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1 TITLE PAGE

2 Title: Feeding ecology of the common dolphin (*Delphinus delphis*) in Western Iberian
3 waters: has the decline in sardine (*Sardina pilchardus*) affected dolphin diet?

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5 Authors: Ana Marçalo^{1,2*}, Lúcia Nicolau^{1,2}, Joan Giménez³, Marisa Ferreira², Jorge
6 Santos^{1,2,4}, Hélder Araújo^{1,2,4}, Alexandra Silva⁵, José Vingada^{1,2} and Graham J.
7 Pierce^{1,6,7}

8

9 ¹Centre for Environmental and Marine Studies (CESAM), Universidade de
10 Aveiro, Campus Universitário de Santiago, 3810–193 Aveiro, Portugal

11 ²Centro de Biologia Molecular e Ambiental (CBMA)/Sociedade Portuguesa de Vida
12 Selvagem (SPVS), Departamento de Biologia, Universidade do Minho, Campus de
13 Gualtar, 4710–057, Braga, Portugal

14 ³Departamento de Biología de la Conservación, Estación Biológica de Doñana–Consejo
15 Superior de Investigaciones Científicas (EBD–CSIC), Americo Vespucio s/n Isla de la
16 Cartuja, 41092 Sevilla, España.

17 ⁴Campus do Mar, International Campus of Excellence, Spain and Portugal.

18 ⁵ IPMA –Portuguese Institute for the Sea and Atmosphere. Avenida de Brasília, Lisboa,
19 Portugal

20 ⁶Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire, AB41
21 6AA, UK

22 ⁷Instituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208, Vigo, Spain

23

24

*Corresponding author: e-mail: amarcalo@gmail.com; current address: Centre of Marine Sciences (CCMAR), University of the Algarve, Campus de Gambelas, FCT Ed. 7, 8005-139 Faro, Portugal

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ABSTRACT

Predator diet is expected to respond to changes in the abundance of important prey items. We investigated whether common dolphin diet has changed with changes in the pelagic fish community off the Iberian Peninsula in recent years, in particular with reference to the decline of sardine (*Sardina pilchardus*) and the increase of Atlantic chub mackerel (*Scomber colias*) and scads (*Trachurus* spp.), and estimated how much fish was removed by common dolphins in coastal waters of mainland Portugal. Based on analysis of stomach contents of stranded animals from 2010 to 2013 (n=150), we related diet composition to sardine abundance, dolphin size and sex, season and region. Despite the decline in sardine stocks in recent years, sardines were the most important prey of common dolphins, as was previously reported in the 1990s, followed by chub mackerel and scads. However, small sardines have disappeared from the diet, consistent with recent poor recruitment to the stock. The relative importance of these pelagic species in the diet increased significantly with increasing dolphin length. The dietary importance of chub mackerel also varied regionally, with higher intake on the southern coast. Finally, we compared the estimated biomass of fish removed by dolphins with that taken by fisheries. We found that even with the severe quota restrictions on sardine catches, total biomass removed by fisheries was over five times greater than the estimated removal by common dolphins. Our results confirm the previously reported preference for energy-rich prey, especially sardine, suggesting that common dolphins in Portuguese waters specialise in feeding on this species.

Keywords: Common dolphin, diet analysis, stomach contents, pelagic fish, Portuguese coast, sardine

INTRODUCTION

Studies on diet and feeding ecology of cetaceans are key to obtaining the data needed to assess cetacean impact on fish stocks (Trites et al. 1997). Such work can improve knowledge on predator and prey biology, and can also provide insights into cetacean distribution, movements, feeding behaviour and trophic relationships. Our knowledge of the role of top predators (marine birds, marine mammals and large predatory fish) needs to be improved as they occur at the same trophic level as local fisheries and can share the same resources (Bearzi 2002, Kaschner 2004, Read 2008, Bearzi et al. 2008, 2010, Cury et al. 2011, Santos et al. 2013, 2014, Scheinin et al. 2014). Furthermore, understanding trophic relationships in marine ecosystems is key to understanding the central role that some fish often play, both as links between zooplankton and top predators and as important fishery targets (Frederiksen et al. 2006).

The common dolphin, *Delphinus delphis*, is an abundant top predator with a worldwide distribution (Evans 1994), and is the most abundant cetacean species off the western Iberian coast (Sequeira et al. 1992, de Sousa 2010, Santos et al. 2012, Hammond et al. 2013). Common dolphins favour diets rich in small, schooling species of high energy content ($>5\text{--}6\text{ kJ g}^{-1}$; Spitz et al. 2010a), but change their diet or energy richness according to seasonal and yearly fluctuations of prey distribution and abundance (Young and Cockcroft 1994, Silva 1999, Santos et al. 2004, 2013, 2014, Spitz et al. 2010a, 2010b). Optimal foraging theory predicts that diet selection will be driven by prey availability, catchability, energetic value and by the specific cost of foraging. This may be especially true of predators leading an energetically expensive life style such as the common dolphin (Spitz et al. 2010b). Fatty fish like sardine, *Sardina pilchardus*,

horse mackerel, *Trachurus trachurus*, anchovy, *Engraulis encrasicolus*, mackerel, *Scomber* spp. or lipid-rich mesopelagic species (see Spitz et al. 2010a for specific energetic values) are important prey of common dolphins around Europe (Silva 1999, Pusineri et al. 2007, Meynier et al. 2008, Spitz et al. 2010b, Santos et al. 2013, Giménez et al. 2018).

Western Iberian waters, with their well-known seasonal coastal upwelling regime (Fiúza et al. 1982, Fiúza 1983, Peliz et al. 2002), sustain a highly productive and diverse system favouring the presence of small pelagic fish species whose reproductive strategies and recruitment success depend on upwelling and other environmental conditions such as sea surface temperature (SST), wind strength and direction and productivity (Santos et al. 2001, Borges et al. 2003, Santos et al. 2012). In recent years, important environmental changes in western Iberia have been reported, related to the North Atlantic Oscillation (NAO) index and SST, which have triggered shifts in the pelagic fish community, notably the decline of the abundance in sardine (Lemos 2004, Leitão et al. 2014, Santos et al. 2012, Teixeira et al. 2016).

