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Prey selection by the common dolphin: fulfilling high energy requirements with high quality food

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17

18 ABSTRACT

Which characteristics define the prey species constituting the diet of a given predator? 19 Answering this question would help predict a predator's diet and improve our understanding 20 of how an ecosystem functions. The aim of this study was to test if the diet of common 21 dolphins, Delphinus delphis, in the oceanic Bay of Biscay reflected prey availability or a 22 selection shaped by prey energy densities (ED). To do this, the community of potential prey 23 species, described both in terms of relative abundance and energy densities, was compared to 24 the common dolphin diet in this area. This analysis of a predator's diet and its prey field 25 26 revealed that the common dolphin selected its diet on the basis of prey energy densities (significant values of Chesson's index for ED>5kJ.g⁻¹). High-energy prey were positively 27 selected in the diet [e.g. Notoscopelus kroeyeri, ED=7.9 kJ.g⁻¹, 9% of relative abundance in 28

the environment (%Ne); 62% of relative abundance in the diet (%Nd)] and low-energy prey disregarded (*Xenodermichthys copei*, ED=2.1kJ.g⁻¹, 20%Ne, 0%Nd). These results supported the hypothesis that common dolphins selected high energy density prey species to meet their energetically expensive life style and disregard prey organisms of poor energy content even when abundant in the environment.

34

35 *Keyworld:* field of prey; energy density; active prey selection; trophic *cul-de-sac*

36

37 **1. Introduction**

Beyond the simple description of the diet, a major ecological issue is also to understand its ecological significance: why does the observed array of prey species compose the diet of a given predator? What are the prey key traits for this predator? Answering this would help predict a predator's diet and its variations according to the availability of prey functional traits, improve our understanding of ecosystem functioning and anticipate the consequences of possible changes.

The optimal foraging theory (OFT) is a classical paradigm used to explain or even 44 predict the diet of a forager (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976). In 45 initial studies placed in the OFT framework, some predictions depended on unrealistic 46 assumptions and OFT was a much debated theory (Zach and Smith, 1981; Stephen and Krebs, 47 1986; Pierce and Ollason, 1987). However, numerous studies provided results which matched 48 quantitatively or qualitatively OFT predictions (Sih and Christensen, 2001). Today, three 49 major robust and fundamental predictions are commonly assumed (Stephens and Krebs, 1986; 50 Sih and Christensen, 2001): (1) predators should prefer prey that yield more energy compared 51 to foraging costs, (2) as abundance of higher profitable prey species increases in the 52 environment, lower profitable prey should be dropped out from the diet and predators should 53

54 become more specialised, and (3) foragers should obey a quantitative threshold rule for when 55 specific prey types should be included or excluded from an optimal diet. Thus, predators have 56 to develop an adapted foraging strategy related with their specific energy requirements.

From killer whales eating marine mammals to herbivorous dugong, marine mammals 57 exhibit a broad range of biological models and have developed diverse feeding strategies 58 (Berta and Sumich, 1999). But, some species, particularly small cetaceans and pinnipeds, are 59 often described as opportunistic feeders: predators which consume their prey without 60 selection, *i.e.* proportionately to their availability in the environment. Contrastingly, active 61 prey choice by marine mammals has rarely been actually tested. The difficulty to describe the 62 63 prey field exposed to a predator species (species diversity and abundance, distributions, energy contents...) is an important limitation in such investigations (e.g. Santos and Pierce, 64 2003). 65

The common dolphin Delphinus delphis is the most abundant delphinid in offshore warm-66 temperate waters in the Atlantic (Perrin, 2002). This small delphinid is likely an energetically 67 expensive biological model because it is fairly small among cetaceans and a very active 68 swimmer, both of these characteristics being associated with high metabolic costs per unit 69 body mass (Berta and Sumich, 1999; Costa and Williams, 1999). In the Bay of Biscay, 70 common dolphin feed preferentially on small schooling pelagic fish: scads Trachurus spp., 71 pilchard Sardina pilchardus, anchovy Engraulis encrasicolus and mackerels Scomber 72 scombrus. Between seasons or years, the specific composition of its diets can change 73 significantly (Meynier et al., 2008), but, if the proximate composition of forage species was 74 considered (Spitz et al., 2010), dolphins seemed always to switch from a fat and high-quality 75 prey species to another high-quality prey species. Low-quality prey would be neglected; 76 indeed several of them, such as gadids, are very abundant in the area (Poulard and Blanchard, 77 2005), but never constitute a measurable share of the common dolphin diet (Meynier et al., 78

