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

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ABSTRACT

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

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.

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

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

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

From killer whales eating marine mammals to herbivorous dugong, marine mammals exhibit a broad range of biological models and have developed diverse feeding strategies (Berta and Sumich, 1999). But, some species, particularly small cetaceans and pinnipeds, are often described as opportunistic feeders: predators which consume their prey without selection, *i.e.* proportionately to their availability in the environment. Contrastingly, active prey choice by marine mammals has rarely been actually tested. The difficulty to describe the 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, 2003).

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

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.

2. Materials and methods

2.1. Composition of the epi- and mesopelagic fish community

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°N and 2.40–5.11°W (Table 1). Fish were counted and identified following published guides (*e.g.* Quéro et al., 2003).

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

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

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

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

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

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

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

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,

1994, Spitz et al., 2006). The diet was dominated by myctophid fish, mostly *Notoscopelus 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).

2.3. Comparison between diet and prey availability

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):

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

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).

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

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

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

feeding at random whereas values greater (*versus* smaller) than 1/m correspond to positive (*versus* negative) selection of prey *i*.

Pearson's correlation tests between species abundance in the hauls *versus* in the diet was performed to examine if the diet reflected prey availability (percentage by number >1% either in diet or in hauls). Similar tests were carried out between Chesson's index of selectivity and energetic density to investigate if prey choice was associated to prey quality. All correlations were computed by using the *R* software (Ihaka and Gentleman, 1996).

3. Results

3.1. Composition of the epi- and mesopelagic fish community

From the fourteen epi- to mesopelagic trawl hauls, 3258 fish were captured. The pelagic fish community was composed of 26 species from 12 families. Three families accounted for up to 88% of total number of fish caught (Table 4). The alepocephalid *Xenodermichtys copei* was the most abundant species with a total contribution of 22.2%N, 95% non-parametric confidence interval being [12.9–32]. Myctophid fish were represented by at least eight species and amounted to 44.5%N; among them *Benthosema glaciale* (17.2%N [2.2–40]) and *Notoscopelus kroeyeri* (8.9%N [5.1–13.8]) were the most prevalent. The sternoptychids were the third dominant family with three species identified: *Argyropelecus olfersii* (11.3%N [4.6–21.8]), *A. hemigymnus* (3.4%N [0.6–8.2]) and *Maurolicus muelleri* (6.6%N [0.1–18.1]). Lastly, the paralepid *Arctozenus risso* accounted for 8.1%N [3.7–14.2]. Abundances of all other species were negligible.

3.2. Comparison between diet and prey availability

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

4. Discussion

4.1. General comments

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

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.

4.2. Considerations on foraging strategies

This active selection based on prey quality suggests that, within a given prey field, predators would adapt the quality of their diets according to their specific energy requirements. Hence, in the oceanic Bay of Biscay the diets of the top predator community studied sympatrically revealed a large diversity of potential prey species (Pusineri et al., 2008). Among this field of available prey, observed differences in the quality of forage species (Spitz et al., 2010) could reflect differences in predator-specific metabolic needs and 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 *Stenella coeruleoalba*, the other homoeothermic top predator (Ringelstein et al., 2006). Thus, predators with high energy requirement would be constrained to feeding on the most profitable food sources constituted of small, gregarious and high energy density prey types. Whereas in the diet of large ectothermic predators, high-quality prey were either rare (<5 %M) in the swordfish *Xiphias gladius* (Chancollon et al., 2006) or absent in the blue shark *Prionace glauca* (Pusineri et al., 2008). These latter predators with lower energy requirements would be better fitted to exploit lower quality food sources made of larger and leaner prey species.

4.3. Ecosystem implications

Beyond a standard description of food habits, to attempt explaining the diet 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, but the challenge is to identify the key functional traits which influence food web structure and ecosystem functioning (Lazzaro et al., 2009). Here, the lowest quality, albeit most abundant, mesopelagic fish species, such as *X. copei*, were neglected, or negatively selected, by all top-predators studied so far in the area (Pusineri et al., 2008) and should therefore be considered as trophic *cul-de-sacs*. In contrast, the highest quality prey (e.g. *N. kroeyeri* and *M. muelleri*) are positively selected by predators with energetically expensive life styles and 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 adaptations allowing predation risk to be reduced, such as toxicity, camouflage or specific behavioral characteristics (Caro, 2005). Thus, prey with traits which reduce predation risk would be favored within a trophic level (Preisser et al., 2007). In this evolutionary context, one may interpret low energy density and associated poor nutritional quality as a successful adaptation for mesopelagic fish that would limit predation risk and could explain their high abundance within this fish community.