The southern stock of sardine, also known as the Iberian sardine stock, is managed by Portugal and Spain. For both countries the bulk of sardine landings (97% in weight and 98% in value) are made by purse seine boats (Silva et al. 2015). Sardine abundance is dependent on the magnitude of recruitment, which has been poor in the southern-Iberian stock since 2004, leading to a recent historical low level of biomass (Silva et al. 2015). To protect the stock, a new management plan for the southern Iberian sardine stock was implemented from 2011 onwards by Portuguese and Spanish administrations, with severe restrictions on catches. This led to sharp annual declines in landings of 70% and

above from 2011 to 2014. In order to remain economically viable, the fishing sector has since been forced to target other pelagic species, namely Atlantic chub mackerel, *Scomber colias*, and horse mackerel, *Trachurus trachurus*. Both species have recently shown increased biomass off the Portugal–Cadiz region and, for chub mackerel, especially an inverse relationship with abundance of sardine has been found (Martins et al. 2013, ICES 2016).

In the late 1980's and the 1990's, common dolphins off the Portuguese mainland coast were found to feed mainly on sardine (Silva 1999). Although the sardine stock was suffering recruitment fluctuations (with marked highs and lows) during this period, leading to a suggested decline, abundance was still higher than currently: the stock is presently at a historically low level (see Silva et al. 2015). The decline of the Iberian sardine stock in recent years has not only been a problem for the purse seine fishing sector, but may also have impacted the diet composition of common dolphins due to their preferred prey being less available. More specifically, in view of common dolphin's apparent preference for fatty fish, a **decline in the abundance of a “favoured”** prey species (Silva 1999, Santos et al. 2013) might be expected to lead to a change in diet towards other fatty species, assuming comparable foraging costs.

The main aim of the present study, therefore, was to re-assess dietary variation of the common dolphin along the Portuguese mainland coast. Specifically, we aimed to determine whether specific changes in diet composition have occurred over the last two decades, by analysing stomach contents of dead stranded animals. We attempted to determine the relationship between diet and a series of intrinsic (e.g. biological) and extrinsic (e.g. area/coasts) variables. This work also provided the opportunity to

estimate for the first time the amount of commercially important small pelagic fish species consumed annually by common dolphin off mainland Portugal. This allowed us to compare dolphin consumption with the biomass removed annually by the fisheries, thus providing insight into the likelihood of competition between dolphins and fisheries.

MATERIALS AND METHODS

Sample collection

One hundred and fifty stomach contents samples were collected from stranded common dolphins found dead along the Portuguese mainland coast from 2010 to 2013. Samples were obtained from regions where dedicated local stranding networks operate, coordinated by the Portuguese Wildlife Society. These regions were the north-central western coast from Caminha to Peniche (Cape Carvoeiro), which is 310 km long, and the southern-Algarve coast, which is 170 km long and extends from Odeceixe on the western coast to the southern tip of Cabo São Vicente and onwards to Vila Real Santo António (Fig 1). Animals were necropsied according to a standardized dissection protocol (Kuiken and Hartmann, 1993), including collection of biological information (length, sex) and tissue samples for subsequent studies (stored at the Portuguese Marine Animal Tissue Bank (MATB, Ordinance 7: 3PT0124/S). Determination of the cause of death was based on external and internal examinations. Cause of death was divided into 5 classes: (1) by-catch, (2) probable by-catch (attributed to animals with pronounced decomposition preventing establishment of cause of death, but which had intact prey in the oesophagus and abundant stomach contents, suggesting recent feeding; Moore et al. 2013), (3) boat collision, (4) live stranding, and (5) undetermined. Diagnosis of death

due to by-catch was based on evidence such as presence of netting and/or net marks on the body surface and anterior margins of flippers and fins, amputation of the tail and other criteria as described in Kuiken (1996) and Read and Murray (2000). The available diet samples comprised stomachs from 88 females, 55 males and 7 animals in which sex remained undetermined due to body parts being damaged or missing. Whole stomachs were removed and stored at -20°C in polyethylene bags until further analysis.

Prey identification and estimation of prey size

Frozen stomachs were thawed and opened with a scalpel blade. The contents were washed through a 0.5 mm mesh sieve; diagnostic parts (*i.e.* fish bones, sagittal otoliths and cephalopod beaks) and fresh prey items were recovered and identified to the lowest possible taxonomic level using published guides (Clarke 1986, Härkönen, 1986; Tuset et al. 2008) and reference material stored in the MATB. Fish bones and sagittal otoliths were stored dry, whereas cephalopod beaks were kept in 70 % ethanol. The minimum number of fish of each species/taxon was determined as half the highest number of paired structures (*i.e.* sagittal otoliths, opercula, dentaries, maxillae or premaxillae). The number of upper or lower beaks, whichever was higher, was used for cephalopods. Diagnostic hard parts were measured to the nearest 0.02 mm under a binocular microscope fitted with a digital eye-piece probe following established standards (Clarke 1986; Härkönen 1986). Only undamaged (unbroken and not obviously eroded) otoliths were used in order to avoid errors associated with reduction in otolith size due to erosion by stomach gastric acids. When more than thirty diagnostic remains were present in a sample, a random subsample of thirty was measured (after Silva 1999, Santos et al. 2004, 2013, Tollit et al. 2010). Individual prey body length and mass were

calculated using regressions from the published literature (Silva 1999, Santos et al. 2004, Giménez et al. 2016). When no regression was available, a new regression was constructed using data from our reference collection (Table S1). Otolith length was measured in most cases, except for the otoliths of sardine, scads (*Trachurus* spp.; two species of this genus are abundant in Portuguese mainland waters, which have similar otoliths and bones: horse mackerel *Trachurus trachurus* and the less common blue-jack mackerel *Trachurus picturatus*), Atlantic chub mackerel and Gobiidae, for which width is suggested as the standard measurement (Härkönen 1986, Silva 1999). For otoliths identified only to genus, family or order, regressions based on combined data from the species in the group were used when available (Silva 1999, Tollit et al. 2010). Where damage to the otoliths of an identified species prevented reliable measurements or when no measurable structures were available, the mean individual weight (MIW), *i.e.* mean of the estimated weights of the individuals of this species found in all the stomachs examined, was used (after Silva 1999). For cephalopods, dorsal mantle length and weight were estimated from hood length of sepiid and sepiolid lower beaks and from rostrum length of lower beaks for other cephalopods (Clarke, 1986).

