Differences in foraging activity of deep sea diving odontocetes in the Ligurian Sea as
determined by passive acoustic recorders.

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33 **ABSTRACT**

34 Characterizing the trophic roles of deep-diving odontocete species and how they vary in space
35 and time is challenged by our ability to observe foraging behavior. Though sampling methods
36 are limited, foraging activity of deep-diving odontocetes can be monitored by recording their
37 biosonar emissions. Daily occurrence of echolocation clicks was monitored acoustically for five
38 months (July – December 2011) in the Ligurian Sea (Mediterranean Sea) using five passive
39 acoustic recorders. Detected odontocetes included Cuvier's beaked whales (*Ziphius cavirostris*),
40 sperm whales (*Physeter macrocephalus*), Risso's dolphins (*Grampus griseus*), and long-finned
41 pilot whales (*Globicephala melas*). The results indicated that the foraging strategies varied
42 significantly over time, with sperm whales switching to nocturnal foraging in late September
43 whereas Risso's dolphins and pilot whales foraged mainly at night throughout the sampling
44 period. In the study area, winter nights are about five hours longer than summer nights and an
45 analysis showed that pilot whales and Risso's dolphins adjusted their foraging activity with the
46 length of the night, foraging longer during the longer winter nights. This is the first study to
47 show that marine mammals exhibit diurnal foraging patterns closely correlated to sunrise and
48 sunset.

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51 **Keywords:** Deep-diving odontocetes, foraging, Mediterranean Sea, echolocation, beaked
52 | whales, sperm whales, pilot whales, Risso's dolphin

1. Introduction

Deep-diving odontocetes like sperm, beaked, and pilot whales, and Risso's dolphins are all top predators that feed in the deep sea using echolocation to hunt their prey. Like other marine top predators, they have an important ecologic role in the ecosystem through top down trophic effects. While some information exists on predator-prey roles (e.g. stomach contents data, Blanco et al., 2006; MacLeod et al., 2003), characterizing species-specific, temporal and spatial variations in foraging behavior is limited by our inability to directly observe these animals beneath the sea surface. Passive Acoustic Monitoring (PAM)¹ provides a cost-effective way to detect the presence of acoustically active animals in remote areas. This is particularly true for cetaceans, since these marine mammals use sound for communication, foraging and navigation (Wartzok and Ketten, 1999). Indeed, PAM techniques have been successfully applied to marine mammal research to study foraging activity (e.g. Giorli et al., 2015), occurrence and distribution (e.g. Gedamke & Robinson, 2010; Au et al., 2013; Au et al., 2014), and the estimation of density (e.g. Marques et al., 2009; Martin et al., 2013; Küsel et al., 2011).

Species-specific monitoring using PAM requires the detection and classification of species-specific sounds, and a number of algorithms have been developed for this task (Jarvis et

¹Abbreviations:

NATO-CMRE :North Atlantic Treaty Organization Centre for Maritime Research and Experimentation

PAM :Passive Acoustic Monitoring

FM: Frequency Modulated

DTAG :Digital Acoustic Tag

DSL: Deep sea Scattering Layer

EAR :Ecological Acoustical Recorders

CS-SVM : Class-Specific Support Vector Machine

M3R :Marine Mammal Monitoring on Navy Ranges

ECM :Eco Cluster Machine

ICI : Inter-Click Interval

%OBSP : Percentage of Observation Periods

OBSP : Observation Period

DOY :Day of the Year

al., 2008; Yack et al., 2010). Spectral peaks and notches were used to classify Risso's dolphin echolocation clicks (Soldevilla et al., 2008), while bandwidth and click spectrum median and center frequency discriminated pilot whale clicks (Baumann-Pickering et al., 2011). Sperm whales are the only odontocetes that produce low frequency clicks with peak frequencies between 5 and 15 kHz and a duration of 100 ms (Møhl et al., 2003), and these features have been used to acoustically monitor their presence in many parts of the world (Morrissey et al., 2006). Beaked whales (family Ziphiidae) also produce distinctive echolocation clicks that are frequency modulated (FM). Cuvier beaked whales (*Ziphius cavirostris*) emit FM clicks with peak frequencies ~40 kHz, durations of ~200 μ s and inter-click intervals (ICI) of ~0.4 s (Zimmer et al., 2005). FM clicks are also produced by Blainville's beaked whales, *Mesoplodon densirostris*, (Johnson et al., 2006), Longman's beaked whales, *Indopacetus pacificus*, (Rankin et al., 2011) and Gervais beaked whales, *Mesoplodon europaeus* (Gillespie et al., 2009), though only Cuvier's beaked whale is known to inhabit the Mediterranean Sea.

