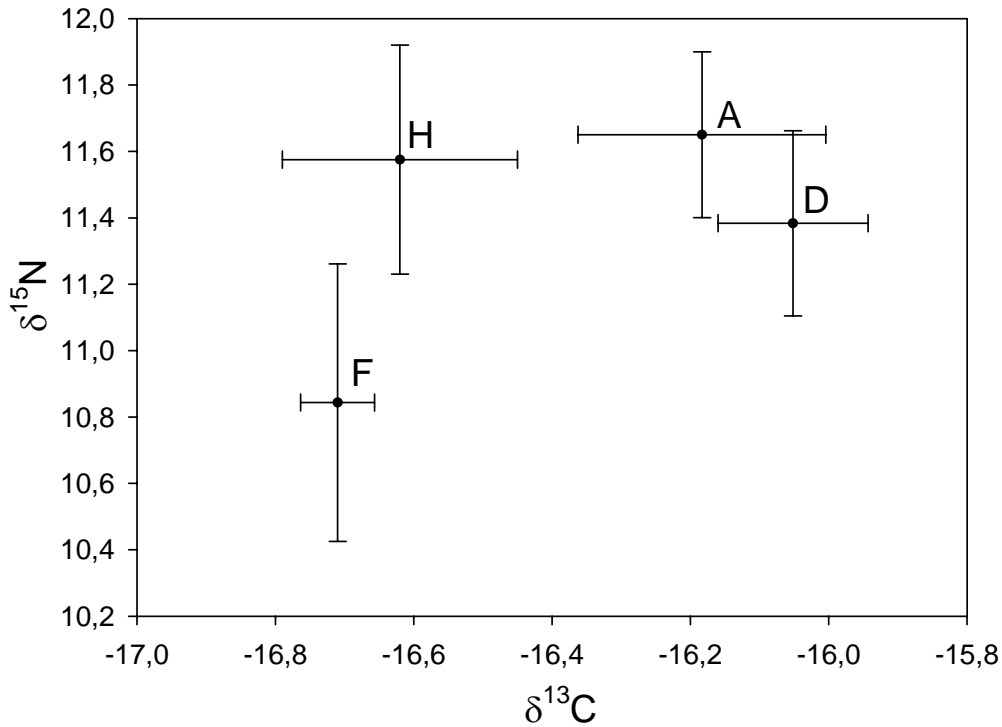


Figure 3.- $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with SD for the groups A, D, F and H described in De Stephanis *et al* submitted b.

DISCUSSION

In the absence of any change of the of the $\delta^{13}\text{C}$ values between summer and fall supports the hypothesis that pilot whales remain and forage in the same water mass. This result is consistent with our previous photo-identification work establishing that this community of pilot whale is year-round resident in the strait of Gibraltar (De Stephanis *et al* (submitted a)). The change in the isotopic values of $\delta^{15}\text{N}$ of pilot whales between the summer and the autumn could be due to pilot whales shifting prey species between summer and fall. An alternative possibility is that their prey remains the same, but that their diet is shifting to a higher trophic level between summer and fall. However, the higher range observed in the $\delta^{15}\text{N}$ isotopic signatures in fall compared to summer, despite the smaller sample size in fall, suggests that pilot whales feed on a broader range of prey species in fall compared to summer. This change in diet is concomitant to a change in the spatial distribution of pilot whales through the strait area, with pilot whales foraging over a broader area in fall compared to summer (De Stephanis *et al* submitted a). Cephalopods are expected to be at a lower trophic level than fish (ie Abend and Smith 1997, Sydeman *et al* 1997, Awkerman 2007), therefore our results would suggest that in summer, the diet of pilot whales is dominated by a cephalopod diet, while in fall diet was more diverse and included a greater proportion of fish.

Differences in stable isotope signature, between social units of the same community suggest segregation by diet specialisation or some differences in the water masses exploited. We can rule out the possible effect of the timing between biopsies on the stable isotope values obtained as samples were collected within 7 days and the stable isotope turnover rate of the skin is unlikely to vary much over such a short period of time. Closely associated animals were more likely to share a similar $\delta^{13}\text{C}$ signature compared to individuals belonging to the same clan (De Stephanis *et al.* b) but which associate less often. These results tend to indicate that individual of the same social units tend to exploit prey species in the same water masses while the absence of differences in the $\delta^{15}\text{N}$ values suggest that during summer the trophic level did not vary between long lasting social units. One possible interpretation of these results would be that social units tend to target different location, (either along a bathymetric gradient) to feed. As the strait of Gibraltar is a highly stratified environment (Lacombe and Richez 1982, Echevarría *et al.* 2002) this may reveal that some pilot whale social units target prey species living in different water masses within the strait of Gibraltar. The possible horizontal vs. vertical variation in the spatial distribution of pilot whales according to their social units should be investigated in a future studies, the horizontal variation according to the social units being the easiest to investigate by looking at the horizontal distribution of individuals belonging to these different social units. If no differences are found, this would rather suggest that either there is some kind of a vertical segregation between social units, or that different social units tend to select different type of prey (more likely to be squid species or different age classes of the same prey species). These results suggest that there is some level of social specialization in habitat or prey choice between social units of pilot whales. Future studies should investigate if those differences between social units persist through the year and in particular in periods like fall when diet appear to be much more diverse.

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