Dietary Variation

Dolphin diet was quantified in terms of prey occurrence, abundance, reconstituted mass, and size distribution, following general procedures for diet analysis of marine top predators (Pierce et al. 2007, Santos et al. 2004, 2013, 2014, Tollit et al. 2010). The relative importance of each food item in the diet was quantified using three standard indices: (a) numerical percentage of each prey *i* in relation to the total number of prey individuals found in the stomachs (%N); (b) percentage of frequency of occurrence of each prey type (%F, *i.e.* number of stomachs where prey *i* was found divided by the

total number of stomachs); and (c) the percentage of total reconstructed prey biomass (%W). The %W of each prey category was calculated as the product of the number of individuals and the average reconstructed body mass, in each stomach, summed throughout the sample set, divided by the grand total for all prey categories and expressed as a percentage. Although prey mass provides the best proxy for the energetic importance of each prey type, not all prey remains could be used to estimate prey size, nor were regressions available for all prey species, and the mass data are thus slightly less complete than data on prey numbers or presence (Table 2). Additionally, we used the Index of Relative Importance (IRI, Eq. 1) to measure the overall importance of each type of prey (Hyslop 1980):

$$\text{IRI} = (\%N + \%W) * \%F \quad (\text{Eq. 1})$$

Sampling errors for overall %N, %F, %W and IRI on overall data were assessed by generating non-parametric 95 % confidence intervals using bootstrap simulations as per Santos et al. (2014). The procedure involves the addition of all prey numbers or weights from a sample to the total diet each time a sample is selected. The bootstrap routine was written using R (R Development Core Team 2016); *n* samples were drawn randomly with replacement, and the procedure repeated 1000 times.

Dolphin diet variability was characterized graphically using the Costello diagram (Costello 1990, modified by Amundsen et al. 1996), in which prey-specific importance of each prey taxon (%P, equation 2 below) is plotted against frequency of occurrence (% F).

249 where w_{ij} is the contribution by weight of prey taxon j to the stomach contents, and
250 W_i is the total stomach contents weight for those individual predators with prey taxon j in
251 their stomachs. This tool has been used to characterize diet variability and feeding
252 behaviour of several marine predators including cetaceans (Pusineri et al. 2007, Romero
253 et al. 2012, Reisser et al. 2013, Varela et al. 2016). The position of prey types within the
254 diagram provides information on the relative importance of prey, predator feeding
255 strategy and niche width (Amundsen et al. 1996). It also allowed graphical comparison
256 with previous results from Silva (1999). Prey species positioned in the upper left corner
257 of the diagram are those with high prey-specific importance but low occurrence in the
258 diet, indicating specialization by individual predators. Prey species located in the upper
259 right of the plot are abundant species with high occurrence in the diet, which indicates
260 population specialization. For a generalist predation strategy, prey species occur at high
261 frequency but each individual species account for only a small proportion of the total
262 diet when present (lower right corner). Also suggestive of a generalist diet are prey
263 types with low prey-specific importance and low occurrence (lower left), i.e. “rare”
264 species.

265

266 Generalized Additive Models (GAMs) were used to analyze the effects of several
267 explanatory variables on the numerical importance (%N) of the main prey types
268 consumed, *i.e.* small pelagics (sardines, scads and chub mackerel). This analysis was
269 applied to 135 animals with complete datasets (*e.g.* sex, total length). Initial models
270 were fitted using a discrete probability distribution, namely a Poisson distribution due to
271 our data characteristics (*i.e.* count data). High overdispersion was found in most cases,
272 so a negative binomial distribution was finally chosen. The following explanatory

variables were treated as continuous and were therefore included as smoothers: year, day in year, dolphin length. Sex and area (western vs southern coasts) were included as factors. If the year effect was significant and annual stock abundance data were available for the prey species in question, prey species biomass was included as a smoother in place of year. The complexity of smoothers was constrained by setting a maximum of three degrees of freedom ($k=4$) to avoid overfitting. We checked heteroscedasticity and presence of outliers (**the latter based on “hat” values ≥ 1**), which may bias the results of such analyses (Zuur et al. 2007), however hat values were always < 0.2 . Starting with a model that included main effects of all explanatory variables, we used backwards selection to identify the best model, *i.e.* at each step the least important non-significant variable was dropped and the model was re-run. The best model was the one that presented the lowest Akaike Information Criterion value (AIC, Akaike (1974)).

Each dolphin was assigned to one of two size/maturity classes according to body length: values presented for common dolphins from the Portuguese coast (Silva 1999). They were classified as mature at ≥ 190 cm length and immature at < 190 cm.

Lengths of male and female dolphins were compared using the Mann–Whitney nonparametric test using the stats package in R (R Core Team, 2016). This was necessary because the assumptions of normality (Shapiro–Wilk test) and homoscedasticity (Equal Variance Test) were not fulfilled. We also investigated whether the length of prey and total prey biomass found in the stomachs varied with dolphin length. Preliminary examination of the data suggested a linear relationship, so a linear model was fitted using the function *lm* from the stats package.

Annual consumption rates

Annual consumption by the common dolphin population in Portuguese mainland water was calculated for the three main prey types (sardine, chub mackerel and horse mackerel). Annual food consumption (I_i , tons) of a given species i by the common dolphin population in Portuguese mainland waters was estimated using the following equation based on Santos et al. (2014):

$$I_i = N \times (IB/1000) \times P_i \times T \quad (\text{Eq. 3})$$

where IB is the average daily food intake of an individual dolphin (in kg), P_i is the previously calculated proportion by weight of prey species i in the diet, T is the number of days when prey and predator are in contact (assumed to be 365 days), and N is the common dolphin population size. N was taken from a recent estimate (Life MarPro aerial surveys estimates 2010–2015; Araújo et al. 2015) within the continental platform out to 200 m depth. A population size of 20170 (95% CI 10792–37699) common dolphins was assumed to be constant during the study period in Portuguese mainland waters. This approach ignores seasonal and regional variation in diet (Santos et al. 2014) and treats **each dolphin as an “average dolphin” (ignoring size-related dietary variation)**. However, the available data do not allow a more detailed approach.

The values used for importance of the main prey species were based on %W values obtained from the stomach contents analysis (see above). Following the approach used in Bearzi et al. (2010), average daily food intake of common dolphins (IB) was estimated using four different published relationships:

(1) $IB = 0.123M^{0.8}$ (Innes et al., 1987)

(2) $IB = 0.482M^{0.524}$ (Leaper and Lavigne, 2002; Kaschner, 2004)

(3) $IB = 0.035M$ (Tamura, 2003; Kaschner, 2004)

(4) $IB = 0.1M^{0.8}$ (Trites et al., 1997)

where M is the body mass in kg. Body mass (M, Kg) was calculated based on body length L (in cm) as in Kastelein et al. (2000):

$M = 7.5814 (L - 140)^{0.5345}$ (Kastelein et al. 2000).