The Ligurian Sea (a basin of the Mediterranean Sea) is located between the Italian Riviera (Liguria and Tuscany) and the island of Corsica and is the home of a number of odontocete species including Risso's dolphins (*Grampus griseus*), striped dolphins (*Stenella coeruleoalba*), common dolphins (*Delphinus delphis*), Cuvier's beaked whales (*Ziphius cavirostris*), sperm whales (*Physeter macrocephalus*), long-finned pilot whales (*Globicephala melas*) and bottlenose dolphins (*Tursiops truncatus*; Di Sciara et al., 1993). In the Ligurian sea, odontocete distribution is species-specific, with bottlenose dolphins found mainly in neritic waters (Gnone et al., 2011) and other dolphin species like striped and common dolphins found mainly in oceanic waters (Gannier, 2005). Sperm whales and Cuvier's beaked whales mainly frequent oceanic waters in the Ligurian Sea, ranging in depths between 1000 and 2000 m (Moulins et al., 2007; Azzellino et

al., 2008), while Risso's dolphins and long-finned pilot whales are found over the continental slope (Bearzi et al., 2011, Gannier, 2005). These species-specific distributions are thought to be shaped by foraging behavior. Pilot whales, Risso's dolphins, sperm whales and Cuvier's beaked whales all forage in deep water. Stomach contents of stranded Risso's dolphins in the Mediterranean Sea revealed that this species feeds mainly on Ommastrephidae, Histioteuthidae and Onychoteuthidae squids (Blanco et al., 2006). These squids perform diel vertical migration staying between 600 and 800 m depth during the day and many migrating to surface waters at night. Previous studies using digital acoustic tags showed foraging dive depths of > 600m for sperm whales (Watwood et al., 2006), 1000m for pilot whales (Jensen et al., 2011) and 1800m for Cuvier's beaked whales where most of their hunting time is spent in the lower part of the deep scattering layer (DSL) or near the bottom of the ocean (Tyack et al., 2006; Arranz et al., 2011).

Sperm whales, beaked whales, pilot whales and Risso's dolphins are all top predators in the Mediterranean Sea with foraging activities affecting prey abundance and timing, and associated food web dynamics. Since these are non-migratory species, their presence in an area will be mainly dictated by the presence of prey, and thus characterizing whale foraging activities is necessary to explain population dynamics of associated prey species, as well as for whale conservation. Here, we characterize foraging activity patterns of deep-diving odontocetes (Cuvier's beaked whales, pilot whales, Risso's dolphins, and sperm whales) in the Ligurian Sea, both daily and across seasons, with an emphasis on species-specific variability and implications for associated prey populations.

2.Methods

2.1 Research Site and Data Acquisition

The instruments used in this study were Ecological Acoustic Recorders (EARs; Lammers et al., 2008; Au et al., 2013). The EAR acquires data at a sample rate of 80 kHz using a calibrated Sensor Technology SQ26-01 hydrophone with a relatively flat frequency response from 1 to 40 kHz and a sensitivity of $-193.5 \pm 1 \text{ dB re } 1 \mu\text{Pa/V}$. The EAR can be deployed to depths down to 990 m and is controlled by a Persistor Instrument CF2 micro-controller allowing it to be programmed to operate on a duty cycle. Five EARs were deployed at the end of July 2011 and recovered at the beginning of December 2011 as part of the North Atlantic Treaty Organization Centre for Maritime Research and Experimentation (NATO-CMRE) SIRENA11 sea trial. The trial took place in three legs from late July to mid-December 2011 (Table 1). All EARs were deployed at the beginning of leg one, refurbished during leg two, and recovered during leg three. EAR1 and EAR2 were also recovered, refurbished and redeployed at the end of leg one to allow us to obtain preliminary data.

Table 1. SIRENA 11 sea trial legs schedule

1st Leg :22 nd July 2011 - 1 st August 2011
2nd Leg: 20 th October 2011- 30 th October 2011
3rd Leg: 8 th December 2011- 18 th December 2011

The five EARs were deployed at depths between 700 and 900 m at the locations shown in Figure 1. The deployment locations were chosen along the 800m depth isobath which, according to previous surveys, is the depth where deep diving odontocetes are likely to be found (NATO CREM).

