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

3

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17

18 **ABSTRACT**

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

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

34

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

36

37 **1. Introduction**

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

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

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.

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

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

79 2008). Hence, prey selection by common dolphins based on prey energy densities was
80 suggested to occur in this neritic habitat. Recently and for the first time in a fully oceanic
81 area, the diet of common dolphins off the Bay of Biscay was shown to be largely constituted
82 of myctophids (Pusineri et al., 2007). By comparison with other predators studied in the same
83 area and collected in the same condition, *i.e.* living in the same prey field, it appeared that
84 similarly-sized pelagic predators such as blue shark, *Prionace glauca*, or swordfish, *Xiphias*
85 *gladius*, ate larger and probably leaner prey types (Pusineri et al., 2008).

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

93

94 **2. Materials and methods**

95

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

97

98 The epi- to mesopelagic oceanic fish community off the Bay of Biscay was
99 investigated during EVHOE (*EValuation des ressources Halieutiques de l'Ouest Européen*)
100 research cruises onboard the R/V *Thalassa* in October 2002, 2003 and 2008. Fourteen hauls
101 were performed with a 25 m vertical opening pelagic trawl. The mesh size decreases
102 gradually from 76 mm to 44 mm in the bag. The trawl-haul duration was one hour at 4 kn.
103 The hauls were carried out during the night at various depths supposedly accessible to

104 dolphins from sub-surface to 500 m deep off the continental slope from 43.91–46.60°N and
105 2.40–5.11°W (Table 1). Fish were counted and identified following published guides (*e.g.*
106 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
$$\% N_i = x_i / X * 100$$

115 where x_i is the number of individuals belonging to species i and X the total number of fish
116 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

124 The dietary composition of common dolphin used in the present work comes from a
125 previous analysis of stomach contents carried out from dolphins incidentally caught in tuna
126 driftnet fisheries during the summers 1992-1993 off the Bay of Biscay (Pusineri et al. 2007;
127 summary in Table 2). Briefly described, stomach contents from 63 common dolphins were
128 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*.

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

134

135 *2.3. Comparison between diet and prey availability*

136

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

140

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

141

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

145

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

147

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

148 where α_i is the selectivity for prey type i ; r_i is the percentage by number of species i in the diet
149 of the common dolphin; p_i percentage by number of species i in hauls and m is the total
150 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 *R* 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 *Xenodermichthys 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].
173 Abundances of all other species were negligible.

174

175 *3.2. Comparison between diet and prey availability*

176

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

188

189 **4. Discussion**

190

191 *4.1. General comments*

192

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

Both stomach content analysis and trawling are subject to their own selectivity and 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 difficulty of controlling the sampling design and to the differential digestion of ingested prey (e.g. Tollit et al., 1997; Pierce et al., 2007). Especially for protected species such as marine mammals, the dietary results were often limited by the size, the spatio-temporal coverage, or 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 still the best and most widely used approach to investigate marine top predator diets and 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 sampling design (*i.e.* number of trawls, spatio-temporal coverage, immersion/depth/daytime 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. However, oceanic fish communities are often poorly described around the world, in particular because the cost of fish survey is generally higher in oceanic habitats than in coastal ones. The present study provides original data on the eastern North Atlantic mesopelagic fish community off the Bay of Biscay. Despite the fairly limited number of trawl hauls on which the description of the mesopelagic fish community was based, the results obtained were consistent with previous data in the same region (Quéro, 1969; Quéro et al., 2002) or in adjacent areas (Roe et al., 1984; Fock et al., 2004). Myctophids with *N. kroeyeri* and *B. glaciale*, alepocephalids with *X. copei*, sternoptichids with *A. olfersii*, *A. hemigymnus* and *M. muelleri* and paralepids with *A. risso* were the main species amongst a highly diversified fish community. Given the sources of uncertainty and biases both in diet and fish community descriptions, the composition values used in the present work should be considered as

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

230

231 *4.2. Considerations on foraging strategies*

232

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

249

250 *4.3. Ecosystem implications*

251

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

269

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276

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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)