Body lengths of the sampled animals were assumed to be representative of the population. Body lengths below the mean body length minus one standard deviation (i.e. common dolphins below 153 cm) were not included in the calculations, as these values probably included young animals, including nursing individuals. Body masses were calculated for all remaining animals for which total length was available (n=116). Food consumption of each animal was calculated using the four methods and the average taken, then the overall average derived as the average of the values for each animal.

RESULTS

Composition of the sample

Numbers of dolphin stomachs analyzed each year, in each category, are shown in Figure 1 and summarized in table 1. Approximately 61 % of the whole sample (n = 91) were thought to be by-catches in fishing gear, including suspected interactions with set-nets (n= 23, either gill or trammel nets) and, less frequently, animals showing evidence of

interaction with purse seine (n= 5) and beach seine nets (n= 1). In addition, around 30 animals were considered to have died from probable by-catch events. In 26 individuals the cause of death was not determined (although samples for pathological and histopathological analysis have been collected for further analysis), one dolphin was live stranded (dying shortly after it was discovered) and another showed signs of boat collision. Most strandings (60 %) occurred in the first and last quarters of the year. Of the 143 dolphins for which the sex was determined, 59 % were females. Total length was available for 135 animals and ranged between 107 and 239 cm with mean $\pm$ SD = 181.4 ± 26.1 cm, with females (n= 84; mean $\pm$ SD = 179.2 ± 23.7 cm) being significantly (Mann Whitney; $p < 0.001$) smaller than males (n = 51; mean $\pm$ SD = 185.2 ± 29.5 cm).

Overall diet composition

In total, we identified the remains of 7776 individual fish, 2976 cephalopods, 33 polychaetes and 1 crustacean, corresponding to a total reconstructed mass of 283 kg (an average of approximately 1.9 kg per stomach, amounting to roughly 2/3 of the estimated mean daily food consumption (see below). We identified 26 fish taxa and 7 cephalopod taxa, belonging to 26 families, using fish otoliths and bones and cephalopod lower beaks, with 91.8 % of all prey items identified to at least genus level (Table 2). The diet of common dolphins consisted mainly of fish (72.0% N, 100% F, 95.6% W, 16756.0 IRI), and to a lesser extent of cephalopods (27.7% N, 52.7% F, 5.5% W, 1749.7 IRI).

Overall, sardine, chub mackerel and scads were the most important prey categories, in terms of abundance (%F), biomass (% W) and relative importance (IRI). Sardine

occurred in 83 % of the stomachs, as compared to 61 % and 49 % respectively for scads and chub mackerel. By reconstructed weight, these three prey types together made up about 76 % of the diet, with sardine corresponding to about 36 % and chub mackerel and scads to 24% and 16 % respectively. Sardine was also the most important according to the IRI (4381) followed by scads (1867) and chub mackerel (1515). According to overall numerical importance, sardine was the most important prey species (16%), followed by *Sepiolo atlantica* and scads (both 15 %).

The distribution of estimated lengths of prey eaten by common dolphins presented two peaks (modes) at about 1–4 and 17–20 cm (Figure 2 A). Prey from the smaller group was composed mainly of benthic and meso-benthic species such as Gobiidae sp, *Citharus linguatula*, *Sepiolo Atlantica*, and *Trisopterus sp.*, and juvenile hake, *Merluccius merluccius*. These fish and cephalopods are mostly benthic and demersal. The larger group is composed of pelagic species such as sardines, chub mackerel and scads. There were significant positive correlations between predator length and both prey length ($R^2=0.077$, $p < 0.0001$) and prey biomass ($R^2=0.094$, $p < 0.0001$). Sardines eaten ranged from 13.8 to 24.9 cm total length, with a mean at 19.0 and SD of 11.7 cm. Chub mackerel eaten were similarly sized (19.6 ± 2.9 cm, range 13.5 to 32.1 cm), while scads were slightly smaller on average (15.5 ± 3.5 cm, range 8.4 to 37.0 cm). Compared to Silva (1999), sardines in particular had a larger average size (Figure 2 B).

The modified Costello diagrams (Figure 3) show that the common dolphins sampled showed varying degrees of specialization and generalization on different prey types. Comparing our results with stomachs analysed from the 1980's–1990's (Silva 1999, Figure 3 B), the situation has not substantially changed. Our data (Figures 3B, 3C and

3D) show sardines as the dominant food item of common dolphins. In Silva's study, blue whiting *Micromesistius poutassou* and *Atherina* sp. were of intermediate importance, also in the upper part of the plot, but lower in frequency. Currently, scads and chub mackerel (the latter especially in the southern area, Figure 3 D) follow sardines as the next most important prey species. Most other prey species are located in the lower left corner or close to the vertical axis, indicating low values for prey-specific importance. However, common dolphins from the western coast (Figure 3 C), show feeding preferences for *Alloteuthis* sp. and *Sepiolo atlantica*, with these cephalopods occurring with high frequency in stomachs from this area, although only accounting for a small biomass proportion of the diet when present.

Dietary variation

Results from the GAMs indicated that there was no significant inter-annual variation in the numerical importance of the three pelagic fish species in the stomach contents. The numbers of sardines in common dolphin stomachs were significantly related only to individual dolphin length ($P < 0.001$). The final model (chosen based on the lowest AIC value) explained 11.0% of deviance (Table 3). The numerical importance of sardines in the diet increases with increasing common dolphin length, reaching an asymptote around 210 cm (Fig 4A). The final model for the numerical importance of scads explained 7.4% of the deviance and included a weaker but significant effect of length ($p < 0.01$). Again, for scads, numerical importance was positively related to dolphin length, reaching an asymptote around 190 cm (Figure 4B). The final model for the numerical abundance of chub mackerel explained 26.1 % of the deviance and included significant effects of length ($p < 0.001$) and region ($p < 0.0001$). Figures 4C and D show

respectively that the numerical importance of chub mackerel in the diet increases with dolphin length, and that chub mackerel occurs more frequently in the stomachs of common dolphins stranded in the southern Portuguese coast than in dolphins stranded in the western coast. The same groups of fish and cephalopods made the bulk of the diet of both adults and juveniles (Table 4).

