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1 **Ecological niche segregation among five toothed whale species off the NW Iberian**
2 **Peninsula using ecological tracers as multi-approach.**

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24

25 **Abstract** This study aims to assess niche segregation among the five main toothed whales
26 that frequent the NW Iberian Peninsula waters: the common dolphin, the harbour porpoise,
27 the bottlenose dolphin, the striped dolphin and the long-finned pilot whale. We used cadmium
28 (Cd) and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as ecological tracers to assess degree of
29 segregation in diet/trophic level and in foraging habitat, over various time-scales. $\delta^{13}\text{C}$ values
30 highlighted different habitat while Cd concentrations highlighted feeding differences between
31 oceanic and neritic species. Moreover, $\delta^{15}\text{N}$ values suggest different trophic levels of prey
32 targeted within oceanic and neritic species. Hence, results revealed long-term ecological
33 segregation among five toothed whales that coexist in the NWIP and demonstrated the ability
34 of ecological tracers to discriminate ecological niches among closely related species.

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39 **Introduction**

40 Hutchinson (1957) defined the central concept of ecological niche as a set of biotic and
41 abiotic conditions in which a species is able to persist and maintain stable population sizes.
42 These conditions can be structured along three main dimensions: trophic (e.g. diet
43 composition, trophic level and prey quality), spatial (horizontally and vertically) and temporal
44 (from diel activity patterns to yearly migratory cycles); temporal and spatial dimensions of the
45 niche include various environmental influences on distribution. Description of these different
46 dimensions allows estimation of inter-specific overlap *versus* segregation within a community
47 or a guild (Pianka 1974). The first mechanism that allows for niche differentiation is resource
48 partitioning (trophic dimension). In this case, different predators living in the same habitat
49 exploit the resources differently, minimizing the overlap in terms of prey composition
50 (Ballance 2002). The second mechanism involves the spatial and/or temporal dimensions of
51 the availability of different resources (Huisman and Weissing 2001).

52 The study of the ecological niche as well as of the segregation processes can help to advance
53 our understanding of ecosystem functioning (Leibold 1995) although this objective presents
54 added difficulties since the ecological niche in marine ecosystems is hard to measure
55 (Newsome et al. 2007). Renewed interest in this concept has arisen due to technological
56 advances such as the use of chemical or ecological tracers in marine organisms, e.g. stable
57 isotopes, in particular of carbon (C) and nitrogen (N), analysis of which has become a
58 powerful tool in the study of ecological niches (Jardine et al. 2006; Newsome et al. 2007),
59 notably because $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provide information on trophic level and foraging area
60 (DeNiro and Epstein 1978; Cabana and Rasmussen 1996 ; Hobson 1999; Fry 2006). Isotopic
61 results are especially relevant in combination with others approaches such as stomach content
62 analysis, habitat modeling or other potential ecological tracers (e.g. trace elements, persistent
63 organic pollutants or fatty acids) to investigated the ecological niches of marine top predators

64 (e.g. Zhao et al. 2004; Herman et al. 2005; Krahn et al. 2007; Cherel et al. 2008; Kiszka et al.
65 2011).

66 Together with stable isotopes, ecological and chemical tracers' elements offer an integrated
67 measure of prey assimilation over different periods of time. This contrast with conventional
68 dietary analyses (e.g. faeces or stomach contents) which provide information on food ingested
69 over a very short-time scale (several days, see e.g. Santos et al. 2001). Depending on the
70 combination of elements and tissues used, the period of integration represented by the specific
71 signature or concentration will differ, relating biological half-life of tracers and tissue
72 turnover rates. Thus, ecological tracers can provide information from a medium-time scale
73 (from several weeks to months, i.e. fatty acids in blubber or stable isotopes in liver and
74 muscle), to long-term time scales (from several years to the life span of the animals) when
75 ecological tracers are analyzed in hard tissues with no turnover such as teeth (Hobson and
76 Clark 1992; Hobson and Sease 1998; Nordstrom et al. 2008, Caurant et al. 2009).

77 Moreover, ecological tracers can be viewed as proxies of habitat, feeding habits and trophic
78 position. Thus the relative abundance of heavy to light carbon isotopes ($\delta^{13}\text{C}$) has been used
79 to discriminate between habitats where phytoplankton is the only source of organic carbon
80 (pelagic and offshore habitats) and those where macrophytes are a significant source of
81 organic carbon (vegetated inshore and benthic habitats) (DeNiro and Epstein 1978; Fry 2006).

82 The relative abundance of heavy to light nitrogen isotopes ($\delta^{15}\text{N}$) is commonly taken as an
83 indicator of trophic level (Cabana and Rasmussen 1996) because $\delta^{15}\text{N}$ increases from prey to
84 predator due to the preferential excretion of the light isotope (Hobson 1999). However, $\delta^{15}\text{N}$
85 also vary strongly by habitat: inshore and offshore systems, latitudes and between oceanic
86 basins. Thus, Ruiz-Cooley et al. (2012) recently showed that the $\delta^{15}\text{N}$ values from
87 zooplankton and/or prey such as squid from similar sizes exhibited large differences in $\delta^{15}\text{N}$
88 ($> 4 \text{ ‰}$) between inshore and offshore systems due to biochemical properties of the habitat. In

89 the same way, Chouvelon et al. (2012) showed marked decreasing $\delta^{15}\text{N}$ values from inshore
90 to offshore into different marine species from the Bay of Biscay, highlighting the role of
91 stable isotopes of N as an indicator of feeding area.

92 Considering trace elements, elevated concentrations of cadmium (Cd) in marine mammals are
93 usually associated to a predominance of cephalopods or crustaceans in the diet (Honda et al.
94 1983; Das et al. 2000) due to the bioaccumulation of this element in their digestive gland
95 where most of the detoxification processes take place (Bustamante et al. 1998b) and the
96 highest concentrations of Cd are found in oceanic species (Bustamante et al. 1998a; Lahaye et
97 al. 2005). The high bioavailability of Cd induces a high potential for its trophic transfer to
98 upper level predators such as marine mammals (Bustamante et al. 2002a, 2002b). In addition,
99 cephalopods show large differences in Cd concentrations depending upon their origin
100 (specifically latitude, with highest Cd enrichment found in sub-polar food webs (Bryan 1976;
101 Miramand and Bentley 1992; Bustamante et al. 1998a). Consequently, marine top predators
102 from polar and sub-polar areas feeding on cephalopods should exhibit high Cd concentrations
103 in their tissues.

104 The Northwest of the Iberian Peninsula (NWIP) is at the northern limit of the East Central
105 Atlantic upwelling system, characterized by high biodiversity and productive fisheries. NWIP
106 represents an important habitat for cetaceans, at least 20 species of marine mammals (16
107 cetaceans and 4 pinnipeds) have been recorded and the rate of stranding is one of the highest
108 in Europe (López et al. 2002). The most frequent species in the area are toothed whales,
109 specifically common dolphin (*Delphinus delphis*), bottlenose dolphin (*Tursiops truncatus*),
110 harbour porpoise (*Phocoena phocoena*), striped dolphin (*Stenella coeruleoalba*) and long-
111 finned pilot whale (*Globicephala melas*) (Cendrero 1993; López et al. 2002, 2004). The
112 ongoing occurrence of cetaceans in the area has permitted, for many years, systematic boat-
113 and land-based surveys, as well as several studies on diet, distribution, habitat preferences and

114 interactions with human activities including fisheries among others (López et al. 2003, 2004;
115 Santos et al. 2007a, b, In press; Pierce et al. 2010; Spyrakos et al. 2011). Several studies have
116 tried to relate coastal and at-sea sightings with environmental parameters (e.g. depth, SST and
117 chlorophyll-a) to improve understanding of spatio-temporal trends in cetacean distribution in
118 the NWIP, and results suggest the existence of mechanisms allowing a fine-scale partitioning
119 of habitats and/or resources. For instance, stable isotopes of C and N were analyzed in
120 muscle tissues (i.e. medium-time scale information) of these five species and in their prey in
121 order to better understand their position in the NWIP food web (Méndez-Fernandez et al.
122 2012). Toothed whales occupy high trophic positions (TPs from 4.3 to 5.3) and no
123 significantly between-species differences have been detected. However, an overlap in TP does
124 not necessarily imply an overlap in diet, since animals may feed on different prey species with
125 similar TPs.

126 Thus, the present study aims to provide further insight into habitat and resource partitioning
127 among these toothed whale species, extending previous stable isotopes of C and N results in
128 muscle (from Méndez-Fernandez et al. 2012) with new analyses on C and N isotopes in teeth
129 as well as Cd in liver and kidney tissues, to cover a wide range of temporal scales. We
130 hypothesized that each toothed whale species occupies its own ecological niche in the area,
131 defined by differences in at least one of the ecological tracers used. Cd and $\delta^{15}\text{N}$ values will
132 determine the trophic dimension of the ecological niche over different time-scales
133 (Bustamante et al. 1998a; Hobson 1999), whereas, information on the spatial dimension
134 (offshore vs inshore, pelagic vs benthic) will be provided by $\delta^{13}\text{C}$ and also $\delta^{15}\text{N}$ isotope values
135 (Hansson et al. 1997; Hobson 1999; Sherwood and Rose 2005; Ménard et al. 2007;
136 Chouvelon et al. 2012). An important aspect of the temporal dimension is the possibility that
137 habitat use and trophic position may change over time. Consequently, effects of seasons and

138 years were studied on common dolphin, the species for which the biggest sample size was
139 available.