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Figure 1. Correlation between relative abundance in the environment for major fish species and their relative abundance in the diet of common dolphin.

Figure 2. Correlation between energetic value for major fish species and their value of Chesson's index.

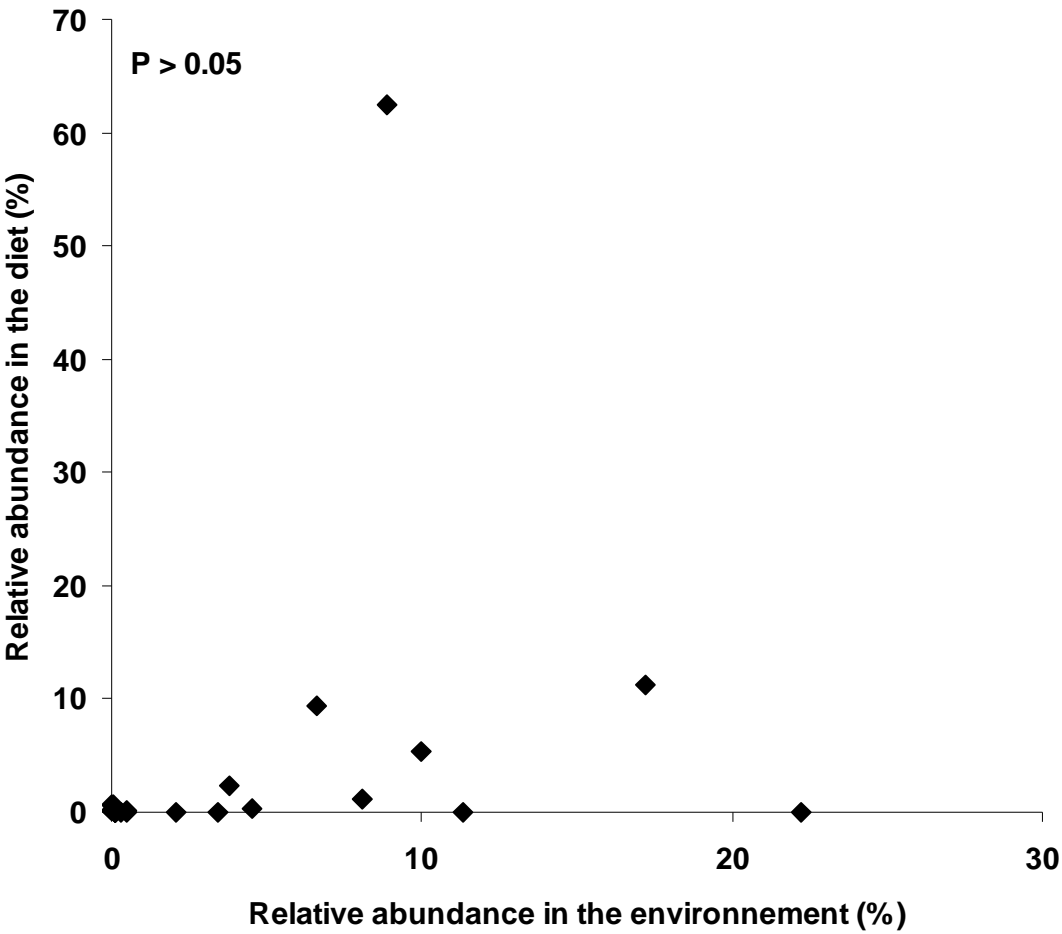
Table 1. Trawling station data for the RV *Thalassa*

Table 2. Composition of the diet of common dolphin off the Bay of Biscay in percentage by number (Pusineri et al., 2007)

