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Spatio-temporal variation in the diet of Cory's shearwater *Calonectris diomedea* in the Azores archipelago, northeast Atlantic

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ABSTRACT

The diet of Cory's shearwater *Calonectris diomedea* in the Azores was studied in four islands of the archipelago over four breeding seasons, using stomach flushings from 959 birds. Fish were identified from flesh, otoliths and vertebrae and cephalopods from flesh and lower beaks. The frequency of occurrence of prey taxa, and the numerical frequency of fish and cephalopods, showed marked variations both spatially, across the breeding cycle and between years. Overall, cephalopods from 37 species representing 17 families and fish from 33 species representing 18 families were identified, representing over 70 prey species and trebling what was previously known. Histioteuthidae, Ommastrephidae and Cranchiidae were the only cephalopod families present every year and represented two thirds of the cephalopods' consumption by number. Blue jack mackerel *Trachurus picturatus* was the most abundant prey species present in 1998 and 2002 but was absent in 1999 and 2000, representing on average 57.2% of prey by number in the years it occurred. Apart from blue jack mackerel, most fish species were present in very low numbers with the exception of *Cubiceps gracilis*, *Scomberesox saurus* and *Maurolicus muellerii*. *Diaphus adenomus*, was recorded for the first time for the Azores archipelago.

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1. Introduction

Studying the diet of top marine predators, such as seabirds, is important for understanding their role in oceanic food webs, ensuring their conservation and monitoring change in ecosystems. Knowing their main prey is important for ecosystem modeling and ecosystem management. Seabirds are at the top of oceanic food webs and can be valuable indicators of change. Seabirds are excellent samplers of the marine environment because they are known to take advantage of situations in which prey are predictably concentrated by the interaction of physical processes, such as upwelling current boundaries (Hunt and Schneider, 1987; Bost et al., 2009).

Studies on the feeding behaviour of pelagic seabirds have shown the importance of feeding associations with other marine predators, especially for some Procellariiform (albatrosses and petrels) species whose prey are only patchily available (Furness and Monaghan, 1987). The largest and most abundant Procellariiforme from the northern subtropical Atlantic is Cory's

shearwater *Calonectris diomedea*. Previous studies have shown inter-annual differences in the diet of this species but studies at a finer scale are needed. The Azores archipelago, Atlantic Ocean, holds the largest population of Cory's shearwaters in the world, estimated at 188 thousand pairs (BirdLife International, 2004). The Azorean population of Cory's shearwaters belongs to the subspecies *C. d. borealis* and forages over large oceanic areas (Magalhães et al., 2008; Paiva et al., 2010a; Boertmann, 2011).

Previous studies on the diet composition of Cory's shearwater in the Azores have shown that marked variations in the prey composition from year to year exist and that Cory's shearwaters feed mainly on pelagic fish of very few species (Granadeiro et al., 1998; Xavier et al., 2011). Aggregations are regularly found in apparent association with upwelling waters at the shelf break and at seamounts (Monteiro et al., 1996; Paiva et al., 2010a). Martin (1986) recorded Cory's shearwater in the Azores feeding on blue jack mackerel *Trachurus picturatus* in association with Atlantic spotted dolphins *Stenella frontalis*. Clua and Grosvalet (2001) observed large aggregations (up to one thousand individuals) of seabirds (mainly Cory's shearwaters) feeding on small fish together with large tunas (yellowfin tuna *Thunnus albacares*, bluefin tuna *Thunnus thynnus*) and dolphins (common dolphin *Delphinus delphis*, Atlantic spotted dolphin *S. frontalis* and bottlenose dolphin *Tursiops truncatus*).

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The Azores are made up by nine islands lying along a 600-km transect and the Cory's shearwaters from the different islands have partially distinct foraging areas during incubation and chick-rearing (Paiva et al., 2010a). It is therefore desirable to determine if spatial segregation is also associated with spatial variations in diet. Also, since the constraints faced by the adults vary throughout the breeding cycle (the most obvious of them being that during chick-rearing, adults have to forage not only for themselves, but also for the chick), does composition of diet vary accordingly?

In this study we investigate the spatial and temporal variability in the diet of Cory's Shearwaters on four islands of the Azores archipelago, covering the entire 600-km transect, during four breeding seasons, i.e., 1998, 1999, 2000 and 2002.

2. Material and methods

Fieldwork was conducted in the Azores archipelago (36–39°N, 25–31°W) between March 1998 and August 2002. The archipelago is formed by nine islands divided in three groups: western, central and eastern—samples were collected from the three groups. Cory's shearwaters start visiting their colonies from February onwards, eggs are laid from mid-May until early June,

and chicks hatch in late July and fledge from mid-October to early November (Monteiro et al., 1996). Food samples were collected from adult Cory's Shearwaters at locations situated in four different islands: (1) Vila islet, off Santa Maria island, (2) Praia islet, off Graciosa island, (3) Morro de Castelo Branco and Capelinhos, on Faial island and (4) Ponta do Pesqueiro, on Corvo island; Table 1 shows the dates of collection of samples and Fig. 1 the geographical positions of collection sites. Diet samples were obtained using the water-offloading technique (Wilson, 1984). For that procedure we used a water pump and a plastic catheter with an external diameter of 0.5 cm. Each bird was stomach-flushed twice to ensure complete collection of the stomach contents (Neves et al., 2006). Birds were immediately released after being sampled and food samples were drained and preserved in 70% ethanol. Samples were examined and sorted under a binocular microscope: otoliths were kept dry; all the other remains from fish, cephalopod and crustaceans were stored in 70% ethanol. Fish were identified to the lowest possible taxon by their otoliths using available keys (Nolf, 1985; Härkönen, 1986; Smale et al., 1995 and reference collections. Otoliths were paired to estimate the number of fish prey in each sample. Cephalopods were identified from their lower beaks and, when the prey was not too digested, from flesh, shape, color and other physical

Table 1
Dates of sample collection. Dates underlined are for pre-laying, in bold for incubation and in italic for chick-rearing.