140

141 **Methods**

142 Study area and sampling

143 Fieldwork was carried out in the North West of the Iberian Peninsula (NWIP), from Northern
144 limit of the Galician coast (43° 31' N, 7° 2' W) to Nazaré on the Portuguese coast (39° 36' N,
145 9° 3' W; Fig. 1). Stranded and by-caught cetaceans were attended by experienced personnel
146 of the Galician (Coordinadora para o Estudo dos Mamíferos Mariños, CEMMA) or
147 Portuguese (Sociedade Portuguesa de Vida Salvagem, SPVS) stranding networks. Animals
148 were identified to species, measured (total length and several other standard measurements are
149 routinely taken), sexed and, if the state of preservation of the carcass allowed it, full
150 necropsies were performed and samples collected following a standard protocol defined by
151 the European Cetacean Society (after Kuiken and Garcia Hartmann 1991). Samples collected
152 between 2004 and 2008 were used for this study, and muscle, teeth, liver and kidney tissues
153 were sampled, whenever possible, from stranded and by-caught individuals of five toothed
154 whales species: common dolphin, bottlenose dolphin, harbour porpoise, striped dolphin and
155 long-finned pilot whale (see Table 1). The common dolphin was the best represented species,
156 as a result of the high number of individuals by-caught in the Spanish and Portuguese
157 fisheries. After the necropsies, all the tissue samples were stored at -20°C until being
158 processed in the laboratory. Since decomposition state can affect results from stable isotope
159 analysis of muscle tissue, individuals selected for analysis were those with condition code 1 to
160 3, i.e. originally stranded alive, freshly dead or moderately decomposed (after Kuiken and
161 Garcia Hartmann 1991).

162 Age determination

163 At least 5 teeth were collected from the mid-section of the left mandible of each sampled
164 individual, selecting the least worn/damaged and least curved teeth, to ensure sufficient
165 material for replicate preparations. Teeth were preserved frozen and age was determined by
166 analysing growth layer groups (GLGs) in the dentine of teeth, following adapted methods
167 based on Lockyer (1993), Hohn and Lockyer (1995) and Rogan et al. (2004). Teeth were
168 decalcified and sectioned using a freezing microtome. The most central and complete sections
169 (including the whole pulp cavity) were selected from each tooth, stained with Mayer's
170 haematoxylin (modified by Grue) and 'blued' in a weak ammonia solution, mounted on glass
171 slides, and allowed to dry. GLGs were counted under a binocular microscope. All readings
172 were initially made blind (without access to individual biological data) and replicate counts
173 were made by at least two readers. If the age estimates obtained by the two readers differed by
174 more than 1 year, readings were repeated. If the increments were difficult to count, both
175 readers discussed the interpretation and either reached an agreed age or judged the tooth to be
176 unreadable.

177 Stable isotope analyses

178 Muscle samples were previously analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (see Mèndez-Fernandez et al.
179 2012) and, as for whole tooth samples, they were freeze-dried and then ground into a fine
180 powder before isotopic analyses. Since lipids are highly depleted in ^{13}C relative to other tissue
181 components (DeNiro and Epstein 1978), they were extracted from muscle tissues using
182 cyclohexane. To this end, an aliquot of approximately 100 mg of muscle powder was agitated
183 with 4 mL of cyclohexane for 1h. Next, the sample was centrifuged for 5 min at 4000 g, and
184 the supernatant containing the lipids was discarded. Then, the sample was dried in an oven at
185 45°C for 48 h, and 0.35 ± 0.05 mg subsamples of lipid-free dry powder were finally weighed
186 in tin capsules for stable isotope analyses. Any sample for $\delta^{13}\text{C}$ analysis that may contain
187 biogenic carbonates (i.e. inorganic carbon) must be acidified and carbonates can be removed

188 in the dry powder leaving only the organic portion of the sample, composed of collagen.
189 Thus, carbonates were removed from powdered whole tooth samples by digesting with
190 approximately 1 mL of a 4 M-hydrochloric acid solution at 45°C for 48 h. The digested
191 contents were taken up in milli-Q ultrapure quality water, homogenized and freeze-dried at
192 -80°C for 2 days. Finally, 1.45 ± 0.05 mg subsamples of each homogenized carbonate-free
193 dried dental sample were weighed into tin capsules.

194 These analyses were performed with an elemental analyzer coupled to an Isoprime
195 (Micromass) continuous-flow isotope-ratio mass spectrometer (CF IR-MS). The results are
196 presented in the usual δ notation relative to Pee Dee belemnite marine fossil limestone for
197 $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$, in parts per thousand (‰). Replicate measurements of
198 internal laboratory standards (acetanilide) during each run indicate measurements errors < 0.2
199 ‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

200 Trace element analyses

201 The equipment used in the sample processing was cleaned and subsequently decontaminated
202 for 24 h in a solution composed of 35 ml HNO_3 (65%) and 50 mL HCl (36%) for 1 L of Milli-
203 Ro quality water. Fresh samples were freeze-dried, ground to powder and then each sample
204 was treated in duplicate.

205 For Cd analysis, aliquots of the liver and kidney samples (i.e. the main storage tissues; 0.1-0.3
206 g) were digested with 6mL 67-70% HNO_3 and 2 mL 34-37% HCl . Acid digestion was
207 performed overnight under ambient temperature before been heated in a microwave
208 (ThermoFisher Scientific Milestone Start D) during 30 min with increasing temperature up to
209 105°C, and 15 min at 105°C (1200 W). After the mineralization process, each sample was
210 diluted to 30 or 50 mL with milli-Q quality water, according to the volume of acid added to
211 the mineralization (3.0 mL or 4.5 mL). Thus, for samples with a weight $< 0.1\text{g}$ the mixture
212 was 3mL 67-70% HNO_3 / 2mL 34-37% HCl and the milli-Q water complement was 25mL.

213 Elements were analysed using a Varian Vista-Pro ICP-OES and a Thermo Fisher Scientific
214 XSeries 2 ICP-MS. Three control samples (two CRMs and one blank) treated and analysed in
215 the same way as the samples were included in each analytical batch. CRMs were DOLT-4
216 (dogfish liver; NRCC) and TORT-2 (lobster hepatopancreas; NRCC) and the detection limit
217 was $0.15 \mu\text{g g}^{-1}$ dry weight (d.wt). Finally, this protocol was validated by an international
218 intercalibration method (Christopher et al. 2007).

219 Data treatment

220 Cadmium concentration data showed a marked departure from normality which was
221 substantially improved by log transformation. The distribution of $\delta^{13}\text{C}$ values (at least for
222 model residuals) was normal and no transformation was needed. Although $\delta^{15}\text{N}$ values were
223 not exactly normally distributed, transformation did not improve the distribution and
224 untransformed data were therefore used in analysis.

225 To investigate the possible role of confounding factors, notably age and season but also
226 interannual differences, on niche segregation, generalized additive models (GAMs; Hastie and
227 Tibshirani 1990) were used. GAM is a semi-parametric extension of generalized linear
228 modelling (McCullagh and Nelder 1989). GAMs are more flexible; they permit both linear
229 and complex non-linear relationships between species and environmental predictors, as well
230 as combinations of the two within the same model (Wood and Augustin 2002), without the
231 problematic step of postulating response curve shape or parametric response function. GAMs
232 estimate response curves with a non-parametric smoothing function (“smoothers”) instead of
233 parametric terms, and as such are said to be data-driven methods. Differences between the
234 sexes were also tested but since there was no effect for any species and tracers we removed
235 this parameter from the final GAMs.

236 For common dolphin, Gaussian GAMs with an identity link function were fitted to stable
237 isotope values and Cd concentrations (log-transformed) (response variables) with age, season

238 and year as potential explanatory variables. In these GAMs, age was considered as a
239 continuous explanatory variable, while the year and the season of sampling of individuals
240 were treated as categorical explanatory variables. Season was defined as a categorical variable
241 with 4 values: spring (March, April and May), summer (June, July and August), autumn
242 (September, October and November) and winter (December, January and February). The age
243 smoother was constrained to take a relatively simple form, avoiding overfitting, by setting to
244 the number of knots to $k = 4$. Overfitting occurs when the model learns the training data
245 extremely well but is not able to generalize well. To test for significant interactions between
246 age-season and age-year effects, models were fitted both with single age smoothers and with
247 separate age smoothers for each season or year and, in both cases, the two versions were
248 compared using a F test. If the seasonal effect was significant, we also explored using month
249 instead of season as an explanatory variable, fitting it as a smoother, to provide greater detail
250 on the form of the seasonal pattern. The general form of the model performed for each tracer
251 was then:

252
$$\text{Tracer value} \sim \text{s}(\text{age}, k = 4) + \text{s}(\text{month}, k = 4) + \text{year} [+ \text{interaction terms}]$$

253 In principle this approach could be extended to species comparisons but sample sizes for all
254 species except common dolphin were too small to allow fitting a common model (with
255 relevant interaction terms) for all species, testing species differences using models such as the
256 following, taking into account the fact that age effects and seasonal patterns are likely to
257 differ between species (i.e. that there are species-age and species-season interaction):

258
$$\text{Tracer value} \sim \text{species} + \text{s}(\text{age}, k = 4, \text{by} = \text{as.factor}(\text{species}))$$

259
$$+ \text{s}(\text{month}, k = 4, \text{by} = \text{as.factor}(\text{species})) + \text{year} [+ \text{other interaction terms}]$$

260 In practice, because sample sizes were small for most species, full models could not be tested.
261 However, relationships between tracers and explanatory variables found in common dolphins

262 were used as a guide for the construction of species comparison models, e.g. if the common
263 dolphin model contained an age effect, this structure was used in the all species model.