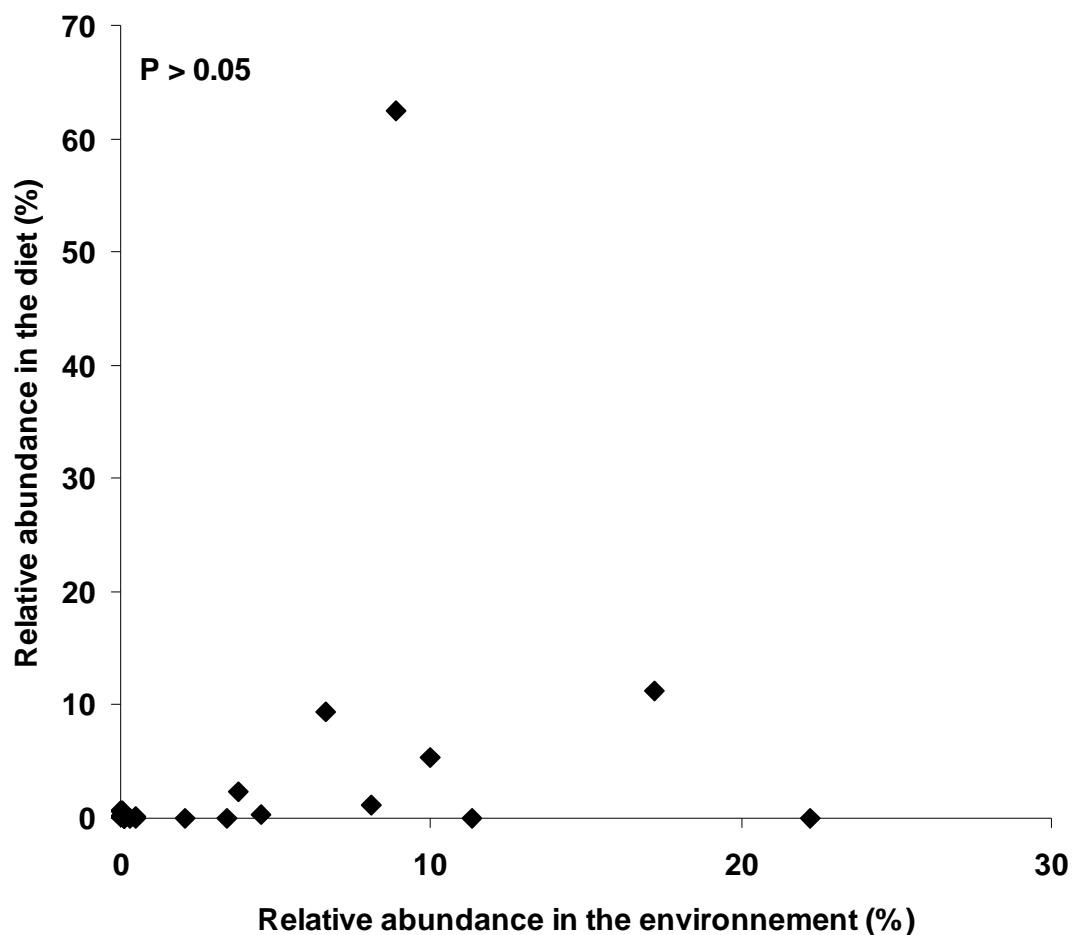
371

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)

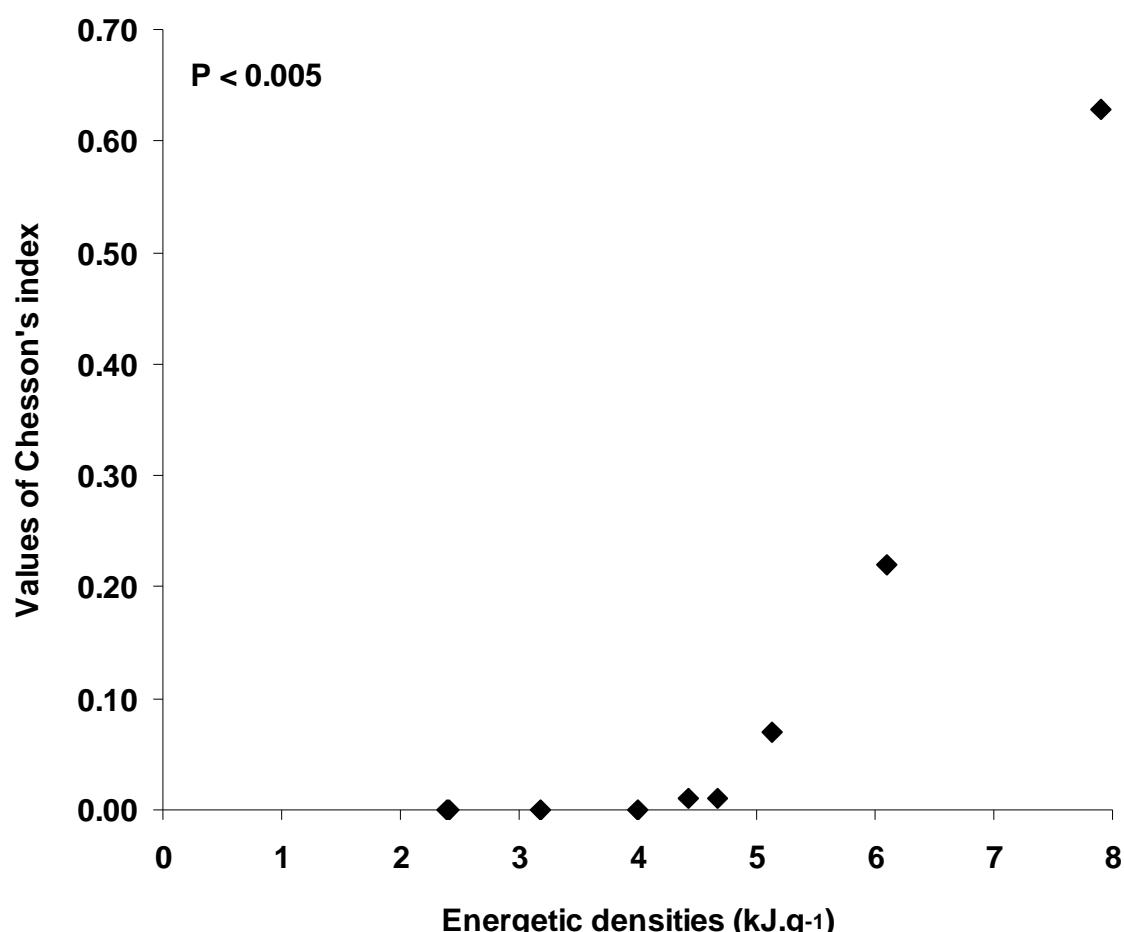
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378 Figure 1