Island	1998	1999	2000	2002
Corvo island	<i>24–27 July</i>	<i>28 July–1 August</i>		
Graciosa island	<i>5–9 August</i>	<i>9–14 August</i>		9–12 July
Santa Maria island	29 and 30 March <i>10–12 August</i>	22–26 March <i>3–7 August</i>	20–24 April	20 April–15 May 2 June–2 July <i>27 July–1 August</i>
Faial island	15–22 March 13–15 April 7–11 May 8–11 June 3–15 July <i>31 July–2 August</i> <i>10 and 17 September</i>			

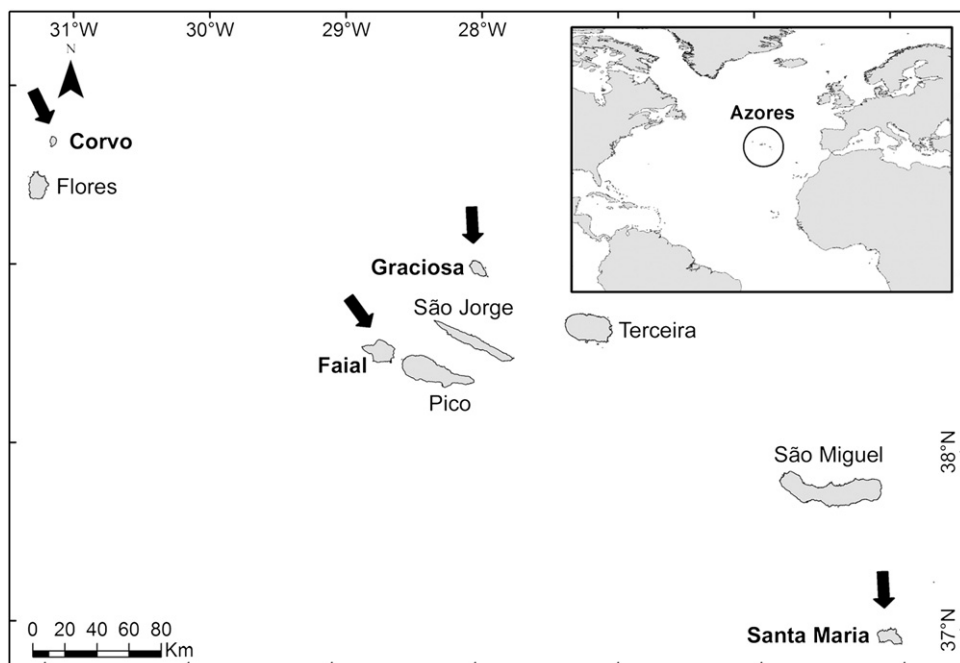


Fig. 1. Location of the Azores Islands showing the islands where samples were collected in bold arrows.

features (Clarke, 1986; Nesis, 1987). The rostral lengths (LRLs) of intact lower beaks were measured with vernier callipers or a microscope, as appropriate for their size, and previously published relationships for each cephalopod family (or lower taxon) enabled the estimation of body mass (M) and mantle lengths (ML) for each taxon. When weight estimates were not available for a given species, we calculated a weighted average Family-specific weight. Given that the length of the arms of cephalopods in relation to ML varies considerably among species, we also provided estimates of standard length (SL), which is the length of a squid excluding the tentacles. SL may give a better idea of the size of the prey from the predator's point of view and enables better comparisons with the size of the fish prey. Estimates of SL are based on ML–SL relationships from drawings published by Nesis (1987).

We report biomass estimates and fish length estimates for blue jack mackerel based on the following equations: Fork Length = $0.568 + 34.79 \times VL$ (mm); VL = vertebra length between vertebrae C10 and C13 (V. Neves, unpublished results) and $Wt(g) = 0.00819 \times FL^{3.11}$ (cm) (Isidro, 1990). Diet composition is described by frequency of occurrence (%O—percentage of samples containing each type of prey), numerical frequency (%N—individual numbers of each prey species expressed as % of all same type prey; e.g., %N *Taonius pavo* = Total number *T. pavo*/Total number of cephalopods) and weight frequency (%W weight contribution of a given prey type as % of total weight). Comparisons in prey occurrence between years, location and across the breeding cycle for a given year were made using chi-square tests calculated with SPSS 17. Means are presented \pm SD.

We estimated the annual consumption of fish and cephalopod by the Azorean population of Cory's shearwaters throughout the year. The breeding population is estimated at 188,000 pairs (BirdLife International, 2004) and the non-breeding population was assumed to be 70% of the number of breeders (Furness, 1994 cited in Granadeiro et al., 1998) so the global population was assumed to be 639,200 individuals. Field and basal metabolic rates (FMR and BMR) were estimated using Ellis and Gabrielsens (2002) allometric equations for Procellariiformes. The length of the breeding season was set as 245 day (March to October; Monteiro et al., 1996). We considered the length of the incubation period to be 54 day (Monteiro et al., 1996). We considered that for half of the incubation period (27 day) breeders had a BMR and that for the other half of the incubation period and throughout the rest of the year they had a FMR. For non-breeders we assumed a FMR throughout the year. This estimation assumes that the diet of Cory's shearwater is similar during the breeding and the non-breeding season. We assumed an average calorific value of 6 kJ g^{-1} for fish (Lea et al., 2002) and 3 kJ g^{-1} for cephalopods (Croxall and Prince, 1982).

3. Results

A total of 959 stomach contents were collected—Table 2 presents the frequency of occurrence of different prey for all the years studied

Table 2
Frequency of occurrence (FO%) of oil, crustacean, cephalopods and fish in food samples of Cory's shearwaters in the Azores. Number of samples in parentheses. A total of 959 samples were collected.