264 For each GAM performed, a stepwise procedure was used to select the most parsimonious
265 model using the Akaike Information Criterion (AIC; Akaike 1981). The best model was found
266 using backwards selection (successive eliminations), removing the least important non-
267 significant terms sequentially until all remaining effects were significant. Stepwise procedures
268 have been criticized by several authors (e.g. Whittingham et al. 2006), for example because
269 they effectively update the hypothesis tested at each step. However, resulting models can be
270 viewed more as a refinement of the original hypothesis than a hypothesis test per se. Thus all
271 such models require tests with independent data sets and we therefore argue that stepwise
272 procedures remain a useful tool to guide future work. The percentage of deviance explained
273 by the final model was calculated as follows:

274 Explained deviance = ((Null model deviance – final model residual deviance)/Null model
275 deviance)*100, with the null model that only contains the intercept terms.

276 Final models were checked for normality and trends in residuals and for outliers and other
277 influential data points (Zuur et al. 2007). The models performed for common dolphin,
278 including respective AIC values, are summarized in Table 2.

279 To provide a quick and easily understandable summary of between species differences in
280 accumulation/assimilation of trace elements and stable isotopes, ANOVA (analysis of
281 variance) with Tukey tests was also performed, specifically to test for differences in Cd
282 concentrations ($\mu\text{g g}^{-1}$ wet weight, w.wt) and stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (log-
283 transformed) between species.

284 Statistical analyses mentioned above were performed using R version 2.11.1 (R Development
285 Core Team 2010) and BRODGAR 2.5.1 statistical software.

286

287 **Results**

288 The number of samples available by tissue, species and year are summarized in Table 1.

289 Cadmium concentration in kidney

290 Concentrations of Cd were higher in the kidney than in the liver for all species; ranges and
291 values (mean \pm SD) are summarized in Table 3.

292 ANOVA confirmed that Cd concentrations ($\mu\text{g g}^{-1}$ w.wt, log-transformed) in kidney varied
293 significantly between species (ANOVA, $F_{(4)} = 5.31$, $P < 0.001$), being significantly higher in
294 striped dolphin than in common dolphin and harbour porpoise and significantly higher in pilot
295 whale than in harbour porpoise (Tukey tests). However, no significant differences were found
296 between pilot whale and striped dolphin ($P > 0.05$, Tukey test). The final GAM for Cd
297 concentrations ($\mu\text{g g}^{-1}$ w.wt, log-transformed) in the kidney of common dolphins explained
298 37.9% of deviance ($N = 96$, $\text{AIC} = 133.6$; Table 2) and included only a significant effect of
299 age ($P < 0.0001$, d.f. = 2.81). Cd concentrations increased with increasing age, although
300 leveling off after around 10 years (Fig. 2a).

301 A GAM model for all species which included separate age-smoothers for each species
302 performed better than one assuming a common age smoother across all species (F test, $P <$
303 0.0001) and explained 47.7% of deviance. The age effect was significant and showed
304 different trends among species (Fig. 3), except for bottlenose dolphin ($P = 0.060$). This was
305 probably a result of the low number of samples and high proportion of young (immature)
306 animals of this species. Significant between-species variation is confirmed, with pilot whale,
307 striped dolphin and common dolphins all showing higher age-corrected accumulation of Cd in
308 the kidney than harbour porpoise and striped dolphin having a higher concentration than
309 common dolphin ($P < 0.0001$ in all cases).

310 Cadmium concentration in liver

311 In liver, Cd concentrations also varied significantly between species (ANOVA, $F_{(4)} = 13.85$,
312 $P < 0.0001$), being significantly higher in striped dolphin than in all the other species except
313 pilot whale, significantly lower for harbour porpoise than in all the other species except
314 bottlenose dolphin and significantly higher in pilot whale than in common dolphin (Tukey
315 tests). The final model for Cd in liver of common dolphin explained 47.4% of deviance ($N =$
316 95 , $AIC = 110.3$; Table 2). Cd concentrations in liver increased with increasing age (d.f. =
317 2.99 , $P < 0.0001$) up to around age 7 (Fig. 2b). As for Cd in kidney, seasonal and between-
318 year differences were non-significant.

319 The final GAM for Cd concentrations in liver for all species included separate age smoothers
320 for each species and explained 52.4% of deviance ($N = 143$, $AIC = 253.9$). The age effects
321 were significant for all the species except for striped dolphin and pilot whale. Again,
322 differences between species were highly significant. Age-corrected concentrations were
323 higher in pilot whale and striped dolphin than in common dolphin or harbour porpoise, and
324 higher in common dolphin than in harbour porpoise ($P < 0.0001$ in all cases).

325 $\delta^{13}\text{C}$ values in muscle and teeth

326 A summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the different tissues (muscle and tooth) of the five
327 toothed whales from the NWIP is presented in Table 3. Results for muscle are based on data
328 from Mèndez-Fernandez et al. (2012)

329 $\delta^{13}\text{C}$ values (‰) in muscle and teeth varied significantly between species, as shown by
330 ANOVA analysis (ANOVA, $F_{(4)} = 11.1$ and 10.91 , respectively, $P < 0.0001$). Striped dolphin
331 showed significantly lower $\delta^{13}\text{C}$ values in both muscle and teeth (Tukey tests) compared to all
332 other species, except for common dolphin in teeth. Common dolphin also showed
333 significantly lower $\delta^{13}\text{C}$ values than harbour porpoise in both muscle and teeth, and lower
334 $\delta^{13}\text{C}$ values than pilot whale and bottlenose dolphin in teeth (Tukey tests) (Fig. 4).

335 The final GAM for $\delta^{13}\text{C}$ values (‰) in the muscle of common dolphin explained 34.9% of
336 deviance (N = 104, AIC = 119.8; Table 2). There was no effect of age but the effect of season
337 was highly significant ($P < 0.0001$, d.f. = 2.3), with the highest values in April and the lowest
338 in September (Fig. 5a).

339 GAM results for $\delta^{13}\text{C}$ in muscle of all species confirmed clear differences between species
340 and that the effect of season also differed between species, with the seasonal trends for
341 common dolphin, harbour porpoise and bottlenose dolphin all being statistically significant
342 (Figs. 5a-c). The model explained 45.7% of deviance. Seasonally adjusted $\delta^{13}\text{C}$ in muscle was
343 higher in pilot whale, porpoise and bottlenose dolphin than in common or striped dolphin, and
344 higher in common dolphin than in striped dolphin. The GAM for $\delta^{13}\text{C}$ in teeth gave similar
345 results, although deviance explained was only 26.5% (Table 2).

346 $\delta^{15}\text{N}$ values in muscle and teeth

347 ANOVA confirmed that $\delta^{15}\text{N}$ values (‰) in muscle and teeth also varied significantly
348 between species (ANOVA, $F_{(4)} = 25.92$ and 40.61 , respectively, $P < 0.0001$), being
349 significantly lower in striped dolphin than in all the other species, except in teeth of pilot
350 whale, and significantly higher in teeth of harbour porpoise than in teeth of all the other
351 species (Tukey tests). Finally, $\delta^{15}\text{N}$ values in muscle of common dolphin were significantly
352 lower than in muscle of bottlenose dolphin (Tukey tests) (Fig. 4).

353 The final GAM for $\delta^{15}\text{N}$ values in muscle of common dolphin explained 19.7% of deviance
354 (N = 97, AIC = 151.9; Table 2). There was no effect of season or year but a strong negative
355 and linear effect of age ($P < 0.001$, d.f. = 1.0) where $\delta^{15}\text{N}$ values decreased with increasing
356 age (Fig. 6).

357 GAM results for the all-species analysis of $\delta^{15}\text{N}$ in muscle indicated that a model with
358 separate age-smoothers for each species was not a significant improvement on a model with a
359 common smoother for age. Although there were some influential outliers (“hat” values

360 approaching 1.0), using separate smoothers and/or transformation of $\delta^{15}\text{N}$ data produced no
361 marked improvement in fit. The final model therefore contained a significant age effect ($P <$
362 0.0001 , d.f. = 2.8), depicting a decline in $\delta^{15}\text{N}$, at least until age 7 and also a significant
363 species effect ($P < 0.0001$). It explained 52.3% of deviance. Harbour porpoise, pilot whale
364 and bottlenose dolphin all had higher (age-corrected) $\delta^{15}\text{N}$ values than common dolphin and
365 striped dolphin, while values for common dolphin were also higher than for striped dolphin.
366 Finally, for $\delta^{15}\text{N}$ in teeth of all species, the best model included separate age effects for each
367 species (with these being significant for all species except the pilot whale) and a species effect
368 ($P < 0.0001$), explaining 77.3% of deviance. Although there were some influential data points,
369 the distribution of residuals appeared to be satisfactory. $\delta^{15}\text{N}$ values were higher in porpoise
370 than in pilot whales and common dolphins, while all three of these species had higher values
371 than striped dolphin.