2008). Hence, prey selection by common dolphins based on prey energy densities was suggested to occur in this neritic habitat. Recently and for the first time in a fully oceanic area, the diet of common dolphins off the Bay of Biscay was shown to be largely constituted of myctophids (Pusineri et al., 2007). By comparison with other predators studied in the same area and collected in the same condition, *i.e.* living in the same prey field, it appeared that similarly-sized pelagic predators such as blue shark, *Prionace glauca*, or swordfish, *Xiphias gladius*, ate larger and probably leaner prey types (Pusineri et al., 2008).

The present study aimed at testing if, within the fish prey field available to top predators, common dolphins would select the most profitable food sources, *i.e.* high energy density prey, to fulfil their high energy requirements. To investigate this issue, we compared the composition of the community of potential dolphin prey species off the Bay of Biscay, both in terms of relative abundance and energy density with the diet of common dolphins in order to test if the diet reflected prey availability or a selection shaped by prey energy densities.

93

94 **2. Materials and methods**

95

96 2.1. Composition of the epi- and mesopelagic fish community

97

The epi- to mesopelagic oceanic fish community off the Bay of Biscay was investigated during EVHOE (*EValuation des ressources Halieutiques de l'Ouest Européen*) research cruises onboard the R/V *Thalassa* in October 2002, 2003 and 2008. Fourteen hauls were performed with a 25 m vertical opening pelagic trawl. The mesh size decreases gradually from 76 mm to 44 mm in the bag. The trawl-haul duration was one hour at 4 kn. The hauls were carried out during the night at various depths supposedly accessible to dolphins from sub-surface to 500 m deep off the continental slope from $43.91-46.60^{\circ}$ N and $2.40-5.11^{\circ}$ W (Table 1). Fish were counted and identified following published guides (*e.g.* Quéro et al., 2003).

107 The occurrence of a given species was the number of haul in which this species was 108 observed. The relative abundance was given by the number of individuals of the same species 109 found throughout the complete haul series. These two indices can be expressed by their 110 percentage frequency as percentage of occurrence (%O) and percentage by number (%N), 111 respectively.

112
$$%O_i = n_i / N*100$$

113 where n_i is the number of hauls where species *i* was found and N the total number of hauls;

114
$$\% N_i = x_i / X * 100$$

where x_i is the number of individuals belonging to species *i* and X the total number of fish caught.

117 Confidence intervals around relative abundance were generated by bootstrap 118 simulations. The bootstrapping routine was written by using the *R* software (Ihaka and 119 Gentleman, 1996). Random samples were drawn with replacement and the procedure was 120 repeated 1000 times.

121

122 2.2. Diet of common dolphin and energy content of prey species: origin of data

123

The dietary composition of common dolphin used in the present work comes from a previous analysis of stomach contents carried out from dolphins incidentally caught in tuna driftnet fisheries during the summers 1992-1993 off the Bay of Biscay (Pusineri et al. 2007; summary in Table 2). Briefly described, stomach contents from 63 common dolphins were analyzed by prey occurrence, number and mass, following standard methods (*e.g.* Ridoux, 129 1994, Spitz et al., 2006). The diet was dominated by myctophid fish, mostly *Notoscopelus*130 *kroeyeri*.

Quality of forage species from the Bay of Biscay was recently explored by analysis of proximate composition and energy content for a wide range of species including mesopelagic fish (Spitz et al., 2010; Table 3).