Taxon	1998	1999	2000	2002	All
Oil	8.6 (46)	8.1 (16)	—	7.8 (14)	7.9 (76)
Crustaceans	21.6 (115)	24.8 (49)	18 (9)	8.4 (15)	19.6 (188)
Cephalopods	88.2 (469)	50.6 (63)	46 (25)	22.3 (40)	62.3 (597)
Fish	(269) 53.2	0 (91)	34 (17)	76.5 (137)	53.6 (514)
N		198	50	179	959

and Figs. 2–7 present the frequency of occurrence of different prey across different years, locations and time of the breeding season. Samples varied in wet weight from 0.1 to 179.1 g (average = 14.6 ± 22.0 [SD] g). Remains of flesh and pieces of pen were present for 13 out of the 37 species identified by lower beaks (Table 3). Individual cephalopods ranged in mass from 1.3 g (*Helichocranchia*

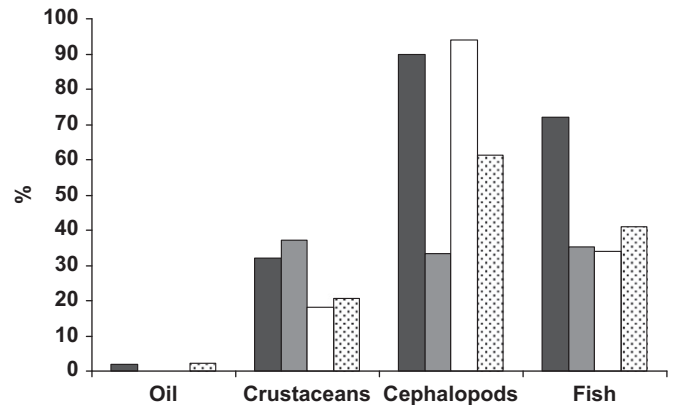


Fig. 2. Frequency of occurrence (%) of different prey types in food samples of Cory's shearwaters in Santa Maria pre-laying during 1998 (black columns; 50 samples), 1999 (grey columns; 51 samples), 2000 (white columns; 50 samples) and 2002 (dotted columns; 44 samples).

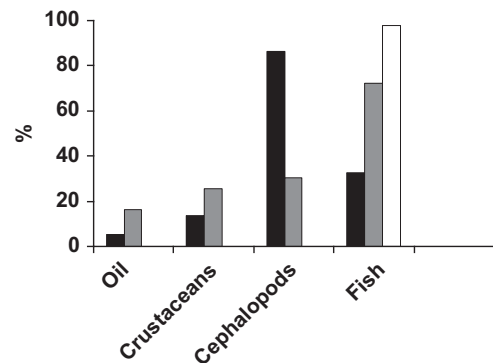


Fig. 3. Frequency of occurrence (%) of different prey types in food samples of Cory's shearwaters in Santa Maria chick-rearing during 1998 (black columns; 37 samples), 1999 (grey columns; 43 samples) and 2002 (white columns; 48 samples).

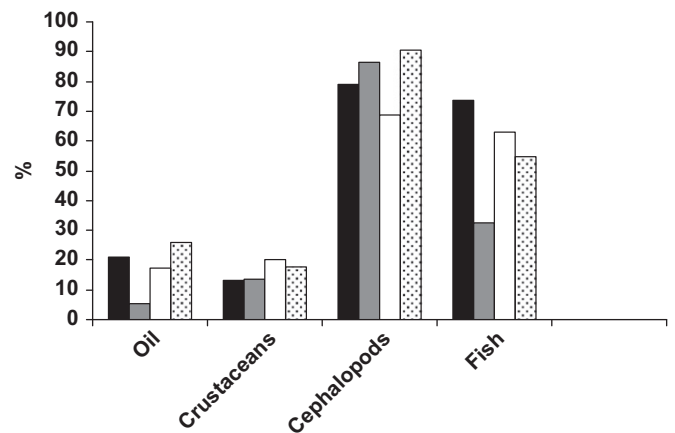


Fig. 4. Frequency of occurrence (%) of different prey types in samples of Cory's shearwaters in Faial (black columns; 38 samples), Santa Maria (grey columns; 37 samples), Graciosa (white columns; 35 samples) and Corvo (dotted columns; 73 samples) during chick-rearing in 1998.

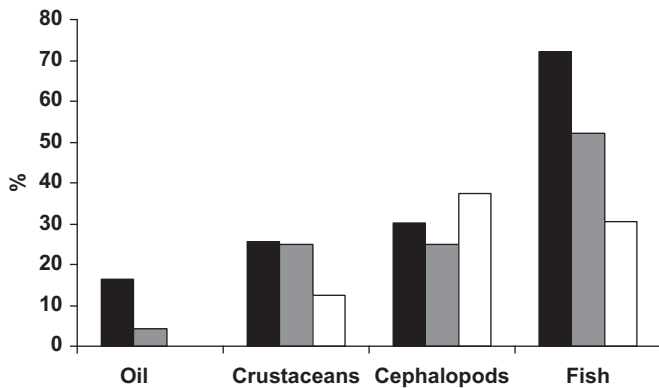


Fig. 5. Frequency of occurrence (%) of different prey types in food samples of Cory's shearwaters in Santa Maria chick-rearing (black columns; 43 samples), Graciosa chick-rearing (grey columns; 48 samples) and Corvo chick-rearing (white columns; 56 samples) in 1999.

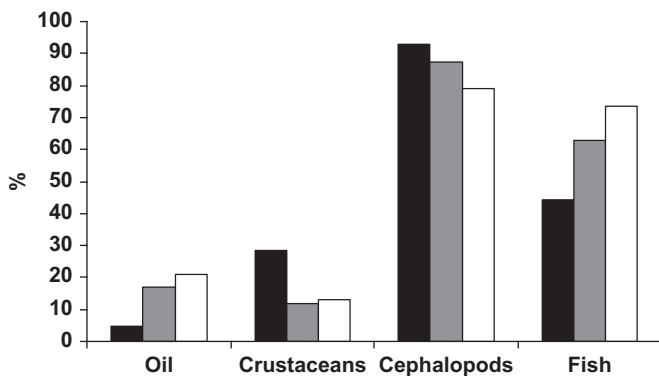


Fig. 6. Frequency of occurrence (%) of different prey types in food samples of Cory's shearwaters on Faial during pre-laying (black columns; 197 samples), incubation (grey columns; 102 samples) and chick-rearing (white columns; 38 samples) in 1998.