372

373 **Discussion**

374 **General comments**

375 We have shown how the application of a multi-tracer approach has allowed the evaluation of
376 the foraging niche of the five most common toothed whales in the NWIP. This approach has
377 permitted the investigation of the foraging niche in two dimensions (i.e. trophic and spatial)
378 covering a range of different time spans. Moreover, this approach also provided
379 complementary information to the studies using conventional methods previously carried out
380 in the area (e.g. based on stomach contents analysis or direct observations). Overall, the main
381 finding in this work is that none of the individual ecological tracers examined alone reveals
382 complete ecological segregation amongst the five species studied whereas the integration of
383 results from all these tracers indicates segregation of all five species in the long-term
384 (conceptually represented in Fig. 7). The NWIP represents only a part of the range of these

385 species within the NE Atlantic and each individual may not spend a substantial proportion of
386 its time within this area. This is why a possible segregation found by tracers may attest to a
387 different distribution of the species on a broader geographic scale out of the NWIP. A further
388 and important consideration is that all the ecological tracers are mainly transmitted *via* food
389 with only differences in tracer signatures are really informative (similar signatures could arise
390 from different combinations of different prey).

391 Identifying the limitations of the study is necessary to delineate its range of validity. Sampling
392 from stranded individuals does not often allow examination of inter-annual or seasonal
393 variation since it is very unlikely that sufficient individuals covering all seasons over several
394 consecutive years are available. However, and despite the potential biases of the sampling
395 regime, the stranded and by-caught animals used in this study reflects the ecology of the
396 different species in the study area and provide evidence of their distinct ecological niches.

397 Resource partitioning inferred from Cd concentrations

398 It is well-known that diet, size, weight, longevity and metabolic rates (i.e. ingestions and
399 assimilation) have an influence on Cd bioaccumulation and variations of concentrations
400 among species (Caurant et al. 1994; Aguilar et al. 1999; Das et al. 2003a). Thus, as shown
401 (Figs. 2 and 3), Cd is a metal which accumulates in cetacean tissues, but with different
402 accumulation rates according to the species. In common dolphin, the species for which we
403 had the largest sample size, concentrations increased with age up to around 10 years old, after
404 which concentrations reached a plateau (Fig. 2a). Similar results are well-documented in the
405 literature for several marine mammal species (Caurant et al. 1994; Bustamante et al. 2004;
406 Lahaye et al. 2006) and this pattern seems to be the result of an equilibrium between
407 absorption and excretion in the animals and not due to a shift in diet with time. These results
408 emphasize the need to take age into account when carrying out comparison between species.

409 Differences in Cd concentrations between areas have already been reported in several marine
410 mammal species. As an example, in common dolphin from the Bay of Biscay, the
411 consumption of cephalopods appeared to be a major route of exposure to Cd and the use of
412 Cd as a tracer confirmed the existence of dietary segregation between oceanic and neritic
413 common dolphins over a long time scale (Lahaye et al. 2005). In the present study, Cd
414 concentrations in both liver and kidney differentiated pilot whale and striped dolphin from the
415 other three species (Table 3). High Cd concentrations in tissues of both species are consistent
416 with their teuthophagous feeding habits. In the NWIP, pilot whales mainly feed on neritic
417 and/or benthic cephalopods such as common and curled octopuses *Octopus vulgaris* and
418 *Eledone cirrhosa* (González et al. 1994; Pierce et al. 2007; Santos et al. In press). However,
419 striped dolphin feeds on both cephalopods (mainly *Gonatus* sp. and ommastrephids) and fish
420 (including blue whiting *Micromesistius poutassou*, scads *Trachurus trachurus*, sand smelt
421 *Atherina presbyter* and silvery lightfish *Maurolicus muelleri*, Santos et al. 2007b) as well as
422 on crustaceans (specifically pelagic shrimp species, Jose Cedeira pers comm). Therefore, their
423 fish consumption could explain their lower Cd concentrations (Table 3) in comparison with
424 pilot whales.

425 Conversely, bottlenose dolphins and harbour porpoises are mainly fish feeders (Santos et al.
426 2007a, b) and in this area, harbour porpoise is mainly a coastal species (López et al. 2002;
427 Pierce et al. 2010). This can explain the significantly lower Cd concentrations found in
428 harbour porpoise compared to the main teuthophagous species over a medium and long time-
429 scale, and the absence of differences between porpoises and bottlenose dolphin at any time-
430 scale. This last result suggests that trophic competition can occur between these two species
431 as reported in adjacent areas of the Northeast Atlantic by Spitz et al. (2006). However,
432 consumption of different prey species, revealed by stomach contents analyses carried out on

433 stranded Iberian Peninsula porpoises and bottlenose dolphins (Santos et al. 2001, 2007a, b),
434 would mitigate the competition in this area (discussed below).

435 The low hepatic and renal Cd concentrations recorded for common dolphin suggests a lower
436 proportion of cephalopods in its diet than expected (Evans 1994; Santos et al. In press; Table
437 3). Significant differences were found between common dolphin and pilot whale, over a
438 medium time-scale (hepatic concentrations), and with striped dolphin, over both medium
439 (hepatic) and long (renal) time-scales, indicating that segregation occur among these species
440 even though common dolphin also frequents oceanic habitats.

441 Spatial and trophic segregation inferred from stable isotopes

442 Results on $\delta^{13}\text{C}$ values obtained in the present study are generally in agreement with the
443 habitat preferences inferred from direct observations and/or from habitat modeling carried out
444 in the study area for some of the study species (López et al. 2004; Pierce et al. 2010; Spyrakos
445 et al. 2011).

446 The $\delta^{13}\text{C}$ values in the tissue analyzed (i.e. muscle and teeth) allowed a good differentiation of
447 the most oceanic from the most coastal species. Thus, the significantly lower $\delta^{13}\text{C}$ values
448 exhibited in striped and common dolphins compared to the other species confirm, over
449 medium and long time-scales, the mostly oceanic distribution observed for both species in this
450 area. Striped dolphin is most frequently seen over depths of 100-500 m along both the western
451 and northern coasts (López et al. 2002; Spyrakos et al. 2011). Common dolphin is the most
452 abundant cetacean in the NWIP (Aguilar 1997; López et al. 2004) and mainly found in waters
453 deeper than 200m depth (Syrakos et al. 2011). Despite this, common dolphin is the second
454 most frequently sighted species from the coast, albeit seen most often in areas where the shelf
455 is narrower (Pierce et al. 2010). This characteristic would explain their low and intermediate
456 $\delta^{13}\text{C}$ values, between those of striped dolphin and the other toothed whales studied (Fig. 4).
457 This information could suggest that common dolphins move following pelagic schooling fish

458 in the area (such as sardine and blue whiting; Moura et al. 2012; Santos et al. In press) and, as
459 a consequence, seasonal overlap and/or competition or habitat with striped dolphins may
460 occur.

461 Based on $\delta^{13}\text{C}$ values, bottlenose dolphin, harbour porpoise and pilot whale did not show
462 significant differences from each other over medium and long time-scales but showed
463 significantly high $\delta^{13}\text{C}$ values than common and striped dolphins (Fig. 4). Coastal sightings
464 suggest that bottlenose dolphin is associated with coastal areas where the continental shelf is
465 relatively wide and productivity relatively high (Pierce et al. 2010) but this species is also
466 seen in offshore waters (López et al. 2004). Recent studies revealed two ecologically and
467 genetically distinct groups of bottlenose dolphins among strandings in Galicia (northern part
468 of the NWIP), which is consistent with the existence of both inshore and offshore groups of
469 bottlenose dolphin (Fernández et al. 2011a, b). Thus the high variability obtained in our
470 isotopic $\delta^{13}\text{C}$ values for bottlenose dolphin may be due to the presence of some offshore
471 individuals in our sampling (Fig. 4). Again based on coastal sightings, harbour porpoise tend
472 to be seen where the shelf is narrower while boat-based sightings studies suggest association
473 with water depths of 100-200m (Spyrakos et al. 2011).

474 Although the pilot whale is essentially known as oceanic and deep water feeder, it shows
475 some degree of dietary plasticity and can apparently forage successfully in both oceanic and
476 neritic habitats (Spitz et al. 2011). This fact, together with the age/maturity of sampled
477 animals, might explain the high muscular and dental $\delta^{13}\text{C}$ values obtained in this study.
478 Nitrogen isotopic signatures are the main source of information on feeding habitat and on
479 resource utilization and trophic positions (TP) of the marine mammals in the food web. Here
480 we used the TP obtained in Mèndez-Fernandez et al. (2012) complementing $\delta^{15}\text{N}$ values
481 obtained from hard tissues, i.e. long-term information, to compare species showing overlap in

482 $\delta^{13}\text{C}$ values and/or Cd concentrations, i.e. living in the same habitat and feeding in the same
483 type of prey.

484 The age effect on muscular $\delta^{15}\text{N}$ values was previously tested for common dolphin (Fig. 6)
485 and showed a negative relationship. Several studies found the same negative effect of age (or
486 body length) on $\delta^{15}\text{N}$ values. In younger animals, this is consistent with individuals switching
487 from primarily feeding on milk to individuals primarily feeding on living prey (Hobson et al.
488 1997; Das et al. 2003b; Knoff et al. 2008; Fernández et al. 2011a; Meissner et al. 2011).
489 Additionally, it was demonstrated that the consumption of blue whiting, one of the main prey
490 of common dolphin in the Iberian Peninsula, increased with (post-weaning) dolphin body
491 length (Fernández et al. 2011a, Santos et al. In press). Since blue whiting have low $\delta^{15}\text{N}$
492 values (Méndez-Fernandez et al. 2012), the decrease of $\delta^{15}\text{N}$ values with common dolphin age
493 makes sense (Fig. 6).