Consumption rates

The estimated body mass for the common dolphins analyzed here ranged from 30.5 to 88.4 kg (average weight = 61.0 kg, n=116). These weights correspond to lengths ranging from 153.5 to 239.0 cm. The average and standard deviation of the food consumption estimates found using the four formulae was 3.1 ± 0.50 kg of food consumed daily by an average common dolphin on the Portuguese mainland coast. Of the total consumed food 36.4 % in mass is sardine, 15.7 % scads and 23.5 % chub mackerel. This corresponds to an individual daily consumption of sardines, scads and chub mackerel of 1.1, 0.5 and 0.7 kg respectively. Estimates of the biomasses removed daily and annually by common dolphins for all prey, and the three main pelagic species combined and individually, are presented in Table 4. Comparing biomass removal by predation (annual consumption by dolphins) and by fisheries (annual landings) of the three small pelagic species, our results suggest that the quantity of fish removed by dolphins is roughly 1/5 of that removed by fisheries (Fig 5). For sardines, estimates of biomass removal by predation are equivalent to around 18.6 % (CI 9.9–34.7 %), and for scads and chub mackerel, 21.8 % (CI 11.7–40.8 %) and 16.3 % (CI 8.7–30.4 %), respectively, of the amounts removed by fisheries.

DISCUSSION

Diet composition

Although at least 26 fish species and 7 cephalopod species were identified from the stomach contents of common dolphins along the Portuguese mainland coast, our study demonstrates a preference for sardine which has been maintained since at least the late 80`s (Silva 1999). We here highlight the importance of small fatty pelagic fish in the diet, in particular sardine, chub mackerel and scads.

Sardine, chub mackerel and scads represented about 38 % and 76% by number and weight respectively, of the combined reconstituted stomach contents. However, cephalopods from the Sepiolidae and Loliginidae families also appeared to be important, especially on the western coast, as shown by the % N and IRI values for stomachs from this area. However, the majority of these cephalopod prey were small and light, and represented a small proportion of ingested prey weight. This consumption of numerous small cephalopods is consistent with Silva's (1999) previous work in Portugal and with findings of other studies in Northwestern Iberia (Santos et al. 2013) and other world regions (Young and Cockcroft 1994). It should be noted that the importance of cephalopods, the beaks of which are well known to have long retention times in dolphin stomachs, is sometimes overestimated (Glaser et al. 2015). Also, we cannot rule out cephalopod occurrence **in the dolphins' stomachs as secondary prey**, which would also result in over-estimation of their relative importance. However, available literature regarding diet and trophic ecology of several fish species found in the diet of common dolphins from the Portuguese coast, namely the small pelagics

(Garrido and Murta 2011, Garrido et al. 2015), and blue whiting and hake (Cabral and Murta 2002), suggest that cephalopods are not an important component of the diet of these fish.

Sardine and other small pelagics as the main prey

Our results show that sardine have an Index of Relative Importance (IRI) 2–3 times higher than the IRI of other important prey species (scads and chub mackerel), a lower value than that obtained from Silva's (1999) work but nevertheless suggesting a clear preference for sardine. A preference for sardine is also supported by the modified Costello diagrams (Figure 3 B–D) for both Portuguese studies and in both regions. Following previous studies in the area (Silva 1999, Santos et al. 2004, 2013, 2014), we would expect variation over time in the composition of the Western Iberia small pelagic fish community to be reflected in the diet of common dolphins. Even at lower stock biomass levels, sardine abundance appears to still be at levels able to satisfy dolphins' energetic needs and justify foraging costs. In addition, we would expect that the current lower fishing effort, especially for the purse seine fleet (Silva et al. 2015), would also tend to increase the resource available to the dolphins (while not compensating for the very much lower stock abundance). As common dolphins are the cetacean species that interacts most with the purse seine fishery (Wise et al. 2007, Marçalo et al. 2015), overestimation of the importance of sardine in dolphin diet may also have resulted from the dolphins taking advantage of the hyper-aggregation of fish in a sardine school when being targeted by the local purse seine fleet. In Silva's (1999) work, proportionately more sardines were found in the diet of by-caught animals, compared with dolphins dying from other causes. However, it is unsurprising that common dolphins should

target such sardine aggregations, irrespective of the presence of purse seiners, and the high proportion of by-caught animals in the present study, rather than introducing sampling bias, could be interpreted as a consequence of dietary preferences.

Dietary preferences in relation to predator and prey size and area

For the important pelagic prey species, from all of the putative explanatory variables analyzed (year, region, quarter-season, biological – sex and dolphin length), the only consistent pattern was a strong length-related variation in their importance in the diet of common dolphins examined. Larger animals tended to consume proportionately higher numbers of sardine, chub mackerel and scads (Figure 4, Table 4), reflected also in higher total biomass (which was positively correlated with dolphin size). As total prey biomass is comprised mainly of those three pelagic species (76 %), as has been suggested in previous studies of this and other cetaceans (Riccialdelli et al. 2013), we assume that juvenile common dolphins could be limited in their ability to capture fast schooling fish, due to either inexperience or physical limitations. Further, dolphin size was also correlated positively with prey size, which has been previously shown in other studies in the area and adjacent waters (Silva 1999, Santos et al. 2013) with smaller dolphins feeding on smaller prey items such as Gobiidae, *Alloteuthis* spp., and *Sepiola atlantica*. For chub mackerel only, there was a significant regional difference in its dietary importance, with higher numbers of this prey consumed in the southern area. This is consistent with higher estimated biomass and landings of chub mackerel in southern Portugal (Martins et al. 2013, ICES 2016). This last observation gives some insight into the plasticity of common dolphin foraging behaviour, which not only demonstrates selection for favoured prey (sardine) and size-based selection, but also an

element of opportunistic foraging, namely a diet composition which reflects regional abundance of prey.

Feeding behaviour

As predicted by optimal foraging theory (e.g. Pulliam, 1974), common dolphin specialisation on energy-rich prey might be expected to be less evident when abundance of such prey is low. Studies of common dolphin from different parts of the world suggest a range of foraging strategies, from selective predation (Meynier et al. 2008, Spitz et al. 2010b) to opportunistic feeding (Young and Cockcroft 1994, Santos et al. 2013). In Portuguese mainland waters, Silva (1999) described sardines (an energy-rich species, Bandarra et al. 1997, 2018) as the main prey of common dolphins. Sardines were also the most abundant small pelagic fish species in the Portuguese shelf waters at the time. Our results provide evidence against common dolphins being purely opportunistic feeders given that sardines have become less abundant in recent years, and would have been expected to decline in importance in the diet of an opportunistic predator.

Horse mackerel (*Trachurus trachurus*), is currently more abundant than it was during Silva's (1999) study (ICES, 2016), which is also reflected in the diet composition seen in the two studies (Figure 3 B and D). Hence, as previously described in Spitz et al. (2010b) for oceanic common dolphins in the Bay of Biscay, we also observed a diet composition that supports prey selection based on prey fat content and most probably also net energy gain by the common dolphin.