134

135 2.3. Comparison between diet and prey availability

136

The overlap between hauls and stomach contents was assessed by calculating the Pianka index of overlap on relative abundance data of fish species in the water *versus* in the diet (Pianka, 1973):

140
$$O = \frac{\sum p_{iA} p_{iB}}{\sqrt{\sum p_{iA}^2 \sum p_{iB}^2}}$$

141

where p_{iA} is the percentage by number of species *i* in hauls and p_{iB} is the percentage by number of the species *i* in the diet of the common dolphin. This index varies from 0 (no overlap) to 1 (complete overlap).

145

146 Prey selectivity was tested by using the Chesson's index (Chesson, 1978):

147
$$\alpha_{i_{(1\to m)}} = \frac{p_i r_i}{\sum p_i r_i}$$

where α_i is the selectivity for prey type *i*; r_i is the percentage by number of species *i* in the diet of the common dolphin; p_i percentage by number of species *i* in hauls and *m* is the total number of species found in hauls and in stomach contents. Values of α_i close to 1/m represent 151 feeding at random whereas values greater (*versus* smaller) than 1/m correspond to positive
152 (*versus* negative) selection of prey *i*.

153	Pearson's correlation tests between species abundance in the hauls versus in the diet
154	was performed to examine if the diet reflected prey availability (percentage by number >1%
155	either in diet or in hauls). Similar tests were carried out between Chesson's index of
156	selectivity and energetic density to investigate if prey choice was associated to prey quality.
157	All correlations were computed by using the <i>R</i> software (Ihaka and Gentleman, 1996).
158	
159	3. Results
160	
161	3.1. Composition of the epi- and mesopelagic fish community
162	
163	From the fourteen epi- to mesopelagic trawl hauls, 3258 fish were captured. The
164	pelagic fish community was composed of 26 species from 12 families. Three families
165	accounted for up to 88% of total number of fish caught (Table 4). The alepocephalid
166	Xenodermichtys copei was the most abundant species with a total contribution of 22.2%N,
167	95% non-parametric confidence interval being [12.9–32]. Myctophid fish were represented by
168	at least eight species and amounted to 44.5%N; among them Benthosema glaciale (17.2%N
169	[2.2-40]) and Notoscopelus kroeyeri (8.9%N [5.1-13.8]) were the most prevalent. The
170	sternoptychids were the third dominant family with three species identified: Argyropelecus
171	olfersii (11.3%N [4.6-21.8]), A. hemigymnus (3.4%N [0.6-8.2]) and Maurolicus muelleri
172	(6.6%N [0.1–18.1]). Lastly, the paralepid Arctozenus risso accounted for 8.1%N [3.7–14.2].

3.2. Comparison between diet and prey availability

Abundances of all other species were negligible.

A first approach to the comparison between common dolphin diet and prey availability 177 was by using the Pianka index of overlap which revealed a fairly low degree of overlap (<0.4) 178 between the two datasets. Similarly, no correlation (Pearson test, P>0.05) existed between 179 relative abundances of each prey species observed in hauls *versus* in stomach contents (Figure 180 1). Actually, the Chesson's index of selectivity suggested a positive selection by which 181 common dolphin would specifically target *M. punctatum*, *M. muelleri* and even more strongly 182 B. glaciale and N. kroeyeri (Table 5). All other species appeared to be negatively selected by 183 the predator. Finally, a significant correlation (Pearson test, P<0.005) was found between the 184 values of Chesson's index of selectivity and fish energy content (Figure 2), with all species 185 poorer than 5 kJ.g⁻¹ being negatively selected and the other being increasingly selected as 186 their energy content increased. 187

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189 4	4. D	iscus	sion
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191 4.1. General comments

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Prey choice or selection by marine predators is difficult to measure, especially in fully 193 oceanic area. The degree of selectivity or opportunism of such predators was often inferred 194 from dietary analyses only. For instance, predators showing a broad diversity in their diet or 195 feeding upon reportedly abundant prey species were classified as opportunistic feeders (e.g. 196 Bearzi et al., 2009). In combining results of stomach content analysis and description of prev 197 field, the present study revealed a strongly significant relationship between prey selection 198 indices and prey energy densities. Thus, common dolphins selected high energy density prey 199 species to face their energetically expensive life style and disregarded prey organisms poorer 200 than 5 kJ.g⁻¹ even when abundant in the environment. 201