494 The comparison between species showed that striped dolphins exhibited the lowest $\delta^{15}\text{N}$
495 values in muscle and teeth, revealing the low TP of this species and its oceanic habitat (Table
496 3). The presence of crustaceans and oceanic fish species (which usually showed low TP in the
497 food web) may be the main reason for their low TP. Therefore, striped dolphin is well
498 segregated from the other four species in the trophic dimension as well as in the spatial
499 dimension (Fig. 4). The higher $\delta^{15}\text{N}$ values in common dolphin compared to striped dolphin,
500 over medium and long time-scales, are consistent with its more strongly piscivorous feeding
501 habits as its higher presence in coastal waters. However, these values were still low in
502 comparison with the other toothed whale species (Table 3), probably as the consequence of
503 feeding on fish with a low TP such as blue whiting and sardine *Sardina pilchardus* (Méndez-
504 Fernandez et al. 2012), the most important prey of common dolphin in Galician waters
505 (Santos et al. In press). According to its $\delta^{15}\text{N}$ values, common dolphin is not significantly
506 different from pilot whale and one might conclude that there is a large overlap between their

507 diets, if Cd concentrations (this study) did not contradict this, by confirming the higher
508 occurrence of cephalopods in pilot whale diet (Pierce et al. 2007; Spitz et al. 2011; Santos et
509 al. In press). Furthermore and as discussed above, pilot whales exhibit some degree of dietary
510 plasticity allowing them to forage successfully in both oceanic and neritic habitats (Spitz et al.
511 2011). This dietary plasticity can also explain their relatively high $\delta^{15}\text{N}$ values and the
512 variability obtained, and might result from a distribution which shifts seasonally between
513 oceanic and neritic habitats. In the present study, we have insufficient samples of this species
514 to confirm a seasonal trend in isotopic composition. Data from coastal sightings are also
515 limited but 5 out of 6 sightings of the species during 2003-07 were during the months
516 September to November, which would be consistent with seasonal use of coastal waters
517 (Pierce et al. 2010; unpubl data).

518 Bottlenose dolphin and harbour porpoise exhibited elevated $\delta^{15}\text{N}$ values, with harbour
519 porpoise showing significantly higher values in teeth compared to the other species (Table 3),
520 indicating that they feed on prey with a high TP and located at more coastal areas on a long-
521 term basis. Thus, scad, pouting *Trisopterus luscus* and garfish *Belone belone* were identified
522 as the most important prey in their diet (Santos et al. 2004, 2007b; Pierce et al. 2010) and
523 these prey also exhibit high $\delta^{15}\text{N}$ values (Méndez-Fernandez et al. 2012). Bottlenose dolphin
524 is slightly more generalist and its main prey, in terms of both biomass and number, are blue
525 whiting and hake *Merluccius merluccius* of less than 30 cm length (Mahe et al. 2007; Santos
526 et al. 2007a), which exhibit lower $\delta^{15}\text{N}$ values than harbour porpoise prey (Méndez-Fernandez
527 et al. 2012).

528 Time integration of ecological tracers

529 Ecological tracers were analyzed in tissues with different rates of turnover and results thus
530 gave us access to different periods of integration. However, sampling did not give us the
531 opportunity to study segregation over the whole year, except for the common dolphin, and the

532 variations which may occur between seasons. Foraging niche segregation probably depends
533 on the availability of resources in the area. The NWIP is an upwelling area which is
534 characterized by high biological productivity (Fraga 1981) and where primary production,
535 biomass and phytoplankton species composition are influenced by this hydrographic
536 perturbation, which can cause large variations in nutrient availability (González et al. 1979;
537 Tenore et al. 1995). Therefore we expected to find differences in the segregation of these
538 species according to the time of year. Despite the possible seasonal movements demonstrated
539 for common dolphin (Fig. 5a), this species is well-separated from striped dolphin by its $\delta^{13}\text{C}$
540 isotopic composition over a medium time-scale, $\delta^{15}\text{N}$ isotopic composition and Cd
541 concentrations. Thus, over a long time-scale both species mostly share the same habitat but
542 feed on different resources. The other species for which results were highly influenced by the
543 time period of integration is the harbour porpoise. Only dental $\delta^{15}\text{N}$ isotopic composition
544 discriminate harbour porpoise from bottlenose dolphin, the most similar species in terms of
545 ecological niche, which means that although both species can share the same coastal habitat
546 and type of prey, they feed on resources at different TP in the long-term. Such foraging
547 segregation might allow their co-existence in NWIP waters.

548 Conclusions

549 In this work we studied the three main dimensions of the ecological niche of five toothed
550 whale species through the analyses of different ecological tracers in different soft and hard
551 tissues, to test whether there is niche segregation to avoid competition among these five
552 toothed whales which frequent the NWIP waters. Over a medium time-scale period of
553 integration, ecological tracers did not reveal a complete segregation among the five species.
554 Thus, the harbour porpoise and bottlenose dolphin could face competition for habitat in
555 waters off the NW Iberian Peninsula. However, integrating information given by long-term

556 ecological tracers showed complete ecological niche segregation among all species (see Fig.
557 7). We hypothesize the following conceptual scheme to sum up our results:

558 1 – Harbour porpoise has a coastal foraging niche with the highest trophic position among the
559 five species.

560 2 – Bottlenose dolphin has the most similar foraging niche to harbour porpoises but its lower
561 trophic position suggests different targeted prey and/or the use of offshore areas.

562 3 – Common dolphin and pilot whale can forage in both oceanic and neritic waters as shown
563 by their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope ratios but the renal cadmium concentrations revealed a
564 dietary difference (fish-based vs cephalopod-based, respectively).

565 4 – The striped dolphin showed the most oceanic ecological niche.

566 Consequently, the present work provides useful indications on trophic and habitat preferences
567 in toothed whales that frequent the NWIP and demonstrates that ecological tracers provide a
568 relatively simple way to quantify ecological niche differences over different time-scales,
569 especially when looking at closely related species within a common area. However, there is a
570 need for a larger sample sizes and a stronger representation of older animals to strengthen
571 these conclusions.

572

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Table 1 Summary of numbers of samples collected per species, year and tissue from cetaceans stranded and by-caught in the North West of the Iberian Peninsula.

Species	Number of samples			
	Muscle	Teeth	Kidney	Liver
Common dolphin <i>Delphinus delphis</i>	103	98	101	101
2004	4	3	4	4
2005	16	17	16	16
2006	12	12	11	12
2007	41	39	41	40
2008	30	27	29	29
Harbour porpoise <i>Phocoena phocoena</i>	17	15	15	15
2004	5	5	5	4
2005	1	1	1	1
2006	3	3	3	3
2007	5	3	3	4
2008	3	3	3	3
Bottlenose dolphin <i>Tursiops truncatus</i>	8	8	8	8
2004	1	1	1	1
2005	2	2	2	2
2006	3	3	3	3
2007	2	2	2	2
Striped dolphin <i>Stenella coeruleoalba</i>	18	20	18	18
2004	2	1	2	2
2005	4	4	4	4
2006	3	3	3	3

2007	6	9	6	6
2008	3	3	3	3
Long-finned pilot whale <i>Globicephala melas</i>	9	3	9	8
2004	4	0	4	3
2006	1	1	1	1
2007	2	2	2	2
2008	2	0	2	2

Table 2 Results of the GAM models for explaining common dolphin (*Delphinus delphis*) tracers of the North West of the Iberian Peninsula. Explanatory variables, deviance explained and Akaike Information Criterion (AIC) value for each model are given. Significance level of variables is indicated by asterixes: *P < 0.05; **P < 0.01; ***P < 0.001; ns: not significance. Final models chosen are highlighted in bold.

Tracer	Variables	Significance	AIC	Deviance explained
Renal Cd	CdK ~ s(Age, k = 4) + s(Month, k = 4) + Year	ns	135.2	39.1%
	CdK ~ s(Age, k = 4) + s(Month, k = 4)	ns	133.9	38.7%
	CdK ~ s(Age, k = 4)	***	133.6	37.9%
Hepatic Cd (CdL)	CdL ~ s(Age, k = 4) + s(Month, k = 4) + Year	ns	114.2	47.5
	CdL ~ s(Age, k = 4) + s(Month, k = 4)	ns	112.2	47.5%
	CdL ~ s(Age, k = 4)	***	110.3	47.4%
$\delta^{13}\text{C}$ Muscle ($\delta^{13}\text{CM}$)	$\delta^{13}\text{CM} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)} + \text{Year}$	ns	119.8	34.9%
	$\delta^{13}\text{CM} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)}$	ns	121.1	32.4%
	$\delta^{13}\text{CM} \sim \text{s(Month, k = 4)}$	***	122.8	29.8%
$\delta^{13}\text{C}$ Teeth ($\delta^{13}\text{CT}$)	$\delta^{13}\text{CT} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)} + \text{Year}$	ns	111	26.9%
	$\delta^{13}\text{CT} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)}$	ns	109.5	26.5%
	$\delta^{13}\text{CT} \sim \text{s(Month, k = 4)}$	***	115.8	20%
$\delta^{15}\text{N}$ Muscle ($\delta^{15}\text{NM}$)	$\delta^{15}\text{NM} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)} + \text{Year}$	ns	151.5	26%
	$\delta^{15}\text{NM} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)}$	ns	149.8	25.9%
	$\delta^{15}\text{NM} \sim \text{s(Age, k = 4)}$	***	151.9	19.7%
$\delta^{15}\text{N}$ Teeth ($\delta^{15}\text{NT}$)	$\delta^{15}\text{NT} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)} + \text{Year}$	ns	162	52.4%
	$\delta^{15}\text{NT} \sim \text{s(Age, k = 4)} + \text{s(Month, k = 4)}$	ns	163.1	50.8%
	$\delta^{15}\text{NT} \sim \text{s(Age, k = 4)}$	***	161.3	50.7%

Table 3 Age (mean \pm SD, in years), carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values (mean \pm SD, ‰) and cadmium (Cd) concentrations (mean \pm SD, $\mu\text{g g}^{-1}$ wet weight, w.wt) in different tissues of the toothed whale species collected along the North West of the Iberian Peninsula. Ranges (minimum, maximum) are presented in parentheses. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values in muscle tissue are from Mèndez-Fernandez et al. (2012).