Fig.1. (a) Ligurian Sea and (b) the position of the five EAR buoys along the 800m isobath in the study area.

Sample rates, sample duration, duty cycle, depth of each EAR, position and recording periods are shown in Table 2. The sample rate is the number of amplitude measurements per second taken from the analog acoustic signal. The analog signal is converted into 16 bit digital data. The sample duration is the length in seconds of each file recorded. The duty cycle is the time interval between the start of a recording period until the start of the next recording period.

Table2. EAR buoys settings and recording periods over the three legs of the SIRENA11 cruise.

EAR	Sample rate (Hz)	Sample duration (s)	Duty cycle (s)	Depth of the EAR (m)	Location coordinates (Decimal Degree)	Recording periods
1st Deployment						
EAR1	80000	40	120	900	Lat 44.0858° Long 8.4601°	07/22 to 08/1 2011
EAR2	80000	40	120	870	Lat 44.1513° Long 8.5795°	07/22 to 08/1 2011
EAR3	80000	30	240	700	Lat 44.1964° Long 8.6157°	07/22 to 10/20 2011
EAR4	80000	30	240	890	Lat 44.1780° Long 8.6857°	07/22 to 09/22 2011
EAR5	80000	30	240	880	Lat 44.0639° Long 8.9244°	07/22 to 10/20 2011
2nd Deployment						
EAR1	80000	34	240	900	Lat 44.0858° Long 8.4601°	08/1 to 10/20 2011
EAR2	80000	34	240	880	Lat 44.1513° Long 8.5795°	08/1 to 09/10 2011
3rd Deployment						
EAR1	80000	30	120	900	Lat 44.0858° Long 8.4601°	10/31 to 12/8 2011
EAR2	80000	30	120	880	Lat 44.1513° Long 8.5795°	10/31 to 11/3 2011

EAR3	80000	30	120	730	Lat 44.1964° Long 8.6157°	10/30 to 12/9 2011
EAR4	80000	30	120	900	Lat 44.1780° Long 8.6857°	CF2 Persistor failure
EAR5	80000	30	120	860	Lat 44.0639° Long 8.9244°	10/30 to 11/13 2011 Hard drive failure

Recording periods varied due to hard drive (EAR2 & 5) or CF2 Persistor (EAR 4) failure. All times stored by the EARs were recorded in UTC time.

CTD data from July, October and December showed no temporal variation in the sound speed profile below 300 m of depth. Thus, the detectability of animals by the recorders did not vary significantly with season.

2.2 Data Analysis

Automatic classification algorithms were used to identify recorded audio files with echolocation clicks from the different species. The class-specific support vector machine (CS-SVM) portion of M3R (Marine Mammal Monitoring on Navy Ranges) system (Jarvis, 2012; 2008) developed at the Naval Undersea Warfare Center Division in Newport, RI, was used to find files containing biosonar clicks of pilot whales and Risso's dolphins. Jarvis et al. (2008) and Jarvis (2012) give an estimate of the performance of the CS-SVM portion of M3R using a test dataset. Data were re-sampled by interpolation to 96 kHz to match the CS-SVM operational sampling frequency, and then data were run through the CS-SVM. The classification performance of the CS-SVM on our dataset was examined for each species by selecting a sub-sample of 100 random files where the CSVM detected animals in that category. Using a custom MATLAB program, an operator checked visually the validity of the classification. For each click in the file, the program plotted the waveform of the click, its spectrum and the Wigner-Ville distribution. Only those files containing at least 5 clicks resembling the category being checked were considered as a correct classification in a similar manner explained in Au et al. (2013 &

2014). Pilot whale clicks were identified following the methodology in Baumann-Pickering et al. (2011), where pilot whales are reported to have a median peak frequency (i.e. the median among the peak frequencies of all the spectra calculated) and center frequency (i.e. the frequency that divides the energy in the spectrum into two equal parts) of 19 and 23 kHz respectively. At our current level of understanding, we have little choice but to assume that the click characteristics of short- and long-finned pilot whales are approximately the same. The only available species-specific observations described the spectral characteristics of 20 on-axis long-finned pilot whale clicks (Eskeen et al. 2011). These on-axis properties are too restrictive for automatic detection of a species. An acoustic sensor record signals emitted by a marine mammal that could have a random orientation with respect to the sensor. There is a probability of 2.8% that a recorded click would be within $\pm 5^\circ$ of the beam axis and about 97.2% that the clicks are not within $\pm 5^\circ$ of the beam axis.