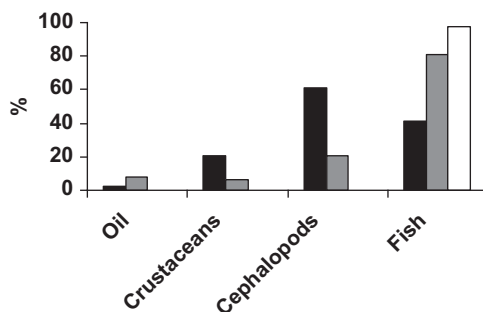


Fig. 7. Frequency of occurrence (%) of different prey types in food samples of Cory's shearwaters in Santa Maria pre-laying (black columns; 44 samples), Santa Maria incubation (grey columns; 62 samples) and Santa Maria chick-rearing (white columns; 48 samples) in the Azores in 2002.

pfefferi) to 1873 g (*Gonatus* sp.) (Table 4). The few intact mantles and pens present confirmed general estimates of body size from lower beaks.

3.1. Inter-annual variations

On Santa Maria the frequency of occurrence of fish during pre-laying was higher in 1998 than in 1999 ($\chi^2_1 = 13.67$, $p = 0.0002$; see Fig. 2), in 2000 ($\chi^2_1 = 14.49$, $p = 0.0001$; see Fig. 2) and 2002

($\chi^2_1 = 9.25$, $p = 0.0024$; see Fig. 2). On the other hand, the frequency of occurrence of cephalopods was lower in 1999 than in 1998 ($\chi^2_1 = 34.2$, $p < 0.0001$; see Fig. 2), 2000 ($\chi^2_1 = 40.03$, $p < 0.0001$; see Fig. 2) and 2002 ($\chi^2_1 = 22.51$, $p < 0.0001$; see Fig. 2). During chick-rearing the frequency of occurrence of fish in Santa Maria was significantly higher in 2002 than in 1999 ($\chi^2_1 = 10.33$, $p = 0.0013$; see Fig. 3) and in 1998 ($\chi^2_1 = 39.17$, $p < 0.0001$; see Fig. 3). It was also significantly higher in 1999 than in 1998 ($\chi^2_1 = 11.04$, $p = 0.0009$; see Fig. 3). Finally, in Santa Maria during chick-rearing, the frequency of occurrence of cephalopods was significantly higher in 1998 than in 1999 ($\chi^2_1 = 31.85$, $p < 0.0001$; see Fig. 3). The opposite happened on Corvo where the frequency of occurrence of fish during chick-rearing was significantly lower in 1999 than in 1998 ($\chi^2_1 = 6.71$, $p = 0.0096$; see Figs. 4 and 5). On Graciosa there was no inter-annual (1998 versus 1999) difference in the frequency of occurrence of the different taxa during chick-rearing.

Overall Figs. 2 and 3 show that there can be marked variations in the diet of Cory's shearwater across different years.

3.2. Variations across the breeding cycle

Considerable variations also occurred among the different phases of the breeding cycle (Figs. 2, 3, 6 and 7). Overall, the frequency of occurrence of fish increased across the breeding season, being highest when birds had chicks (Figs. 6 and 7).

On Faial in 1998 the frequency of occurrence of fish was lower in the pre-laying period than during incubation ($\chi^2_1 = 11.61$, $p = 0.0007$; see Fig. 6) and chick-rearing ($\chi^2_1 = 14.18$, $p = 0.0002$; see Fig. 6). The frequency of occurrence of oil was lower during pre-laying than during chick-rearing ($\chi^2_1 = 20.02$ with Yates' correction, $p < 0.0001$; see Fig. 6). The frequency of occurrence of crustaceans was significantly higher during pre-laying than during incubation ($\chi^2_1 = 5.22$, $p = 0.022$; see Fig. 6) and the frequency of occurrence of cephalopods was significantly higher during pre-laying than during chick-rearing ($\chi^2_1 = 7.71$, $p = 0.0055$; see Fig. 6).

On Santa Maria, the frequency of occurrence of fish was significantly higher during chick-rearing than during pre-laying in 1999 ($\chi^2_1 = 11.23$, $p = 0.0008$; see Figs. 2 and 3). In 2002 the frequency of occurrence of crustaceans and that of cephalopods were significantly higher during pre-laying than during incubation ($\chi^2_1 = 13.90$, $p = 0.0002$, and $\chi^2_1 = 16.2$ with Yates' correction, $p < 0.0001$, respectively; see Fig. 7). Conversely, the frequency of occurrence of fish was significantly lower during pre-laying than during incubation ($\chi^2_1 = 15.98$, $p < 0.0001$; see Fig. 7) and chick-rearing ($\chi^2_1 = 33.28$, $p < 0.0001$; see Fig. 7). The frequency of occurrence of fish was significantly higher during chick-rearing than during incubation ($\chi^2_1 = 6.18$, $p = 0.0129$; see Fig. 7).

3.3. Spatial variations

In 1998 during chick-rearing the frequency of occurrence of fish on Santa Maria was significantly lower than on all the other three islands studied (Corvo: $\chi^2_1 = 4.07$, $p = 0.044$; Graciosa: $\chi^2_1 = 5.52$, $p = 0.0189$; Faial: $\chi^2_1 = 11.21$, $p = 0.0008$; see Fig. 4) and the frequency of occurrence of cephalopods on Corvo was significantly higher than in Graciosa ($\chi^2_1 = 6.63$, $p = 0.01$; see Fig. 4). In 1999, during chick-rearing, the frequency of occurrence of fish was significantly lower in Corvo than in Santa Maria ($\chi^2_1 = 15.33$, $p < 0.0001$; see Fig. 5) and Graciosa ($\chi^2_1 = 4.21$, $p = 0.04$; see Fig. 5). In 1999 the occurrence of fish decreased as latitude and longitude increased (Fig. 5) but in 1998 there was no apparent trend (Fig. 4). The frequency of occurrence of cephalopods was similar across our study islands in 1998 and 1999. However, we found a significant difference in the number of cephalopods found during chick-rearing between Corvo, Santa Maria and Graciosa, both in

Table 3

Numerical frequency (%) of cephalopod species in food samples of Cory's shearwaters in the Azores calculated from lower beaks (no. of individuals in parentheses).