Both stomach content analysis and trawling are subject to their own selectivity and 202 203 biases which could affect our perception of dolphin diets and fish abundance. The representativeness of diet described by stomach content analysis was often subject to the 204 difficulty of controlling the sampling design and to the differential digestion of ingested prey 205 (e.g. Tollit et al., 1997; Pierce et al., 2007). Especially for protected species such as marine 206 mammals, the dietary results were often limited by the size, the spatio-temporal coverage, or 207 208 for instance, the age/sex/reproductive status composition of the individuals providing the stomach content sample set. In spite of these limitations, however, stomach content analysis is 209 still the best and most widely used approach to investigate marine top predator diets and 210 211 provide the most detailed information on prey composition. On the other hand, the representativeness of a fish community described from trawling survey is equally affected by 212 sampling design (*i.e.* number of trawls, spatio-temporal coverage, immersion/depth/daytime 213 214 stratification,...) and the differential escape capabilities of target species for a given trawl (Wardle, 1993). In the present work, the low number of hauls increased these limitations. 215 However, oceanic fish communities are often poorly described around the world, in particular 216 because the cost of fish survey is generally higher in oceanic habitats than in coastal ones. 217 The present study provides original data on the eastern North Atlantic mesopelagic fish 218 community off the Bay of Biscay. Despite the fairly limited number of trawl hauls on which 219 the description of the mesopelagic fish community was based, the results obtained were 220 consistent with previous data in the same region (Quéro, 1969; Quéro et al., 2002) or in 221 adjacent areas (Roe et al., 1984; Fock et al., 2004). Myctophids with N. kroeyeri and B. 222 glaciale, alepocephalids with X. copei, sternoptichids with A. olfersii, A. hemigymnus and M. 223 *muelleri* and paralepids with A. *risso* were the main species amongst a highly diversified fish 224 community. Given the sources of uncertainty and biases both in diet and fish community 225 descriptions, the composition values used in the present work should be considered as 226

revealing general patterns. Hence, the strong significant relationship observed between prey selection indices and prey energy content reveals a general pattern that supports the hypothesis of a quality-based prey selection by the common dolphin.

230

231 *4.2. Considerations on foraging strategies*

232

This active selection based on prey quality suggests that, within a given prey field, 233 predators would adapt the quality of their diets according to their specific energy 234 requirements. Hence, in the oceanic Bay of Biscay the diets of the top predator community 235 studied sympatrically revealed a large diversity of potential prey species (Pusineri et al., 236 2008). Among this field of available prey, observed differences in the quality of forage 237 species (Spitz et al., 2010) could reflect differences in predator-specific metabolic needs and 238 239 associated foraging strategies. Indeed, in addition to being the main prey of the common dolphin, N. kroeyeri, a high-quality prey, was also the main fish prey of the striped dolphins 240 Stenella coeruleoalba, the other homoeothermic top predator (Ringelstein et al., 2006). Thus, 241 predators with high energy requirement would be constrained to feeding on the most 242 profitable food sources constituted of small, gregarious and high energy density prey types. 243 Whereas in the diet of large ectothermic predators, high-quality prey were either rare (<5 244 %M) in the swordfish *Xiphias gladius* (Chancollon et al., 2006) or absent in the blue shark 245 Prionace glauca (Pusineri et al., 2008). These latter predators with lower energy requirements 246 would be better fitted to exploit lower quality food sources made of larger and leaner prey 247 species. 248