Risso's dolphin clicks were identified following the methodology in Soldevilla et al. (2008). Risso's dolphin's click spectrum showed the presence of notches at 19.6, 27.7, and 35.9 kHz, and local peaks at 22.4, 25.5, 30.5, and 38.8 kHz. These features were found to exhibit low variation and were therefore useful for click identification. The classification performance for pilot whale clicks and Risso's dolphin clicks was 86% and 83%, respectively.

A custom MATLAB program, called "Eco Cluster Machine" (ECM) was used to identify files containing sperm and beaked whales' clicks. The ECM automatically recognized echolocation click-trains and classified the clicks to one of the following categories: beaked whale, sperm whale, and dolphin. Using ECM, the echolocation clicks were detected by applying an adaptive threshold that self-adjusted based on the ambient background noise level. For each file analyzed, the average noise level was calculated and the threshold value was set to be 3 dB

above this noise level. ECM contained a clustering algorithm that grouped the individual clicks into click-trains (or clusters) depending on their inter-click intervals (ICI). If the time interval between two consecutive clicks was shorter than 2 s, clicks were considered to be in the same cluster. For each click-cluster, ECM calculated the average ICI, the average duration of the individual clicks and the mean and standard deviation of the peak frequency of the clicks. Click duration was calculated from the envelope of each click, obtained by performing a Hilbert transform. The start and end times of each click occurred when the value of the envelope went above and below the detection threshold value. These parameters were then used to classify the click-train. A click-train was classified as "beaked whale" if the mean peak frequency was higher than 25 kHz, the ICI was between 0.2 s and 0.6 s, and mean click duration was longer than 250 μ s. These parameters were chosen from a literature review on beaked whale clicks (e.g. Baumann-Pickering et al., 2013). A click-train was classified as "sperm whale" if the mean peak frequency was between 8 kHz and 15 kHz, the ICI was between 0.3 s and 1.5 s, and mean click duration of 100 μ s (Møhl et al., 2003).

The probability of correct classification by the ECM was calculated using a binary decision matrix as used in signal detection theory and psychophysical experiments involving the detection of a stimulus (Egan, 1975). For each trial, the detection algorithm is asked to answer "yes" or "no" as to whether a beaked or sperm whale click is present or not in the trial. There are four possible outcomes: two correct responses and two wrong responses. The answer is correct if the algorithm says "yes" when the stimulus is present and "no" when the stimulus is absent. The answer is wrong when the algorithm says "yes" when the stimulus is not present and "no" when the stimulus is present. The probability of correct response can be expressed as:

$$P(C) = P(Y/s) * P(s) + [1 - P(Y/n)] * P(n)$$

where $P(Y/s)$ is the probability of answering "yes" when the stimulus is present; $P(Y/n)$ is the probability of answering "yes" when the stimulus is not present; $P(s)$ is the probability of the stimulus being present; $P(n)$ is the probability of the stimulus being absent (Au and Hastings, 2008). To calculate $P(C)$ in our study, we selected and analyzed 200 files each for beaked and sperm whales, half of which contained the relevant whale click and half without. We obtained a $P(C)$ value of 0.81 for beaked whale clicks and 0.87 for sperm whale clicks. Table 3 shows the results of the algorithm test. It is possible clicks were missed by the detector, but this theoretical bias would not vary with time (time of day or season) and so would not affect the patterns described by our study. This is the classical problem in signal detection theory as to whether one wants to be a liberal or conservative detector. If the threshold is set lower to reduce the percentage of misses, then the false alarm rate will increase as will the correct detection rate. If the threshold is set higher, the false alarm rate will decrease but at the price of more misses (i.e. the correct detection rate decreases).

Table 3. Binary decision matrix values for the testing of the ECM algorithm. $P(Y/s)$ is the probability of answering "yes" when the stimulus is present; $P(N/s)$ is the probability of answering "no" when the stimulus is present; $P(Y/n)$ is the probability of answering "yes" when the stimulus is not present; $P(N/n)$ is the probability of answering "no" when the stimulus is not present; $P(s)$ is the probability of the stimulus being present; $P(n)$ is the probability of the stimulus being absent. $P(C)$ is the probability of correct response.