Species	Age	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Cd	
		Muscle	Teeth	Muscle	Teeth	Liver	Kidney
Common dolphin <i>Delphinus delphis</i>	6.1 \pm 5.3 (0, 20)	-17.0 \pm 0.5 (-18.1, -16.0)	-14.3 \pm 0.5 (-15.6, -13.4)	11.7 \pm 0.6 (10.1, 13.6)	13.0 \pm 0.8 (11.3, 15.2)	0.4 \pm 0.5 (< 0.01, 2.9)	2.3 \pm 2.7 (< 0.01, 16.4)
Harbour porpoise <i>Phocoena phocoena</i>	5.4 \pm 6.1 (0, 18)	-16.5 \pm 0.7 (-17.6, -15.1)	-13.7 \pm 0.7 (-14.7, -12.4)	13.0 \pm 1.2 (11.5, 17.1)	15.5 \pm 0.6 (14.4, 16.2)	0.1 \pm 0.1 (< 0.01, 0.4)	2.2 \pm 5.3 (0.09, 19.0)
Bottlenose dolphin <i>Tursiops truncatus</i>	4.3 \pm 2.0 (0.5, 7)	-16.5 \pm 0.8 (-17.3, -15.2)	-13.8 \pm 0.8 (-14.8, -12.3)	12.6 \pm 0.9 (11.3, 14.0)	13.7 \pm 1.0 (11.6, 15.1)	1.2 \pm 2.8 (0.01, 8.2)	5.7 \pm 13.8 (0.15, 39.8)
Striped dolphin <i>Stenella coeruleoalba</i>	4.1 \pm 5.0 (0, 15)	-17.6 \pm 0.6 (-18.5, -16.5)	-14.6 \pm 0.4 (-15.5, -13.8)	10.8 \pm 0.7 (9.8, 12.4)	12.4 \pm 0.8 (10.8, 14.9)	3.9 \pm 3.8 (0.04, 13.2)	10.3 \pm 11.0 (0.1, 40.7)
Long-finned pilot whale <i>Globicephala melas</i>	7.4 \pm 5.0 (0, 14)	-16.5 \pm 0.5 (-17.3, -15.7)	-13.5 \pm 0.8 (-14.4, -13.0)	12.2 \pm 0.6 (11.0, 13.3)	13.6 \pm 0.5 (13.3, 14.3)	8.3 \pm 8.4 (0.01, 22.2)	30.0 \pm 26.9 (< 0.01, 79.3)

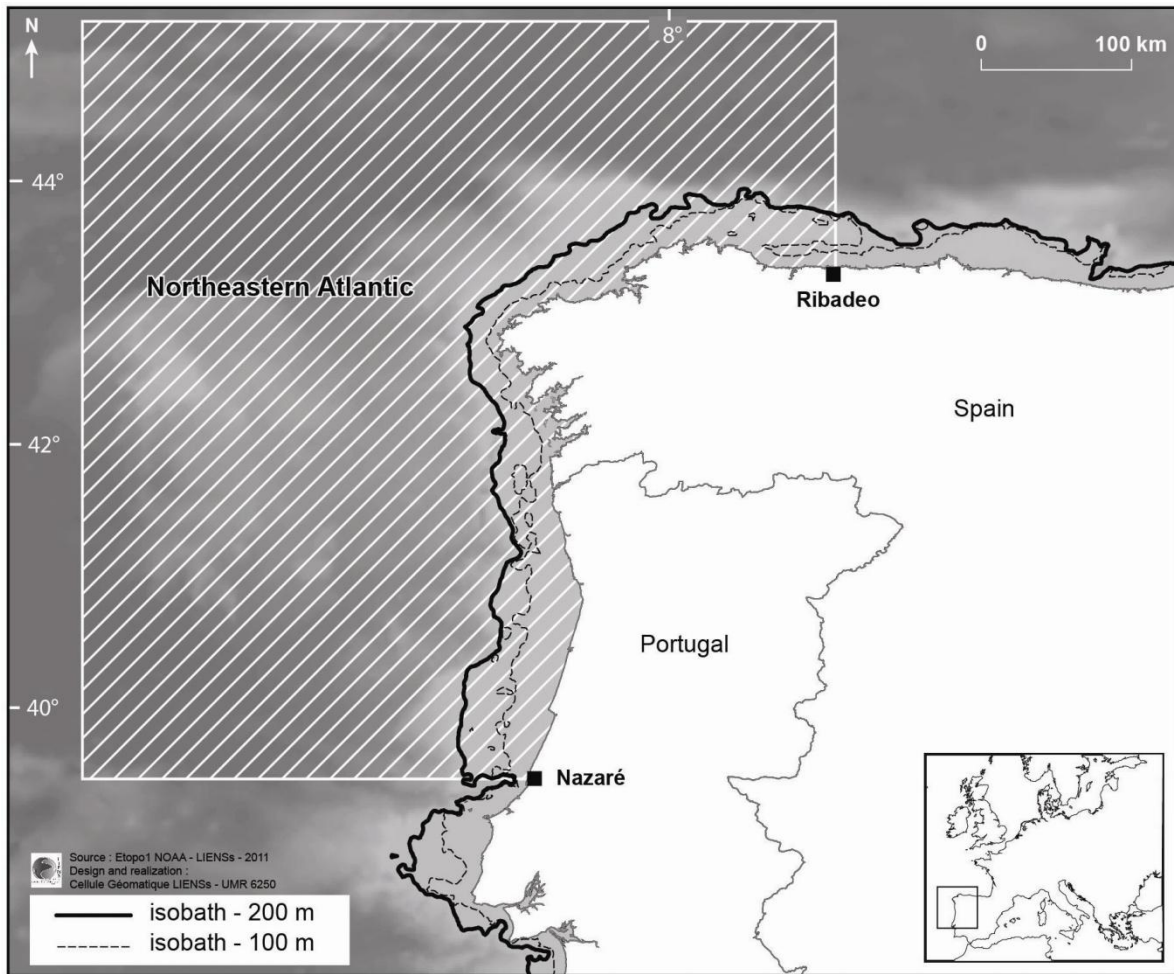


Figure 1 Map of the sampling area with 100 and 200 m isobaths. The 200 m isobaths is taken as the limit for the shelf-break. The sampling area is framed in white, representing the north and south limits for the strandings and the western latitude of the by-catches.

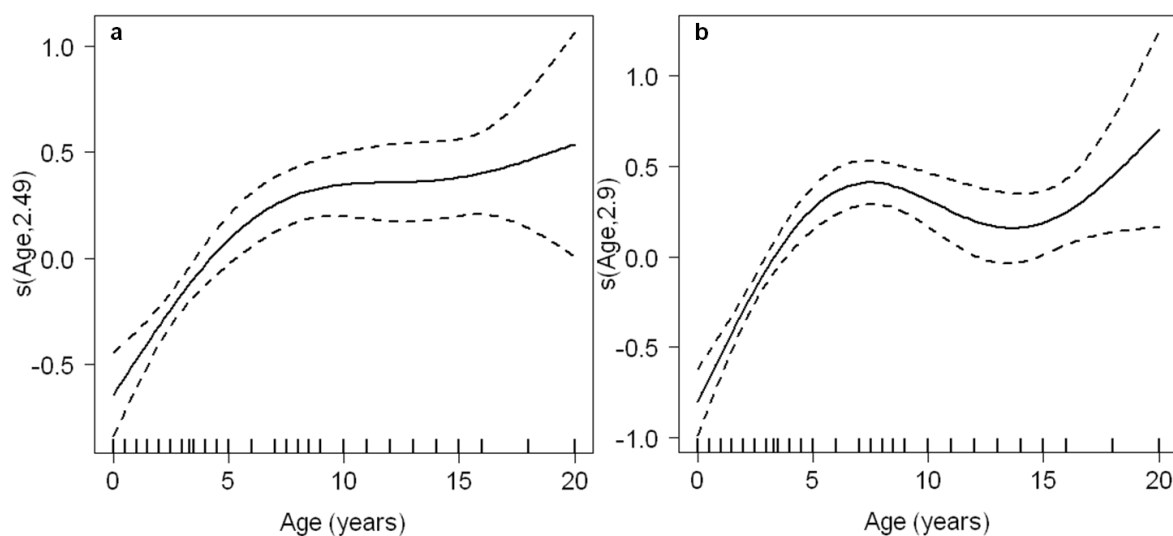


Figure 2 Smoothers for effects of age on Cd concentrations ($\mu\text{g g}^{-1}$ w.wt) in kidney (a) and in liver (b) of common dolphin *Delphinus delphis*. The y-axis shows the contribution of the smoother to the predictor function (in arbitrary units). Smoothers illustrate the partial effect of age, i.e. the effect of age once the effects of all other explanatory variables in the model have been taken into account. Tick marks in x-axis represent sampled individuals. Dashed lines represent 95% confidence bands for the smoothers.