Biomass removal

Taking advantage of recent cetacean population abundance estimates for Portuguese mainland coastal waters (Araújo et al. 2015), we also provide here for the first time information on the potential ecosystem impact of this top predator and compare it with Western Iberian fisheries. We have provided evidence that the average small pelagic biomass removed by fisheries from 2010 to 2013 exceeded that removed by common dolphins by a factor of 5.5. To put these figures into perspective for sardines, for 2010 to 2013, average total fishery catches of sardines from area IXa (representing the Portuguese sardine landings) were about 45000 tonnes from an average spawning stock biomass (SSB) of around 166000 tonnes (down from a peak of around 1 million tonnes in 1993) (ICES, 2016, DGRM 2013, 2014). This represents removal of around 27% of the SSB by fisheries and an estimated average annual consumption of sardine by common dolphins in Portugal equivalent to around 5 % of SSB.

Overlap with fisheries

We also observed an overlap not only in species taken by common dolphins and coastal Portuguese fisheries, but also in the size-classes taken. It is important to note that the sizes of sardine eaten (Figure 2B) have changed over time when compared with Silva's (1999) work. Small sardines have disappeared from the diet, consistent with the absence of strong sardine recruitment events during the period preceding the present study (Silva et al. 2015, supplementary Figure 2). This observation is in line with results already obtained on marine bird diet (Barrett et al. 1990), suggesting that cetacean diet studies could also inform the degree to which recruitment drives the trophic web.

644

645 Our results suggest that the damage caused by common dolphins to fishery yields is
646 likely to be fairly modest. Higher prey depletion resulting from fishing than from
647 dolphin consumption has already been described by Santos et al. (2014) for the Galician
648 coast, where biomass removal rates for several small cetacean species were described.
649 At that time, and for an estimated Iberian Peninsula common dolphin population of
650 close to 14000 individuals (taken from SCANS II 2008), estimated cetacean
651 consumption was a small proportion of the total annual sardine landings from ICES
652 subdivision VIIIcW and IXaN (8–9%).

653

654 Study limitations

655

656 Diet studies based on analysis of stomach contents from stranded animals are repeatedly
657 criticized in relation to the degree to which they represent a free-ranging population's
658 diet (Tollit et al. 2010). However, although the opportunistic sampling of dead animals
659 may result in biases related to animal health and/or cause of death, or related to feeding
660 occurring in the vicinity of fishing boats, thus creating biases towards particular prey
661 items (Gannon et al. 1997), many studies have validated the utility of stomach content
662 analysis as being reasonably representative of the diet of healthy free-ranging
663 individuals, and it has often been used as a baseline for dietary studies (Dunshea et al.
664 2013). Most stomachs analysed in the current work were from common dolphins dying
665 as a result of anthropogenic causes, mostly related to fisheries interaction. We therefore
666 suspected that the sample was unlikely to be biased towards sick animals, but could
667 have been biased towards the specific prey items targeted by the associated fishing
668 boats (although we argue that common dolphins routinely target sardine shoals and that

deaths due to fishery bycatch therefore do not necessarily introduce a bias). Another concern with stomach contents analysis is the underestimation of prey sizes due to otolith erosion (Silva 1999, Santos et al. 2013, Tollit et al. 2010). In our study, most prey were from by-caught animals and were intact, demonstrating recent mortality and yielding undigested otoliths showing that animals had died recently. Finally we were unable to detect any inter-annual variation in diet. However, with only 4 years of data, and a relatively small sample size, we recognize the limited statistical power available to detect interannual dietary changes.

Conclusions

A new quantitative description of the diet of common dolphins along the Portuguese mainland coast, based on stomach content analysis, is provided, and compared with previous observations (Silva 1999). Sardine continues to be the favoured prey, while other high-energetic prey species are also important in the diet. We also provide insights for the first time on consumption rates of their main prey by common dolphins in comparison with total biomass removed by fisheries in Portuguese waters. These data and those from similar studies on top predators are key to better informing the ecosystem models required to evaluate the consequences of fishery management measures, specifically by incorporating where appropriate predator and prey abundances, fully quantified dietary information and information on operational interactions between fisheries and dolphins (i.e. bycatch and depredation).

694

695 COMPLIANCE WITH ETHICAL STANDARDS

696 Research involving Animals

697 The study used only animals found dead on the shoreline.

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699

700 Disclosure of potential conflicts of interest

701 The authors declare that they have no actual or potential conflicts of interest in relation
702 to this work.

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996 FIGURE CAPTIONS

997

998 Figure 1 Maps for location of stranded common dolphins sampled: A. Portuguese
999 mainland coast (n = 150); Distribution by sex along the western coast (B) and along the
1000 southern coast (C).

1001

1002 Figure 2 Distribution of estimated length of common dolphin prey: A–all prey, for
1003 male and female common dolphins; B–Distribution of three main prey types. Solid lines
1004 and dashed lines represent averages from this study and Silva (1999), respectively.

1005

1006 Figure 3 Prey-specific abundance plotted against frequency of occurrence of prey
1007 species for common dolphins stranded along the Portuguese mainland coast. A.
1008 Explanatory axes for foraging patterns are those of Costello (1990) as modified from
1009 Amundsen et al. (1996). The two diagonal axes represent the importance of prey
1010 (dominant vs rare) and the contribution to the niche width (high between-phenotype vs
1011 high within-phenotype contribution); the vertical axis defines the predator feeding
1012 strategy (specialist vs generalist). B. Silva 1999; C. Western coast; D. Southern coast.

1013

1014 Figure 4 Partial effects of selected variables on prey abundance in common dolphin
1015 diet. A . Sardine, *Sardina pilchardus*; B . Scads, *Trachurus sps.*; C . and D . Chub
1016 mackerel, *Scomber colias*.