249

250 4.3. Ecosystem implications

Beyond a standard description of food habits, to attempt explaining the diet 252 253 composition of marine top predators increases the knowledge of prey-predator functional relationship. Indeed, prey selection by top predators could shape the structure of communities, 254 but the challenge is to identify the key functional traits which influence food web structure 255 and ecosystem functioning (Lazzaro et al., 2009). Here, the lowest quality, albeit most 256 abundant, mesopelagic fish species, such as X. copei, were neglected, or negatively selected, 257 by all top-predators studied so far in the area (Pusineri et al., 2008) and should therefore be 258 considered as trophic *cul-de-sacs*. In contrast, the highest quality prey (*e.g. N. kroeyeri* and *M*. 259 muelleri) are positively selected by predators with energetically expensive life styles and 260 261 should be considered as trophic highways to these predators. Predation being a major selective pressure for organisms of intermediate trophic level, forage species developed many 262 adaptations allowing predation risk to be reduced, such as toxicity, camouflage or specific 263 behavioral characteristics (Caro, 2005). Thus, prey with traits which reduce predation risk 264 would be favored within a trophic level (Preisser et al., 2007). In this evolutionary context, 265 one may interpret low energy density and associated poor nutritional quality as a successful 266 adaptation for mesopelagic fish that would limit predation risk and could explain their high 267 abundance within this fish community. 268

269

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358	Figure 1. Correlation between relative abundance in the environment for major fish species
359	and their relative abundance in the diet of common dolphin.
360	
361	Figure 2. Correlation between energetic value for major fish species and their value of
362	Chesson's index.
363	
364	Table 1. Trawling station data for the RV Thalassa
365	
366	Table 2. Composition of the diet of common dolphin off the Bay of Biscay in percentage by
367	number (Pusineri et al., 2007)
368	
369	Table 3. Energy content of main mesopelagic fish species off the Bay of Biscay (Spitz et al.,
370	2010)
371	
372	Table 4. Composition of fish community in the 500 meters depth surface layer off the Bay of
373	Biscay
374	
375	Table 5. Values of Chesson's index (α_i)



378 Figure 1



383 Table 1

Dete	Bottom	Catch	Start of	Latitude	Longitude
Dale	depth (m)	depth (m)	the haul	٩N	W
15/10/2002	1500	500	20:13	44.34	2.46
16/10/2002	1500	200	19:04	44.58	2.40
19/10/2002	2000	20	19:56	44.90	2.57
20/10/2003	700	200	20:13	45.78	3.76
22/10/2003	600	500	19:40	46.60	4.95
24/10/2003	3700	500	20:10	45.30	3.69
25/10/2003	1500	200	20:36	43.92	2.81
26/10/2003	1500	500	19:51	43.91	2.80
02/11/2003	3700	200	20:07	46.27	5.11
22/10/2008	1200	500	19:47	44.33	2.29
23/10/2008	800	200	20:02	43.75	2.24
25/10/2008	3300	20	21:06	44.79	2.74
26/10/2008	1500	500	20:05	44.99	2.67
28/10/2008	700	500	19:35	45.28	3.33

Family	Species	%N
Sternoptichidae		
	Maurolicus muelleri	9.4
Platytroctidae	Platytractidae unidentified	0.1
Stomiidae	r latytroctidae dilidentilied	0.1
	Stomias boa ferox	0.1
Chauliodontidae		
	Chauliodus sloani	0.1
Chiasmodontidae		
	Chiasmodontidae unidentified	0.1
Bathylagidae		0.0
Paralanididaa	All Bathylagidae species	0.2
Paralepididae	Arctozonus risso	1 1
	Paralepis coregonoides	0.7
	Macroparalepis affinis	0.1
Myctophidae		-
	Notoscopelus kroeyeri	62.4
	Myctophum punctatum	5.3
	Benthosema glaciale	11.3
	Symbolophorus veranyi	0.7
	Lampanyctus spp.	2.3
	Ceratoscopelus maderensis	0.4
	Lobianchia gemellarii	0.3
	Electrona risso	0.1
	Myctophidae unidentified	0.5
Nomeidae		
	Cubiceps gracilis	0.2
Others fish species	5	0.6
Cephalopod specie	es estatution estatu	4.0

Table 3

Family	Species	Gross energy (kJ/g)
Serrivomeridae		
	Serrivomer beanii	2.1
Alepocephalidae		
	Xenodermichtys copei	2.2
Platytroctidae		
-	Normichthys operosa	2.6
Sternoptychidae		
	Argyropelecus olfersii	3.5
	Maurolicus muelleri	4.2
Stomiidae		
	Stomias boa ferox	2.8
Paralepididae		
	Arctozenus risso	4.3
Myctophidae		
	Lampanyctus crocodilus	4.1
	Notoscopelus kroeyeri	7.9
	Benthosema glaciale	5.9