	$P(Y/s)$	$P(N/s)$	$P(Y/n)$	$P(N/n)$	$P(s)$	$P(n)$	$P(C)$
Beaked Whale	0.65	0.35	0.03	0.97	0.5	0.5	0.81
Sperm Whale	0.88	0.12	0.14	0.86	0.5	0.5	0.87

All results are presented as percentages of observation periods (%OBSP), with one observation period (OBSP) represented by one file stored to disk by the EAR buoy. Presenting the results in terms of %OBSP allows for comparison of the data despite differences in the duty cycles of the instruments. The nighttime versus the daytime foraging activity was investigated by computing the average percent of observation periods (%OBSP) in which biosonar signals were

detected in each period. Seasonal changes in timing of sunset and sunrise were included in the estimates. For each day, the average %OBSP at daytime and nighttime was calculated by dividing the total number of files with detection at night and day by number of hours in each time period. The average %OBSP can be thought as a rate of foraging activity and averaging takes into account changes in length of day and night as the season changes. For each species, a linear mixed-effects model (R Core Team 2014; Bates et al. 2014) was used to test whether foraging was higher at day or at night. Two models were created, a test model, and a null model:

test model : average %OBSP ~ Day/Night + DOY + 1|EAR

null model : average %OBSP ~ DOY + 1|EAR

where fixed effects were "Day/Night" as a categorical variable indicating daytime or nighttime, and "DOY" as the day of year, and EAR, as the EAR number, was included as a random effect on the intercept. "DOY" was included in the model to include effects of temporal autocorrelation and eliminate possible pseudoreplication errors when each day was considered a sample. A two way ANOVA test was used to compared the two models in order to assess whether Day/Night had an effect on the average %OBPS.

3. Results

3.1 Night-vs day-time foraging

Figure 2 shows the average %OBSP at nighttime and daytime as a function of day for each species and all EARs. Pilot whales and Risso's dolphins clearly show a higher rate of foraging during the night throughout the entire deployment period while beaked and sperm whale foraging during day and night appears more variable. Mixed model results revealed that there was a significantly higher %OBPS during nigh-time than during the day for all species

(ANOVA, $p < 0.0001$, with 0.07 - 1.9 relative increase in %OBSP at night vs. day among species).

Fig.2: Species-specific average %OBSP with foraging clicks at night-time (*, blue) and at day-time (., red) per day for all EARs.

In the case of pilot whales and Risso's dolphins, the difference becomes more evident from October and onward (Figure 2). The difference in foraging activity between nighttime and daytime was greater for Risso's dolphins and pilot whales than for beaked and sperm whales.

To explore possible seasonality in day-night trends, we performed two-way ANOVA tests comparing the test and null models using data subsampled via a 20-day moving window (Figure 3). Only EARs 1 and 3 were included in this analysis as they recorded over the entire

deployment period. The influence of window extent on results was explored and results were found to be similar for all window sizes less than 20 days. The results suggest that Cuvier's beaked and sperm whales show a change in their foraging strategy over the study period. The ANOVA test p-values for Cuvier's beaked whales were below 0.05 until mid-August, indicating more foraging at nighttime. Between mid-August and the beginning of September no differences were observed between night and day foraging rates (ANOVA, $p > 0.05$). Nighttime foraging predominates in September (ANOVA, $p < 0.05$), but from October daytime and nighttime foraging rates are not statistically different (ANOVA, $p > 0.05$).

Fig. 3: Results of ANOVA tests comparing the test and null models for each species at EAR1 and EAR3 performed by sub-sampling data via a 20 day moving window. The horizontal red dashed line represents the 5% significance level of the test (i.e. $\alpha = 0.05$). P-values below the horizontal dashed line indicate that a difference exists between the night and the day value. P-values above the horizontal dashed line indicates no difference between the night and day values at $\alpha = 0.05$.

Sperm whales at EAR1 and EAR3 locations showed little differences between night and day foraging until late September (ANOVA, $p > 0.05$). In general sperm whales seem to switch to foraging mainly at night as the winter approaches (ANOVA, $p < 0.05$). Pilot whales and Risso's dolphins showed a difference between night and day foraging rate over the entire deployment period; foraging was always higher at night for these two species.