1017

1018 Figure 5 Comparison of biomass removal by dolphin predation and by fisheries for the
1019 three small pelagic species: (A) sardine, (B) scads and (C) chub mackerel landed
1020 annually in Portugal for 2010-2013 in ICES areas subdivision 9a (official fishery
1021 statistics). The solid horizontal lines represent the (static) estimates of annual mean
1022 common dolphin consumption; the dashed lines represent the upper and lower 95 %
1023 confidence limits

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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Table 1 Summary of composition of sampled common dolphins in each year period. by season (quarter). area. sex and cause of death. Season: Q1. January–March; Q2. April–June; Q3. July–September; Q4. October–December. Sex: F. female; M. male; U. unknown. Cause of death: BY. By-catch; PBY. Probable by-catch; COL. Boat collision; AL. Alive; ND. Not determined/Unknown

Year	<i>n</i>	Area		Quarter				Sex			Cause of Death				
		Western	Southern	Q1	Q2	Q3	Q4	F	M	U	BY	PBY	COL	AL	ND
2010	28	12	16	9	5	9	5	19	8	1	18	6		1	3
2011	40	21	19	19	9	7	5	22	17	1	25	8	1		6
2012	38	26	12	14	9		15	21	17		22	9			7
2013	44	19	25	12	2	18	12	26	13	5	26	7			10
Total	150	78	72	54	25	34	37	88	55	7	91	30	1	1	27

Table 2 – Diet composition of common dolphins along the Portuguese mainland coast. N=Number of prey. %N=Numerical percentage. F=Occurrence. %F=Percentage of occurrence. W=prey weight. %W=Percentage of reconstructed weight. IRI=Index of relative importance; in parentheses are 95% confidence limits. In square parentheses are IRI values for the most important species in Silva, 1999. For explanations on the calculations see main text.

Family	Species	N	%N	F	%F	W	%W	IRI [IRI Silva 1999]
Clupeidae	<i>Sardina pilchardus</i>	1749	16.22 (11.75-21.31)	125	83.33 (77.33-88.67)	100276.1	36.36 (29.90-42.64)	4381.49 [5734.8] (3220.79-5670.45)
Carangidae	<i>Trachurus</i> sp.	1589	14.73 (9.64-21.15)	92	61.33 (53.33-68.67)	43315.73	15.71 (11.26-20.26)	1866.89 [533.4] (1114.60-2843.62)
Scombridae	<i>Scomber colias</i>	774	7.18 (4.90-10.22)	75	49.33 (42.00-57.33)	64909	23.54 (18.31-29.38)	1515.42 [106.6] (974.82-2270.27)
	<i>Scomber scombrus</i>	107	1 (0.25-2.03)	12	8.67 (4.67-13.33)	13220.98	4.79 (1.69-8.90)	50.20 (9.06-145.70)
Gobiidae	Gobiidae	1414	13.11 (7.69-18.55)	53	35.33 (27.33-43.32)	1004.97	0.36 (0.22-0.57)	475.90 [115.2] (216.18-828.28)
Merluccidae	<i>Merluccius merluccius</i>	342	3.18 (1.88-4.62)	52	35.33 (27.33-43.33)	11610.51	4.21 (2.82-6.12)	261.09 [41.7] (128.45-465.36)
Gadidae	<i>Micromesistius poutassou</i>	440	4.08 (0.40-9.18)	11	7.33 (3.33-12.00)	6893.04	2.5 (0.34-5.21)	48.23 [1227.6] (2.46-172.68)
	<i>Gadiculus argenteus</i>	121	1.12 (0.00-3.46)	2	1.33 (0.00-3.33)	509.76	0.18 (0.00-0.59)	1.73 (0.00-13.49)
	<i>Trisopterus</i> spp.	433	4.01 (1.29-8.19)	35	23.33 (16.67-30.00)	5316.79	1.93 (0.69-3.40)	138.58 (33.01-347.70)
Sparidae	<i>Boops boops</i>	131	1.21 (0.73-1.88)	44	29.33 (22.00-36.67)	7120.62	2.58 (1.58-3.87)	111.16 (50.82-210.85)
	<i>Pagrus pagrus</i>	1	0.01 (0.00-0.03)	1	0.67 (0.00-2.00)	0.61		
	Sparidae sps.	8	0.07 (0.00-0.23)	2	1.33 (0.00-3.33)			
Atherinidae	<i>Atherina</i> sp.	294	2.72 (1.22-4.56)	30	20 (14.00-26.67)	2987.09	1.08 (0.45-1.80)	76.00 (23.38-169.62)
Engraulidae	<i>Engraulis encrasicolus</i>	130	1.2 (0.71-1.91)	33	22 (16.00-28.67)	1836.55	0.67 (0.32-1.09)	41.14 (16.48-86.01)
Belonidae	<i>Belone belone</i>	26	0.24 (0.02-0.70)	5	3.33 (0.67-6.65)	244.57	0.09 (0.00-0.25)	1.10 (0.01-6.32)
Centracanthidae	<i>Spicara smaris</i>	9	0.08 (0.00-0.26)	2	1.33 (0.00-3.33)			
Ammodytidae	<i>Gymnammodytes</i> spp.	28	0.26	3	2	107.19	0.04	0.60

			(0.00-0.90)		(0.00-4.67)		(0.00-0.13)	(0.00-4.81)
Sternoptychidae	<i>Maurolicus muelleri</i>	27	0.25 (0.00-0.93)	1	0.67 (0.00-2.00)			
Citharidae	<i>Citharus linguatula</i>	19	0.18 (0.00-0.46)	2	1.33 (0.00-3.33)	4291.16	1.51 (0.78-4.56)	2.25 (0.00-16.72)
Soleidae	Soleidae sp.	58	0.54 (0.03-1.43)	6	4 (1.33-7.33)	440.92	0.16 (0.01-0.43)	2.80 (0.05-13.63)
Mugilidae	<i>Liza sp.</i>	4	0.04 (0.00-0.11)	2	1.33 (0.00-3.33)	450.93	0.16 (0.00-0.48)	0.27 (0.00-1.96)
Bothidae	<i>Arnoglossus sp.</i>	7	0.06 (0.00-0.22)	1	0.67 (0.00-2.00)	62.65	0.02 (0.00-0.08)	0.05 (0.00-0.60)
Cepolidae	<i>Cepola macrophthalma</i>	3	0.03 (0.00-0.09)	1	0.67 (0.00-2.00)			0.02 (0.00-0.18)
Trichiuridae	<i>Apanopus carbo</i>	1	0.01 (0.00-0.03)	1	0.67 (0.00-2.00)			0.01 (0.00-0.06)
Myctophidae	<i>Myctophum punctatum</i>	4	0.03 (0.00-0.11)	1	0.67 (0.00-2.00)			0.02 (0.00-0.22)
Ophidiidae	<i>Ophidion sp.</i>	1	0.01 (0.00-0.03)	1	0.67 (0.00-2.00)			0.01 (0.00-0.06)
	Unidentified Fish	44	0.41 (0.19-0.70)	18	12 (7.33-17.33)			4.92 (1.39-12.12)
	Total Fish	7776	72.00 (62.84-81.32)	150	100	264599.17	95.56 (91.98-99.04)	16756.00 (15482.00-18036.00)
Sepiolidae	<i>Sepiola atlantica</i>	1636	15.22 (7.77-23.29)	51	36 (28.68-44.00)	2332.87	0.84 (0.37-1.55)	578.16 [<0.0] (233.46-1092.96)
	Sepiolid sps.	42	0.39 (0.13-0.74)	8	6 (2.67-10.00)	68.07	0.02 (0.01-0.04)	2.46 (0.37-7.80)
Loliginidae	<i>Alloteuthis sp.</i>	1239	11.52 (6.73-17.62)	55	38 (30.67-46.00)	6075.51	2.2 (1.09-3.66)	521.36 [229.8] (239.84-978.88)
	<i>Loligo sp.</i>	47	0.44 (0.26-0.72)	26	18.67 (12.67-26)	6382.92	2.31 (0.86-4.49)	51.34 [166.8] (14.19-135.46)
Sepiidae	<i>Sepia spp.</i>	1	0.01 (0.00-0.03)	1	0.67 (0.00-2.00)	22.11	0.01 (0.00-0.03)	0.01 (0.00-0.12)
Ommastrephidae	<i>Illex coindentii</i>	10	0.09 (0.03-0.19)	7	4.67 (1.33-8.00)	441.42	0.16 (0.02-0.38)	1.17 (0.07-4.56)
Octopodidae	<i>Eledone cirrhosa</i>	1	0.01 (0.00-0.03)	1	0.67 (0.00-2.65)	124.15	0.04 (0.00-0.15)	0.03 (0.00-0.48)
	Total Cephalopods	2976	27.68 (18.29-36.63)	70	52.67 (44.67-60.67)	15447.04	5.54 (3.37-8.71)	1749.70 (967.55-2750.78)
Crustacea NI		1	0.01 (0.00-0.03)	1	0.67 (0.00-2.00)			
Polynoidae		33	0.3 (0.01-0.81)	3	2.67 (0.02-5.33)			
	Total	10786	100	150	100	283131.76	100	