Family	Species	% O	Ν	%N	95% IC
Serrivomeridae					
	Serrivomer beanii	21.4	11	0.3	[0-1.1]
Bathylagidae					
	Dolicholagus longirostris	7.1	1	0.0	[0-0.1]
Alepocephalidae					
	Xenodermichtys copei	85.7	724	22.2	[12.9-32]
Platytroctidae					
	Holthyrnia macrops	7.1	1	0.0	[0-0.1]
Sternoptychidae					
	Argyropelecus hemigymnus	57.1	110	3.4	[0.6-8.2]
	Argyropelecus olfersii	78.6	369	11.3	[4.6-21.8]
- ···	Maurolicus muelleri	28.6	214	6.6	[0.1-18.1]
Stomiidae					
	Melanostomias bartonbeani	7.1	1	0.0	[0-0.1]
	Rhadinesthes decimus	7.1	1	0.0	[0-0.1]
0	Stomias boa terox	71.4	69	2.1	[0.9-3.8]
Gonostomatidae	Cualathana miaradan	110	45	0.5	[0 4 4]
Chicomodontidoo	Cyclothone microdon	14.3	15	0.5	[0-1.4]
Chiasmodontidae	Proudosconalus piorbartus	71	1	0.0	[0 0 1]
Paralonidiao	r seudoscopeius pierbartus	7.1	1	0.0	[0-0.1]
	Arctozenus risso	71 4	264	8 1	[3 7-14 2]
	Lestidions affinis	71	.3	0.1	[0-0.3]
	Macroparalepis affinis	57.1	16	0.5	[0.2-0.8]
	Paralepis coregonoides	7.1	1	0.0	[0-0.1]
Myctophidae					[]
	Benthosema glaciale	85.7	561	17.2	[2.2-40]
	Ceratoscopelus maderensis	78.6	146	4.5	[1.9-7.5]
	Electrona risso	7.1	2	0.1	[0-0.2]
	Lobianchia gemellarii	7.1	1	0.0	[0-0.1]
	Myctophum punctatum	78.6	327	10.0	[2.4-25.5]
	Notoscopelus kroeyeri	85.7	290	8.9	[5.1-13.8]
	Lampanyctus spp.	57.1	124	3.8	[0.2-10.4]
	Diaphus mollis	7.1	1	0.0	[0-0.1]
Merluciidae	Cynogadus brachycolus	7.1	1	0.0	[0-0.1]
Syngnathidae	Entelurus aequoerus	14.3	4	0.1	[0-0.4]

intervals at 95%

%O: percentage of occurrence; N: number of fish; %N: percentage by number; CI95%: Confidence

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Species	α	Selection
Serrivomer beanii	0.000	Negative
Xenodermichtys copei	0.000	Negative
Argyropelecus hemigymnus	0.000	Negative
Argyropelecus olfersii	0.000	Negative
Maurolicus muelleri	0.070	Positive
Stomias boa ferox	0.000	Negative
Cyclothone microdon	0.000	Negative
Chauliodus sloani	0.000	Negative
Arctozenus risso	0.010	Negative
Macroparalepis affinis	0.000	Negative
Paralepis coregonoides	0.000	Negative
Benthosema glaciale	0.220	Positive
Ceratoscopelus maderensis	0.002	Negative
Lampanyctus spp.	0.000	Negative
Lobianchia gemellarii	0.000	Negative
Myctophum punctatum	0.060	Positive
Notoscopelus kroeyeri	0.628	Positive
Electrona risso	0.000	Negative
Symbolophorus veranyi	0.000	Negative
Cubiceps gracilis	0.000	Negative
Scomberesox saurus	0.000	Negative
Bathylagidae	0.000	Negative
Chiasmodontidae	0.000	Negative
Platytroctidae	0.000	Negative
Others Stomidae	0.000	Negative
Syngnathidae	0.000	Negative