3.2 Foraging activity in relation to the length of the night.

As winter day length is 5 hours shorter than that in summer, the hypothesis that pilot whales and Risso's dolphins adjust their foraging activity with the length of the night was tested. Pilot whales and Risso's dolphins were chosen as they demonstrated consistently more nighttime foraging at every location throughout the length of the study (Figure 3). As above, only data from EAR1 and EAR3 were included in this analysis since these two recorders collected data over the entire deployment period. The dataset was divided by months and for each month (July through December) the hour of sunset and sunrise was obtained in UTC time. For each month and species, we generated histograms of the number of files with detection per hour (e.g. Figure 4).

Fig.4: Histogram of the number of files with detections per hour for the month of November for Risso's dolphin.

Arrows indicates the hour of the largest negative change in echolocation activity (0600) and the hour of the largest positive change in echolocation activity (1600).

From each histogram, the hour with the biggest negative and positive change in echolocation activity between adjacent hours was calculated. For instance, for Risso's dolphin detections in November, the biggest negative change in echolocation activity occurs at 0600 hour, and the biggest positive change in echolocation activity occurs at 1600 hour (Figure 4). A linear regression was applied to the results to correlate the hours of highest negative change in echolocation activity with the hours of sunrise, and the hours of the highest positive change in echolocation activity with the hours of sunset (Figure 5).

Fig. 5: Linear correlation between hours of negative change in echolocation activity with the hours of sunrise, and the hours of positive change in echolocation activity with the hours of sunset for pilot whales (upper panels) and Risso's dolphin (lower panels). Dashed lines represent the 95% confidence intervals.

There is a significant positive correlation between the hour of negative change in echolocation activity and the hour of sunrise for both pilot whales ($r^2 = 0.84$) and Risso's dolphins ($r^2 = 0.86$). A positive correlation also existed between hours of positive change in

echolocation activity with the hours of sunset for pilot whales ($r^2 = 0.90$) and Risso's dolphins ($r^2 = 0.96$).

4. Discussion

In this study, we found clear species-specific variation in the temporal (seasonal and daily) patterns of foraging activity for deep-diving odontocetes of the Ligurian Sea. Here, we used observations of echolocation clicks as evidence of foraging activity. Echolocation is mainly used as a "tool" for foraging (i.e. searching, detecting, tracking and catching the prey) with searching typically the most time consuming activity. Counting the number of files with detected clicks is a conservative, but arguably less biased, measure of foraging activity vs. simply counting the number of echolocation clicks in a file. The absolute number of echolocation clicks will be biased by the duty cycle, the directional nature of the echolocating beam pattern (e.g. the intensity of bottlenose dolphin echolocation clicks at large off-axis angles can be as much as 50 to 60 dB below the on-axis intensity, Au et al., 2012), and the group size (i.e. more animals echolocating at the same time will result in more echolocation clicks likely to be detected). Moreover, the detection range of any acoustic sensor is dependent on the range, source level, and frequency characteristics of the biosonar signals, the orientation of the animals as well as the sensitivity of the instrument. Reliable information of source level is essentially non-existent and the orientation and range of the animals can be random and highly variable. Given the above uncertainties, "files with detection" offers a robust metric with which to estimate relative differences in potential foraging activity.

Despite the conservative nature of this measure, clear, species-specific patterns were apparent, both daily and across seasons. The foraging behavior of Cuvier's beaked whales

described by our data is variable with no apparent seasonal pattern including periods of predominately night feeding as well as those with feeding both during the day and night (Figure 3). The behavior of the prey would dictate the foraging behavior of Cuvier's beaked whales in the area, and it is possible Cuvier's beaked whales may have been feeding preferentially on different species of prey with different behavior patterns in different seasons. Another explanation is that Cuvier's beaked whales might tend to move between locations to feed at different times of the day, foraging at night preferentially in some areas. Limited data exist on diet of ziphiid whales around the world as data have been opportunistically collected via stranded animals (Ohizumi et al., 2003). Stomach content analysis of Cuvier beaked whales indicated that the absolute majority of prey biomass consists of cephalopods of the families Histiotiuthid, Gonatid, Cranchiid and Onychoteuthid with no obvious preference for bioluminescent or vertical migrating prey species (Macleod et al., 2003). These squids are known to live in depth ranges between 500 m and 800 m, but there are few behavioral data available on these species in the Mediterranean Sea (Quetglas et al., 2010). While there is a prevalent notion that beaked whales feed mainly on squid, there also exists sufficient data to suggest that prey specimens include a variety of demersal and mesopelagic fishes (Heyning, 2002; Ohizumi et al., 2003).