Family	1998	1999	2000	2002	All
<i>Species</i>					
Decapods	94.1 (506)	98.4 (120)	96.0 (24)	91.9 (34)	94.7 (684)
Brachioteuthidae					
<i>Brachioteuthis riisei</i> ^M	10.2 (55)	–	–	13.5 (5)	8.3 (60)
Chiroteuthidae					
<i>Chiroteuthis</i> sp. ^L	2.6 (14)	1.6 (2)	–	5.4 (2)	2.5 (18)
<i>Chiroteuthis</i> B ^L	0.4 (2)	0.8 (1)	–	–	0.4 (3)
<i>Valbiteuthis danae</i> ^L	0.7 (4)	–	–	–	0.6 (4)
Cranchiidae					
<i>Egea</i> sp. ^{*,L}	0.6 (3)	–	–	–	0.4 (3)
<i>Cranchia scabra</i> ^L	0.2 (1)	–	–	–	0.1 (1)
<i>Galiteuthis armata</i> ^L	0.2 (1)	–	–	–	0.1 (1)
<i>Leachia cyclura</i> ^L	0.2 (1)	3.3 (4)	–	–	0.7 (5)
<i>Helichocranchia pfefferi</i> ^L	0.4 (2)	9.8 (12)	–	–	1.9 (14)
<i>Helichocranchia joubini</i> ^{*,L}	–	9.0 (11)	–	–	1.5 (11)
<i>Liocranchia reinhardti</i> ^L	–	0.8 (1)	–	–	0.1 (1)
<i>Taonius pavo</i> ^{*,L}	15.8 (85)	6.6 (8)	4.0 (1)	21.6 (8)	14.1 (102)
<i>Teuthowenia</i> sp. ^L	1.3 (7)	1.6 (2)	4.0 (1)	–	1.4 (10)
<i>Megalocranchia</i> sp. ^L	0.2 (1)	–	–	–	0.1 (1)
Enoploteuthidae					
<i>Abraliopsis</i> sp. ^{*,M,L}	0.6 (3)	–	–	–	0.4 (3)
Gonatidae					
<i>Gonatus steenstrupi</i> ^M	3.9 (21)	9.8 (12)	–	–	4.6 (33)
Grimalditeuthidae					
<i>Grimalditeuthis bonplandi</i>	0.9 (5)	1.6 (2)	–	–	1.0 (7)
Histioteuthidae					
<i>Histioteuthis</i> sp. ^{*,L}	12.3(66)	–	4.0 (1)	2.7 (1)	9.4 (68)
<i>Histioteuthis</i> A ⁺	19.0 (102)	5.7 (7)	20.0 (5)	–	15.8 (114)
<i>Histioteuthis</i> B ^L	0.7 (4)	–	4.0 (1)	–	0.7 (5)
<i>H. arcturi</i> ^L	–	0.8 (1)	–	5.4 (2)	0.4 (3)
<i>H. bonelli</i> ^{*,L}	0.7 (4)	4.9 (6)	–	–	1.4 (10)
<i>H. celetaria</i> ^L	–	–	4.0 (1)	2.7 (1)	0.3 (2)
<i>H. corona</i> ^L	–	1.6 (2)	8.0 (2)	–	0.6 (4)
<i>H. meleagroteuthis</i> ^L	0.2 (1)	7.4 (9)	16.0 (4)	–	1.9 (14)
<i>H. reversa</i> ^{*,L}	0.9 (5)	–	–	–	0.7 (5)
Joubiniteuthidae					
<i>Joubiniteuthis portieri</i> ^L	0.2 (1)	–	–	–	0.1 (1)
Mastigoteuthidae					
<i>Mastigoteuthis</i> sp. ^{*,L}	0.9 (5)	–	–	–	0.7 (5)
<i>Mastigoteuthis magna</i> ^L	0.6 (3)	0.8 (1)	8.0 (2)	–	0.8 (6)
<i>Mastigoteuthis hjorti</i> ^L	–	1.6 (2)	–	–	0.3 (2)
<i>Mastigoteuthis glaukopsis</i> ^L	0.2 (1)	–	–	–	0.1 (1)
Neoteuthidae					
<i>Neoteuthis theilei</i> ^{M,L}	0.4 (2)	–	–	–	0.3 (2)
Octopoteuthidae					
<i>Octopoteuthis</i> sp. ^{*,L}	0.4 (2)	1.6 (2)	–	–	0.6 (4)
Ommastrephidae					
unidentified ^M	7.2 (39)	3.3 (4)	–	–	6.0 (43)
<i>Todarodes sagittatus</i> ^{*,M}	10.0 (54)	–	24.0 (6)	10.8 (4)	8.9 (64)
<i>Ommastrephes bartramii</i> ^{*,M,L}	1.3 (7)	24.6 (30)	–	16.2 (6)	6.0 (43)
Onychoteuthidae					
<i>Onykia carribaea</i> ^{M,L}	0.4 (2)	0.8 (1)	–	–	0.4 (3)
<i>Onychoteuthis banksii</i> ^{*,M,L}	0.4 (2)	–	–	8.1 (3)	0.7 (5)
Pyroteuthidae					
<i>Pyroteuthis margaritifera</i> ^{M,L}	0.2 (1)	–	–	–	0.1 (1)
Sepiolidae					
<i>Heteroteuthis dispar</i> ^{M,L}	–	–	–	5.4 (2)	0.3 (2)
Octopods	4.8 (26)	1.6 (2)	–	–	3.9 (28)
Alloposidae					
<i>Haliphron atlanticus</i> [*]	3.9 (21)	0.8 (1)	–	–	3.0 (22)
Argonautidae					
<i>Argonauta argo</i> ^M	0.9 (5)	–	–	–	0.7 (5)

Table 3 (continued)

Family	1998	1999	2000	2002	All
Tremoctopodidae					
<i>Tremoctopus violaceus</i> ^M	–	0.8 (1)	–	–	0.1 (1)
Unidentified	1.1 (6)	–	4.0 (1)	8.1 (3)	1.4 (10)
N	538	122	25	37	722

* Species whose presence was shown by flesh remains as well as beaks—represent 30.2%.