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381 Figure 2

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383 Table 1

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Date	Bottom depth (m)	Catch depth (m)	Start of the haul	Latitude °N	Longitude °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

385

Family	Species	%N
Sternoptichidae	<i>Maurolicus muelleri</i>	9.4
Platytroctidae	Platytroctidae unidentified	0.1
Stomiidae	<i>Stomias boa ferox</i>	0.1
Chauliodontidae	<i>Chauliodus sloani</i>	0.1
Chiasmodontidae	Chiasmodontidae unidentified	0.1
Bathylagidae	All Bathylagidae species	0.2
Paralepididae	<i>Arctozenus risso</i>	1.1
	<i>Paralepis coregonoides</i>	0.7
	<i>Macroparalepis affinis</i>	0.1
Myctophidae	<i>Notoscopelus kroeyeri</i>	62.4
	<i>Myctophum punctatum</i>	5.3
	<i>Benthosema glaciale</i>	11.3
	<i>Symbolophorus veranyi</i>	0.7
	<i>Lampanyctus</i> spp.	2.3
	<i>Ceratoscopelus maderensis</i>	0.4
	<i>Lobianchia gemellarii</i>	0.3
	<i>Electrona risso</i>	0.1
	Myctophidae unidentified	0.5
Nomeidae	<i>Cubiceps gracilis</i>	0.2
Others fish species		0.6
Cephalopod species		4.0

Table 3

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

391 Table 4

392

Family	Species	%O	N	%N	95% IC
Serrivomeridae	<i>Serrivomer beanii</i>	21.4	11	0.3	[0-1.1]
Bathylagidae	<i>Dolicholagus longirostris</i>	7.1	1	0.0	[0-0.1]
Alepocephalidae	<i>Xenodermichthys copei</i>	85.7	724	22.2	[12.9-32]
Platytroctidae	<i>Holthyrnia macrops</i>	7.1	1	0.0	[0-0.1]
Sternopychidae	<i>Argyropelecus hemigymnus</i>	57.1	110	3.4	[0.6-8.2]
	<i>Argyropelecus olfersii</i>	78.6	369	11.3	[4.6-21.8]
	<i>Maurolicus muelleri</i>	28.6	214	6.6	[0.1-18.1]
Stomiidae	<i>Melanostomias bartonbeani</i>	7.1	1	0.0	[0-0.1]
	<i>Rhadinesthes decimus</i>	7.1	1	0.0	[0-0.1]
	<i>Stomias boa ferox</i>	71.4	69	2.1	[0.9-3.8]
Gonostomatidae	<i>Cyclothona microdon</i>	14.3	15	0.5	[0-1.4]
Chiasmodontidae	<i>Pseudoscopelus pierbartus</i>	7.1	1	0.0	[0-0.1]
Paralepididae	<i>Arctozenus risso</i>	71.4	264	8.1	[3.7-14.2]
	<i>Lestidiops affinis</i>	7.1	3	0.1	[0-0.3]
	<i>Macroparalepis affinis</i>	57.1	16	0.5	[0.2-0.8]
	<i>Paralepis coregonoides</i>	7.1	1	0.0	[0-0.1]
Myctophidae	<i>Benthosema glaciale</i>	85.7	561	17.2	[2.2-40]
	<i>Ceratoscopelus maderensis</i>	78.6	146	4.5	[1.9-7.5]
	<i>Electrona risso</i>	7.1	2	0.1	[0-0.2]
	<i>Lobianchia gemellarii</i>	7.1	1	0.0	[0-0.1]
	<i>Myctophum punctatum</i>	78.6	327	10.0	[2.4-25.5]
	<i>Notoscopelus kroeyeri</i>	85.7	290	8.9	[5.1-13.8]
	<i>Lampanyctus</i> spp.	57.1	124	3.8	[0.2-10.4]
	<i>Diaphus mollis</i>	7.1	1	0.0	[0-0.1]
Merlucciidae	<i>Cynogadus brachycolus</i>	7.1	1	0.0	[0-0.1]
Syngnathidae	<i>Entelurus aequoerus</i>	14.3	4	0.1	[0-0.4]

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394 %O: percentage of occurrence; N: number of fish; %N: percentage by number; CI95%: Confidence

395 intervals at 95%

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398 Table 5

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