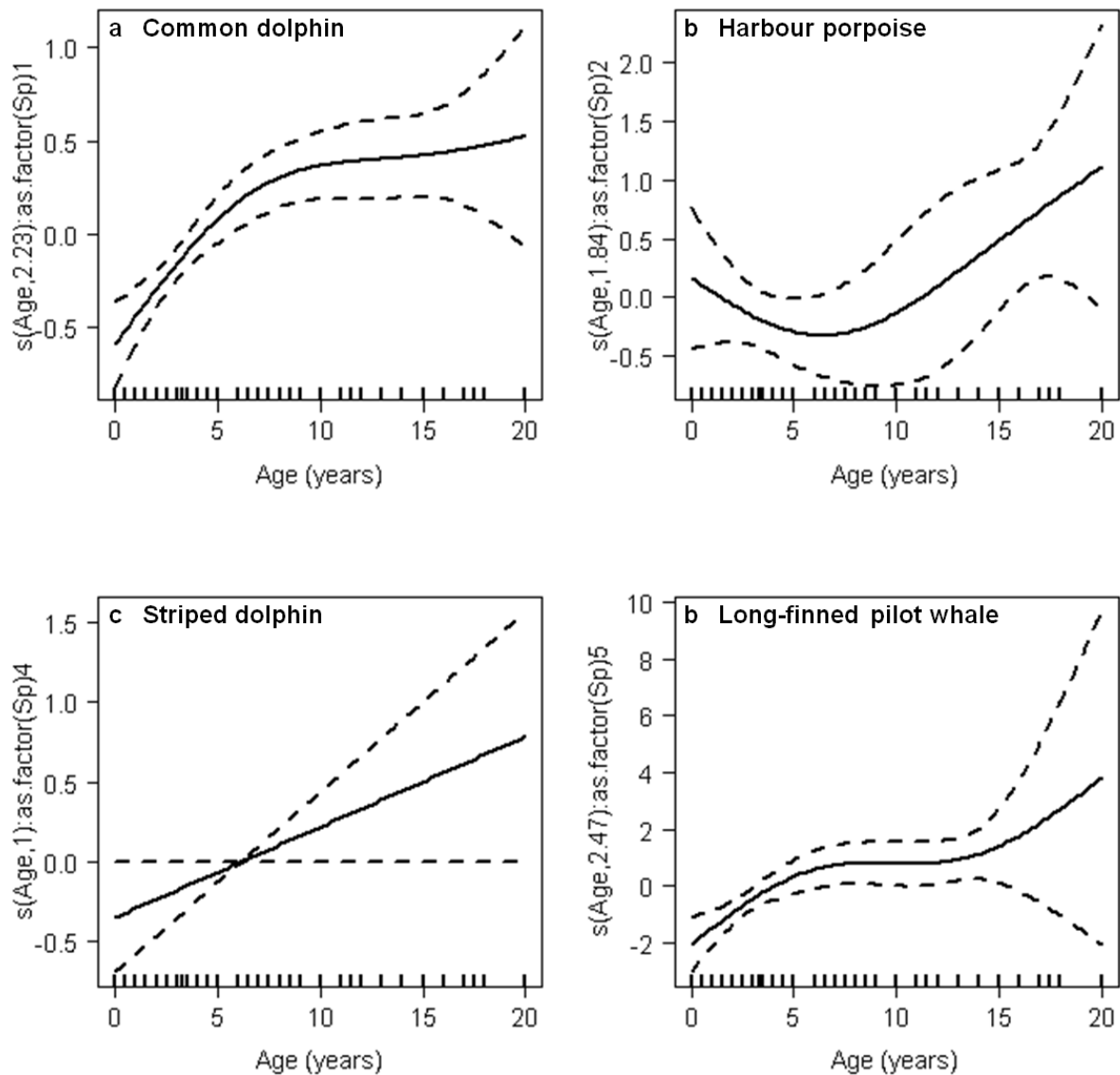


Figure 3 Smoothers for between species differences of age-corrected accumulation of Cd concentrations in kidney ($\mu\text{g g}^{-1}$ w.wt) of common dolphin *Delphinus delphis* (a) harbour porpoise *Phocoena phocoena* (b) striped dolphin *Stenella coeruleoalba* (c) and pilot whale *Globicephala melas* (d). The y-axis shows the contribution of the smoother to the predictor function (in arbitrary units). Smoothers illustrate the partial effect of age, i.e. the effect of age once the effects of all other explanatory variables in the model have been taken into account. Tick marks in x-axis represent sampled individuals. Dashed lines represent 95% confidence bands for the smoothers.

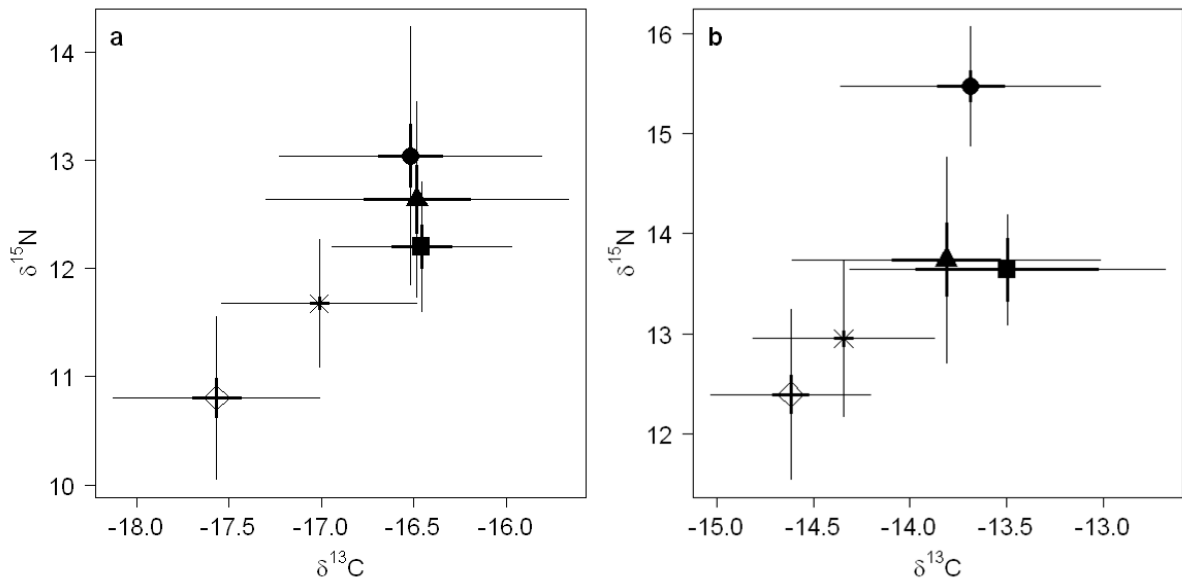


Figure 4 Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values in muscle tissue (a) and in teeth (b) of common dolphin *Delphinus delphis* (*), harbour porpoise *Phocoena phocoena* (●), bottlenose dolphin *Tursiops truncatus* (▲), Striped dolphin *Stenella coeruleoalba* (◇) and long-finned pilot whale *Globicephala melas* (■). Data are mean (‰) \pm SD and SEM (bold). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values in muscle from Mèndez-Fernandez et al. (2012).