^M Muscular species—represent 30.2%.

^L Luminous species—represent 81.4%.

Table 4

Estimated size and weight of cephalopods found in food samples of Cory's shearwaters in the Azores—mean \pm SD. LRL=lower rostral length; ML=mantle length; SL=standard length. Percent W indicates the weight frequency calculated considering only the cephalopod species for which mass was available and considering all years together.

Family	N	LRL (mm)	ML (mm)	SL (mm)	Estimated mass (g)	%W
<i>Species</i>						
Brachioteuthidae						
<i>Brachioteuthis riisei</i> ^a	12	4.8 \pm 1.2	113.3 \pm 23.2	163	16.1 \pm 5.4	2.5
Chiroteuthidae						
<i>Chiroteuthis sp.</i> ^a	7	5.0 \pm 1.6	72.1 \pm 56.7	273	133.0 \pm 39.9	7.2
Cranchiidae						
<i>Egea sp.</i>	2	2.3 \pm 1.9	125.9 \pm 117.3	176	19.0 \pm 24.4	0.2
<i>Leachia cyclura</i> ^a	5	1.1 \pm 0.1	91.6 \pm 3.0	128	4.9 \pm 0.4	0.1
<i>Helichocranchia pfefferi</i>	12	1.0 \pm 0.3	51.2 \pm 18.0	73	2.6 \pm 1.9	0.1
<i>H. joubini</i>	11	0.9 \pm 0.1	44.7 \pm 6.2	64	1.9 \pm 0.4	0.1
<i>Taonius pavo</i> ^a	55	5.6 \pm 1.0	331.6 \pm 58.7	398	98.9 \pm 31.1	26.0
<i>Teuthowenia sp.</i>	8	4.5 \pm 0.9	195.2 \pm 36.0	79	73.2 \pm 32.2	1.9
Enoploteuthidae						
<i>Abraliopsis sp.</i>	3	1.4 \pm 0.4	36.1 \pm 7.3	92	4.0 \pm 2.4	< 0.1
Gonatidae						
<i>Gonatus steenstrupi</i> ^a	29	6.0 \pm 1.9	215.5 \pm 82.7	375	301.3 \pm 431.1	25.6
Histioteuthidae						
<i>Histioteuthis A</i> ^a	45	3.4 \pm 1.3	61.3 \pm 28.8	253	78.2 \pm 59.2	23.0
<i>Histioteuthis B</i>	7	2.4 \pm 0.7	38.8 \pm 14.8	106	35.5 \pm 22.2	0.5
<i>Histioteuthis meleagroteuthis</i> ^a	14	2.8 \pm 0.4	48.3 \pm 9.7	165	47.5 \pm 14.6	1.7
Joubiniteuthidae						
<i>Joubiniteuthis portieri</i>	1	1.7	53	228	3.3	< 0.1
Mastigoteuthidae						
<i>Mastigoteuthis sp.</i> ^a	10	3.9 \pm 0.9	110.7 \pm 25.7	244	67.0 \pm 45.0	2.4
Neoteuthidae						
<i>Neoteuthis theilei</i> ^a	1	2.8	130	260	53.0	0.3
Octopoteuthidae						
<i>Octopoteuthis sp.</i> ^a	2	4.5 \pm 0.6	76.7 \pm 11.0	161	27.0 \pm 8.8	0.3
Ommastrephidae						
<i>Todarodes sagittatus</i>	42	1.4 \pm 0.4	92.6 \pm 12.2	141	14.8 \pm 9.0	2.4
<i>Ommastrephes bartramii</i>	40	2.3 \pm 0.6	116.2 \pm 17.9	176	35.1 \pm 17.6	3.9
Onychoteuthidae ^a	4	2.9 \pm 0.6	149.5 \pm 12.6	223	96.5 \pm 25.8	2.0
Pyroteuthidae						
<i>Pyroteuthis margaritifera</i> ^a	1	1.8	54.4	122	–	–

^a Average adult sizes.

1998 (Pearson's Chi Square Test, goodness of fitness: $\chi^2_2=6.91$, $p=0.032$) and 1999 (Pearson's Chi Square Test, goodness of fitness $\chi^2_2=12.20$, $p=0.002$). The number of cephalopods was highest on Corvo for both years. Overall we also found a higher

diversity of cephalopods on Corvo (27 species) than on Santa Maria and Graciosa islands (11 and 13 species, respectively).

The fish species present in the diet of Cory's shearwater are shown in Table 5. Samples containing fish had on average 2.1 ± 2.4

Table 5

Numerical frequency (%) of fish species in food samples of Cory's shearwaters in the Azores (no. of individuals in parentheses). Identification was based in otoliths and vertebrae. About 53% of the *Trachurus picturatus* could be identified from flesh.