Contrary to previous observations (Laran et al., 2007), our study confirms that sperm whales are present in the Ligurian Sea until December. Sperm whales feed mainly on medium-sized squid and octopuses (Whitehead, 2003) and their foraging activity in the study area was concentrated more at night in the winter months. The possible reasons for such a change in sperm whales' foraging behavior are unknown. It is also possible that sperm whales switched their diet in the winter and hunt for prey that are easier to find and/or capture at night.

In contrast to the beaked and sperm whales, Risso's dolphins and pilot whales exhibited a

nocturnal foraging behavior for the entire research period at every location. Using DTAGs (Johnson & Tyack, 2003), Aguilar de Soto (2008) showed that short-finned pilot whales off of Tenerife, Spain, dove down to 1018 m and stomach contents from Risso's dolphins indicate that they feed on deep living cephalopods (Blanco et al., 2006). It is possible that a nighttime foraging strategy provides an advantage as prey capture may be easier at night (e.g. shallower prey, lower predator avoidance abilities under low light) and hunting at night may maximize the ratio between the energy acquired by feeding versus the amount of energy expended while foraging. In most ocean basins, echosounding techniques revealed that deep sea scattering layers, representing potential prey fields, occurs at depths of 600 to 800 m (Klevjer et al., 2012; Arranz et al., 2011; Hazen & Johnston, 2010); depths that can be reached by deep diving odontocetes. Odontocetes that are able to dive as deep as 1000m to hunt should not have any constraint in hunting migrating mesopelagic organisms that descend to great depths during the day to avoid visual predators.

Previous studies on deep diving odontocete foraging at other locations show variable results. At Cross seamount, in Hawaii, the echolocation activity of beaked whales was found to occur almost entirely at night using long term moored recorders (Johnston et al., 2008). Au et al. (2013) found that the echolocation activity of pilot whales, Risso's dolphins, small dolphins, beaked whales and sperm whales off the island of Kauai occurred mainly at night. Finally, an acoustic monitoring study near Josephine seamount, located in the Atlantic ocean, found foraging patterns consistent with this study, no differences between day and night foraging activity for beaked and sperm whales, but a difference emerged for Risso's dolphins and pilot whales (Giorli et al., 2015). Different environments might host different prey species and deep diving odontocetes might adjust their foraging strategy according to the behavior of the local

prey.

In nature, many animal species show diurnal variations in behavior. Daily rhythms in the physiology and behavior are dictated by an endogenous time keeping mechanism called the circadian clock (Kronfeld-Schor et al., 2013). Our knowledge of circadian cycles in animal biology, or more specifically animal chrono-biology, is vast for terrestrial organisms but not so for marine mammals. The feeding behavior of Hawaiian spinner dolphins (*Stenella longirostris*) is an example of circadian rhythm of a marine mammal (Benoit-Bird & Au, 2009; Thorne et al., 2012). This species feeds offshore at night preying on rising mesopelagic organisms and spends the day resting in safe shallow bays (Norris, 1980). Echolocation signals from deep diving odontocetes also suggest that more than 80% of the foraging activity happens at night (Au et al., 2013). Giorli et al. (2015) found that blackfishes and Risso's dolphins foraged mainly at night in the Josephine Seamount High Seas Marine Protected Area (east Atlantic). It seems reasonable to believe that odontocetes that concentrate their foraging activity at night rely on their internal clock to time their foraging activity so they can feed when the local environmental conditions, abundance or presence of prey, are more favorable. In this study, we find strong evidence of diurnal variation in foraging, with pilot whales and Risso's dolphins even adjusting their foraging activity to the length of the night as it changes with season. This is the first time that such a behavior is reported for deep diving odontocetes. As the season changed, both species seemed to adapt their foraging activity with the local time of sunrise and sunset, foraging longer during the longer winter nights. This behavior may be evidence of a circadian rhythm in these species controlled by the exogenous cue of light levels. While it might not be surprising that nighttime hunters/foragers like pilot whales and Risso's dolphins adjust their foraging behavior to local conditions in order to maximize their feeding outcomes, this aspect of their behavior generates a

series of questions about the behavior of their deep-sea prey. If pilot whales and Risso's dolphins hunt at night because it is easier to access the prey in the deep sea, and they adjust their feeding activity with local time of sunset and sunrise, then the distribution/behavior of the prey must also vary in time. How prey living in the aphotic deep sea adjust their behavior to the change in day light remains an open question for future research.

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