Table 3 – Results of the GAM models for explaining the presence of sardine, scads and chub mackerel in common dolphin stomach contents. Explanatory variables, significant variables, deviance explained. Akaike Information Criterion (AIC) values and Bayesian Information Criterion (BIC) values for best models are presented. Final model chosen is highlighted in bold.

Model	Significant Variables	Explained deviance	AIC	BIC
<i>Sardina pilchardus</i>				
Number <i>Sardina pilchardus</i> ~ s(day in year. k = 4) + s(length. k = 4) + s(sardine biomass. k = 4) + sex + area	LENGTH***	12.4	913.48	937.88
Number <i>Sardina pilchardus</i> ~ s(length. k=4) + s(sardine biomass. k=4) + sex + area	LENGTH***	12	911.87	933.00
Number <i>Sardina pilchardus</i> ~ s(length. k=4) + sex + area	LENGTH***	11.9	910.22	928.78
Number <i>Sardina pilchardus</i> ~ s(length. k=4) + area	LENGTH***	12.1	908.28	924.36
Number <i>Sardina pilchardus</i> ~ s(length. k=4)	LENGTH***	11	908.29	921.77
<i>Trachurus sp.</i>				
Number <i>Trachurus</i> _sp ~ s(day in year. k=4) + s(length. k=4) + s(year. k=4) + sex + area	n.s	9.51	748.75	776.77
Number <i>Trachurus</i> sp ~ s(day in year. k=4) + s(length. k=4) + s(year. k=4) + area	n.s	9.48	746.73	771.84
Number <i>Trachurus</i> sp ~ s(day in year. k=4) + s(length. k=4) + area	n.s	9.34	744.80	766.89
Number <i>Trachurus</i> sp ~ s(length. k=4) + area	LENGTH*	7.81	742.61	758.66
Number <i>Trachurus</i> sp ~ s(length. k=4)	LENGTH**	7.36	741.43	754.89
<i>Scomber colias</i>				
Number <i>Scomber colias</i> ~ s(day in year. k=4) + s(length. k=4) + s(year. k=4) + sex + area	AREA*** LENGTH***	26.1	624.80	649.33
Number <i>Scomber colias</i> ~ s(day in year. k=4) + s(length. k=4) + s(year. k=4) + area	AREA*** LENGTH***	26.2	622.76	644.40
Number <i>Scomber colias</i> ~ s(length. k=4) + s(year. k=4) + area	AREA*** LENGTH***	26.1	620.86	639.49
Number <i>Scomber colias</i> ~ s(length. k=4) + area	AREA*** LENGTH***	26.1	618.95	634.76

Table 4 Percentage number (% N) and weight (% W) of the main prey species identified in the stomach of common dolphins according to different size classes (Small <190 cm; Large $\geq$ 190 cm)

Prey Species	Small (N=86)		Large (N=54)	
	% N	% W	% N	% W
Fish				
<i>Sardina pilchardus</i>	13.5	39.3	21.6	35.4
<i>Trachurus sp</i>	10.7	15.5	19.4	14.6
<i>Scomber colias</i>	5.5	24.8	10.6	24.2
<i>Trisopterus sp</i>	5.3	2.4	1.9	3.1
<i>Gobiidae</i>	19.4	0.5	4.2	0.2
<i>Merluccius merluccius</i>	1.4	2.8	5.9	5.3
<i>Micromesistius poutassou</i>	0.8	0.6	6.9	3.1
<i>Atherina sp</i>	3.2	1.7	1.5	0.5
Cephalopoda				
<i>Alloteuthis sp.</i>	12.4	2.7	11.2	1.9
<i>Sepiolo atlantica</i>	22.5	1.4	5.0	0.3
Total	94.7	89.3	88.2	88.6

Table 5 – Estimated daily and annual consumption for the 3 main species (sardine, chub mackerel, scads) by common dolphins in the Portuguese continental shelf. Figures in parentheses are 95 % confidence limits. For explanation on the calculation see the main text.

Species	Daily consumption rate (tonnes) (95% CI)	Annual consumption rate (tonnes) (95% CI)
<i>Sardina pilchardus</i>	23.0 (12.3-43.0)	8392.7 (4490.0 - 15686.6)
<i>Scomber colias</i>	14.4 (7.7 - 26.9)	5256.5 (2812.5 - 9824.7)
<i>Trachurus sps</i>	9.6 (5.1 - 17.9)	3497.0 (1871.1 - 6536.1)
Total (3 pelagics)	47.0 (87.8 - 25.1)	17146.2 (9174.1 - 32047.4)
Total (all prey)	61.8 (33.1 - 115.6)	22570.0 (12076.1 - 42184.8)

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