Family	1998	1999	2000	2002	All
<i>Species</i>					
Carangidae					
<i>Trachurus picturatus</i>	52.8 (167)	–	–	61.6 (175)	46.8 (342)
Caproidae					
<i>Capros aper</i>	0.3 (1)	–	–	–	0.1 (1)
Centrolophidae	1.9 (6)	–	–	–	0.8 (6)
Coriphaenaidae					
<i>Nematonurus armatus</i>	0.3 (1)	–	–	–	0.1 (1)
Diretmidae					
<i>Diretmus argenteus</i>	0.9 (3)	5.3 (6)	–	–	1.2 (9)
Exocoetidae					
Unidentified	0.9 (3)	–	–	–	0.4 (3)
<i>Exocoetus obtusirostris</i>	–	0.9 (1)	–	–	0.1 (1)
Gadidae					
<i>Gadiculus argenteus</i>	–	0.9 (1)	–	–	0.1 (1)
Gonostomatidae					
<i>Gonostoma denudatum</i>	–	0.9 (1)	–	–	0.1 (1)
Macrouridae					
<i>Malacocephalus laevis</i>	–	–	5.9 (1)	–	0.1 (1)
<i>Nezumia sp.</i>	0.3 (1)	–	–	–	0.1 (1)
Melamphaidae					
Unidentified	–	2.6 (3)	–	–	0.4 (3)
<i>Scopelogadus beanie</i>	1.3 (4)	–	–	–	0.1 (1)
<i>Melamphaes megalops</i>	–	0.9 (1)	–	–	0.1 (1)
<i>Melamphaes suborbitalis</i>	–	1.8 (2)	–	–	0.3 (2)
<i>Poromita sp.</i>	–	0.9 (1)	–	–	0.1 (1)
<i>Poromita megalops</i>	–	2.6 (3)	–	–	0.4 (3)
<i>Poromita capito</i>	–	0.9 (1)	–	–	0.1 (1)
Myctophidae					
unidentified	1.9 (6)	0.9 (1)	–	–	(7)
<i>Benthoosema sp.</i>	0.6 (2)	–	–	–	0.3 (2)
<i>Benthoosema suborbitale</i>	0.3 (1)	–	–	–	0.1 (1)
<i>Bolinycthis sp.</i>	–	0.9 (1)	–	–	0.1 (1)
<i>Ceratoscopus maderensis</i>	1.3 (4)	–	–	–	0.5 (4)
<i>Diaphus adenomous</i>	0.3 (1)	–	–	–	0.1 (1)
<i>Diaphus effulgens</i>	0.3 (1)	–	–	–	0.1 (1)
<i>Diaphus metopoclampus</i>	–	0.9 (1)	–	–	0.1 (1)
<i>Electrona rissoi</i>	0.6 (2)	7.9 (9)	–	–	1.5 (11)
<i>Lampanyctus sp.</i>	0.3 (1)	–	–	–	0.1 (1)
<i>Lampanyctus crocodilus</i>	–	1.8 (2)	–	–	0.3 (2)
<i>Lobianchia gemellarii</i>	–	0.9 (1)	–	–	0.1 (1)
Macrouridae					
<i>Nezumia sp.</i>	–	–	5.9 (1)	–	0.1 (1)
Nomeidae					
<i>Cubiceps gracilis</i>	–	–	–	18.0 (51)	7.0 (51)
<i>Sardina pilchardus</i>	0.3 (1)	–	–	1.1 (3)	0.5 (4)
Opisthoproctidae					
<i>Opisthoproctus soleatus</i>	–	2.6 (3)	–	–	11.4 (83)
Percoidei	–	0.9 (1)	–	–	0.1 (1)
Phycidae					
<i>Phycis blennoides</i>	0.3 (1)	–	–	–	0.1 (1)

Table 5 (continued)

Family	1998	1999	2000	2002	All
Scomberosocidae					
<i>Scomberesox saurus</i>	2.5 (8)	23.7 (27)	29.4 (5)	12.7 (36)	10.4 (76)
Scombridae					
<i>Scomber japonicus</i>	3.2 (10)	–	–	–	1.4 (10)
Sternoptychidae					
<i>Maurolucus muellerii</i>	10.8 (34)	10.5 (12)	–	–	6.3 (46)
Unidentified	18.4 (58)	31.6 (36)	58.8 (10)	6.7 (19)	16.8 (123)
N	316	114	17	284	731

Table 6

Numerical frequency (%) of fish species in food samples of Cory's shearwaters in the Azores (no. of individuals in parentheses) during 2002. For *Trachurus picturatus* we also present data on fork length (FL, mean \pm SD) and weight. Range values in parentheses.

Taxon	Vila pre-laying	Vila incubation	Vila chick-rearing	Praia incubation
Carangidae				
<i>Trachurus picturatus</i>	23.5 (8)	35.9 (33)	99.1 (110)	51.1 (24)
FL* (mm)	191.9 \pm 45.1 (122.3–230.2)	140.5 \pm 13.6 (108.4–160.2)	158.8 \pm 21.5 (122.3–244.1)	158.0 \pm 25.6 (129.3–244.1)
Wt (g)	90.8 \pm 50.0 (19.6–140.7)	31.2 \pm 8.6 (13.4–46.4)	47.5 \pm 21.5 (19.6–169.1)	47.1 \pm 30.2 (23.3–158.0)
Nomeidae				
<i>Cubiceps gracilis</i>	26.5 (9)	45.7 (42)	–	–
<i>Sardina pilchardus</i>	5.9 (2)	1.1 (1)	–	–
Scomberosocidae				
<i>Scomberesox saurus</i>	26.5 (9)	6.5 (6)	–	44.7 (21)
Unidentified	17.7 (6)	10.9 (10)	0.9 (1)	4.3 (2)
N	34	92	111	47

* The length of the fish indicates that their age varied between 0 and a potential maximum of 4 years (Isidro, 1990).

Table 7

Estimations of fork length (FL, mean \pm SD) and weight of *Trachurus picturatus* from samples collected in 1998. Range values in parentheses.

Taxon	Faial pre-laying March–May	Faial incubation May–June	Faial chick-rearing July–September	All ^a
Carangidae				
<i>Trachurus picturatus</i>				
FL* (mm)	170.7 \pm 12.6 (150.2–185.0)	128.6 \pm 29.5 (98.0–191.9)	123.2 \pm 50.5 (98.0–282.4)	146.6 \pm 31.7 (98.0–282.4)
Wt (g)	56.5 \pm 12.5 (37.4–71.4)	27.1 \pm 21.3 (9.9–67.3)	59.9 \pm 72.8 (9.9–266.3)	59.9 \pm 21.5 (9.9–266.3)
N	10	21	18	104

* The length of the fish indicates that their age varied between 0 and a potential maximum of 4 years (Isidro, 1990).