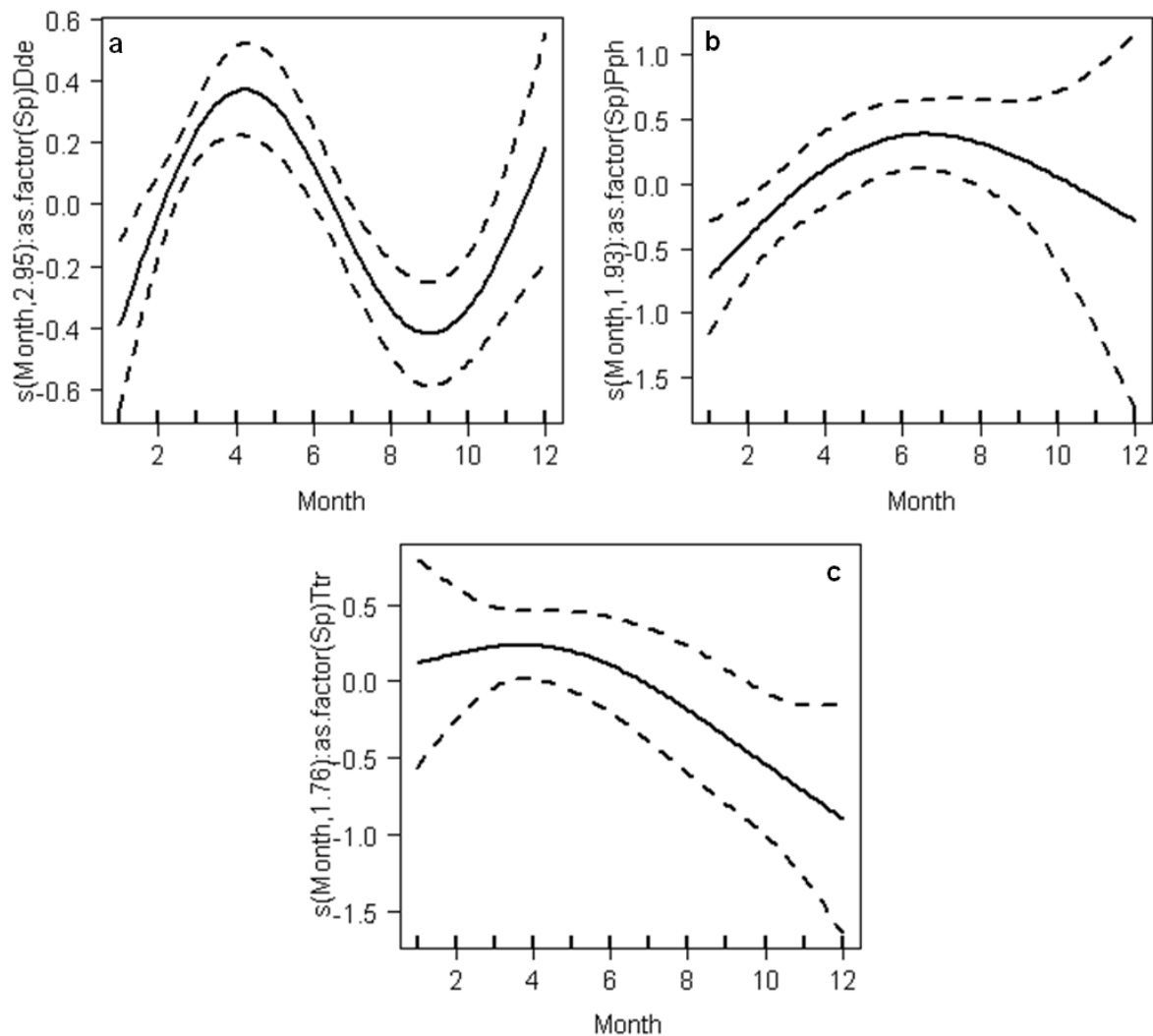


Figure 5 Smoothers for between species differences of season-adjusted effects on $\delta^{13}\text{C}$ values in muscle of common dolphin *Delphinus delphis* (a) harbour porpoise *Phocoena phocoena* (b) and bottlenose dolphin *Tursiops truncatus* (c). The y-axis shows the contribution of the smoother to the predictor function (in arbitrary units). Smoothers illustrate the partial effect of season once the effects of all other explanatory variables in the model have been taken into account. Tick marks in x-axis represent sampled individuals. Dashed lines represent 95% confidence bands for the smoothers.

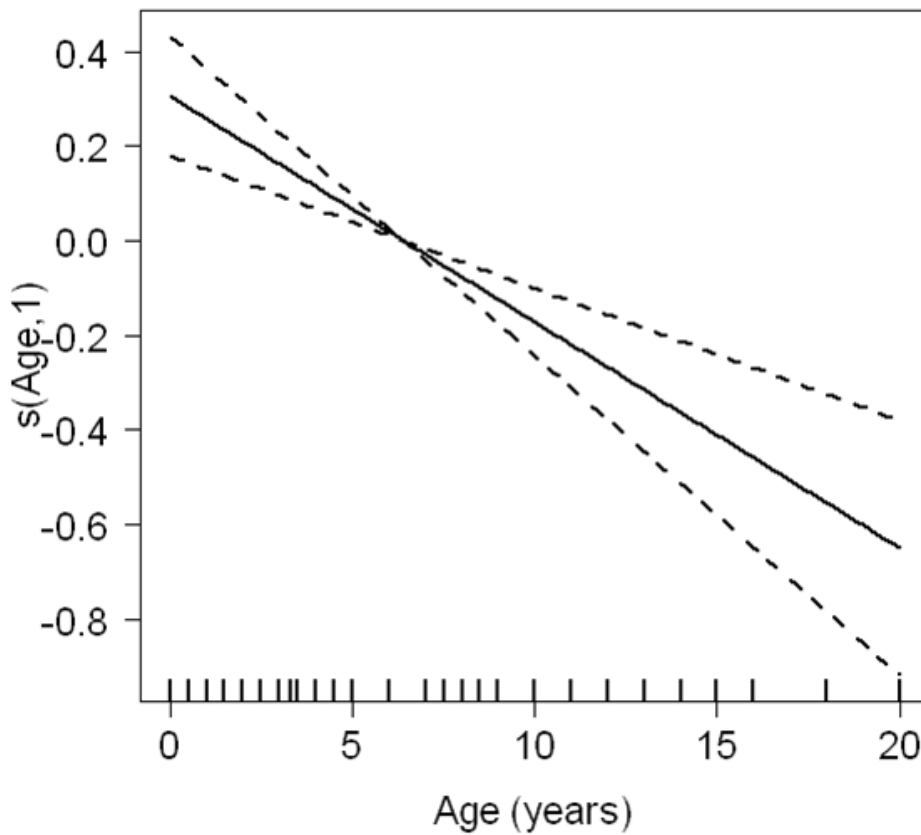


Figure 6 Smoothers for effects of age on $\delta^{15}\text{N}$ values in muscle of common dolphin *Delphinus delphis*. The y-axis shows the contribution of the smoother to the predictor function (in arbitrary units). Smoothers illustrate the partial effect of age once the effects of all other explanatory variables in the model have been taken into account. Tick marks in x -axis represent sampled individuals. Dashed lines represent 95% confidence bands for the smoothers.

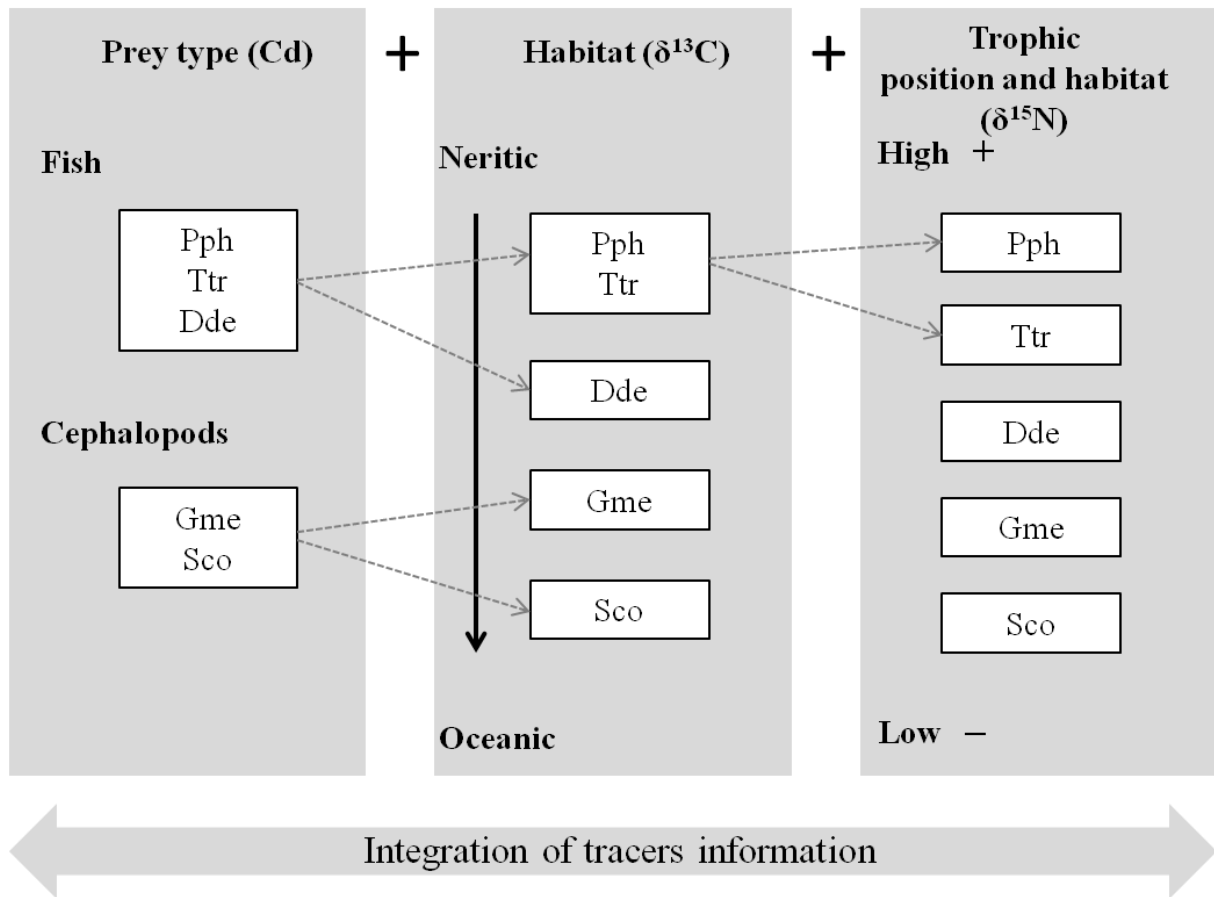


Figure 7 Conceptual scheme of foraging niche segregations obtained by the sum of the information given by ecological tracers' in the long-term (i.e. several years) and in the five toothed whale species. Dde: common dolphin *Delphinus delphis*, Pph: harbour porpoise *Phocoena phocoena*, Ttr: bottlenose dolphin *Tursiops truncatus*, Sco: striped dolphin *Stenella coeruleoalba* and Gme: pilot whale *Globicephala melas*. Ecological tracer values of species lumped together were no significantly different (Tukey test, $P > 0.05$).