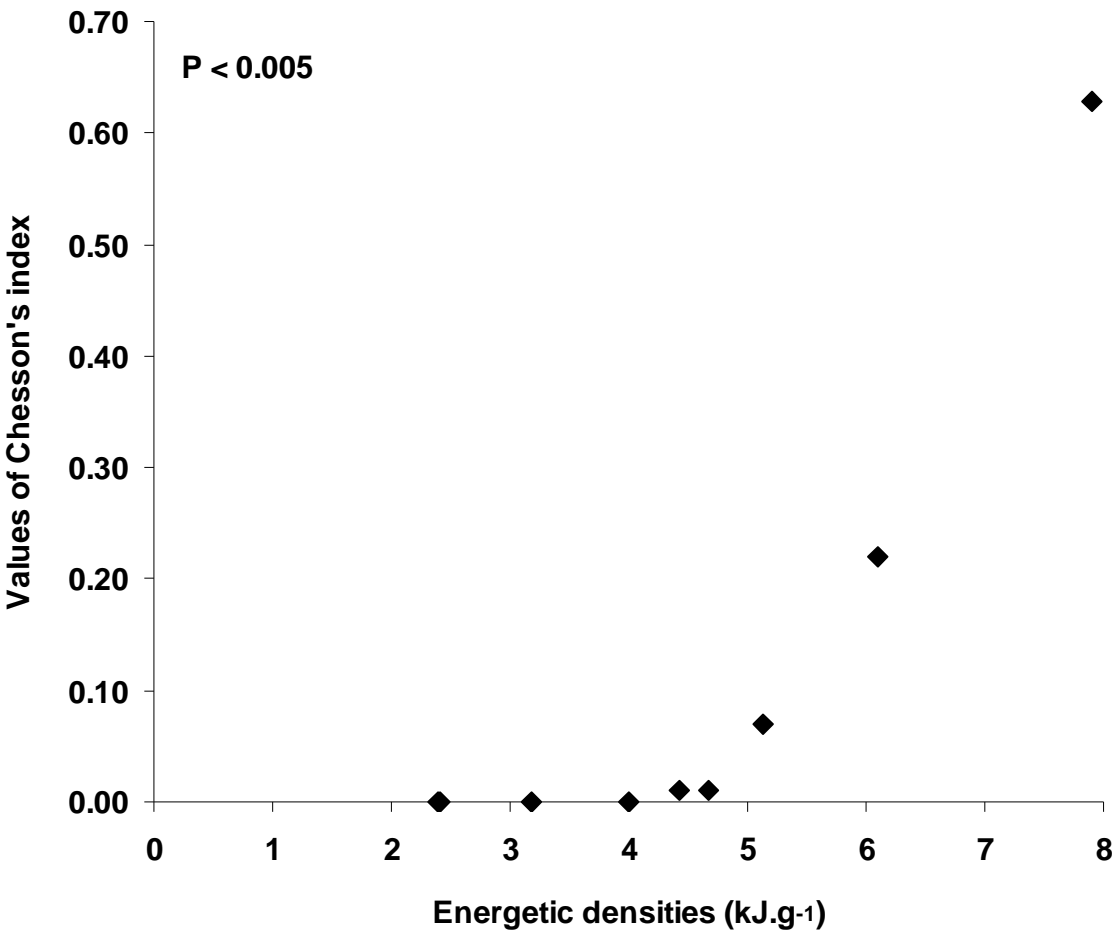
Table 3. Energy content of main mesopelagic fish species off the Bay of Biscay (Spitz et al., 2010)

Table 4. Composition of fish community in the 500 meters depth surface layer off the Bay of Biscay

Table 5. Values of Chesson's index (α_i)



378 Figure 1



381 Figure 2

382

383 Table 1

384

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		
	Chauliodus sloani	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>Ceratospinelus 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

Family	Species	Gross energy (kJ/g)
Serrivomeridae		
	<i>Serrivomer beanii</i>	2.1
Alepocephalidae		
	<i>Xenodermichtys copei</i>	2.2
Platytroctidae		
	<i>Normichthys operosa</i>	2.6
Sternoptychidae		
	<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>Benthoosema glaciale</i>	5.9

Table 4

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>Xenodermichtys copei</i>	85.7	724	22.2	[12.9-32]
Platytroctidae	<i>Holthyrnia macrops</i>	7.1	1	0.0	[0-0.1]
Sternoptychidae	<i>Argyrolepecus hemigymnus</i>	57.1	110	3.4	[0.6-8.2]
	<i>Argyrolepecus 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>Cyclothone 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>Benthoosema 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 aequoeris</i>	14.3	4	0.1	[0-0.4]

%O: percentage of occurrence; N: number of fish; %N: percentage by number; CI95%: Confidence intervals at 95%

Species	α	Selection
<i>Serrivomer beanii</i>	0.000	Negative
<i>Xenodermichtys copei</i>	0.000	Negative
<i>Argyrolepecus hemigymnus</i>	0.000	Negative
<i>Argyrolepecus olfersii</i>	0.000	Negative
<i>Maurolicus muelleri</i>	0.070	Positive
<i>Stomias boa ferox</i>	0.000	Negative
<i>Cyclothone 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>Benthoosema 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
Platyroctidae	0.000	Negative
Others Stomidae	0.000	Negative
Syngnathidae	0.000	Negative