^a Includes samples from Corvo, Santa Maria, Graciosa and Faial.

individuals (range = 1 to 8, but one sample was exceptional containing 33 silvery lightfish *Maurolucus muellerii*). Most species were identified from otoliths with the exception of blue jack mackerel, driftfish *Cubiceps gracilis*, sardine *Sardina pilchardus*, Atlantic chub mackerel *Scomber japonicus* and Atlantic saury *Scomberesox saurus*, which were identified from vertebrae. Blue jack mackerel would have been severely underestimated if we considered otoliths only; for example, in 1998 samples contained 43 specimens considering otoliths only, but 167 considering vertebrae. In 1999 and 2000 the samples contained very few otoliths and most of the vertebrae

present could not be identified given they were not represented in the reference collection. For this reason most fishes were not identified; we include pictures of the unidentified vertebrae in the electronic supplementary material in case identification is possible in the future. Blue jack mackerel was the most abundant fish prey by number in 1998 and 2002 (53.5% and 61.6%, respectively), but was absent from the diet in 1999 and 2000 (Table 5). The size of blue jack mackerel found in the samples in 1998 and 2002 ranged between 98.0 and 282.4 mm and showed no pattern of increase or decrease across the breeding cycle for both 1998 and 2002 (Tables 6 and 7).

The overall numerical frequency of cephalopods and fish varied markedly between years (Fig. 8). The weight contribution of cephalopod and fish also varied considerably between years; we could not estimate weight and length for all the cephalopod and fish prey species because for some species the allometric equations are not available. However, taking into consideration the prey species for which weight is available we estimated that the contribution of fish by weight was 45.2% in 1998 and 94.2% in 2002, while the contribution of cephalopod by weight was 54.8% in 1998 and 5.8% in 2002.

Fig. 9 shows the relative numbers of different cephalopod families in the stomachs of Cory's shearwaters (this study), Bulwer's petrels *Bulweria bulwerii* (Neves et al., 2011) and Barolo shearwaters *Puffinus baroli* (Neves et al., 2012). Table 8 shows the relative numbers of different cephalopod families in the stomachs of Cory's shearwaters (this study), sperm whales *Physeter macrocephalus* (Clarke, 2006), swordfish *Xiphias gladius* (Clarke et al., 1995) and blue sharks *Prionace glauca* (Clarke et al., 1996), and caught by nets (Clarke, 2006); Table 9 compares the average ML of different cephalopod species present in the diet of these predators.

Crustaceans could not be identified but eight samples in 1999 from Graciosa, Corvo and Santa Maria Udekem d'Acoz et al. (2001)

and one sample from Santa Maria in 2002 contained grooveback shrimps *Parapasiphae sulcatifrons*. Two samples contained a specimen of by-the-wind sailor *Vellella vellella* and eight samples contained pieces of plastic.

3.4. Estimation of fish and cephalopod consumption

Adult Cory's shearwaters in the Azores weigh on average 840 g (Monteiro et al., 1996), yielding an estimated daily energy

Table 8

Relative numbers (%) of the different cephalopod families in the stomachs of Cory's shearwaters (this study), nets (Clarke, 2006), sperm whales (Clarke, 2006), swordfish (Clarke et al., 1995) and blue sharks (Clarke et al., 1996).

Cephalopod family	Cory's shearwater	Nets	Sperm whale	Swordfish	Blue shark
Histioteuthidae	32.0	–	75.1	3.5	34.7
Ommastrephidae	21.4	1.1	1.2	13.0	–
Cranchiidae	19.7	18.1	6.8	12.2	5.9
Brachioteuthidae	8.6	1.1	–	5.2	–
Gonatidae	4.7	–	1.4	–	0.5
Chiroteuthidae	3.6	9.6	0.6	7.8	13.4
Alloposidae	3.1	–	1.1	0.9	5.0
Mastigoteuthidae	2.0	5.3	0.3	0.9	19.8
Onychoteuthidae	1.1	–	0.4	7.8	3.0
Grimalditeuthidae	1.0	–	–	0.9	6.9
Argonautidae	0.7	–	–	39.1	0.5
Octopoteuthidae	0.6	1.1	6.1	–	3.5
Enoploteuthidae	0.4	1.1	–	1.7	–
Sepiolidae	0.3	27.7	–	0.9	–
Neoteuthidae	0.3	–	–	–	–
Joubiniteuthidae	0.1	2.1	–	–	1.5
Pyroteuthidae	0.1	22.3	–	1.7	–
Tremoctopodidae	0.1	–	–	–	–
Cirroteuthidae	–	4.3	–	–	–
Bathyteuthidae	–	2.1	–	–	–
Bolitaenidae	–	2.1	–	–	1.0
Cycloteuthidae	–	1.1	4.6	–	1.0
Spirulidae	–	1.1	–	–	–
Ancistrocheiridae	–	–	0.7	–	4.5
Architeuthidae	–	–	0.5	–	–
Pholidoteuthidae	–	–	1.2	4.4	–
Vampyroteuthidae	–	–	–	–	0.5

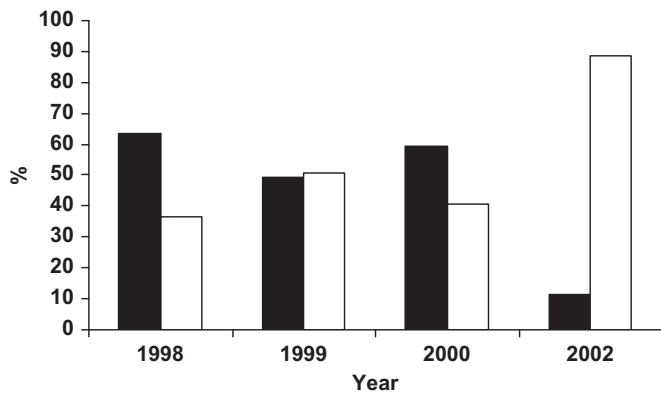


Fig. 8. Numerical frequency (%) of cephalopods (black columns) and fish (white columns) in food samples of Cory's shearwaters in the Azores. Number of prey items equals 854 in 1998, 236 in 1999, 42 in 2000 and 321 in 2002.

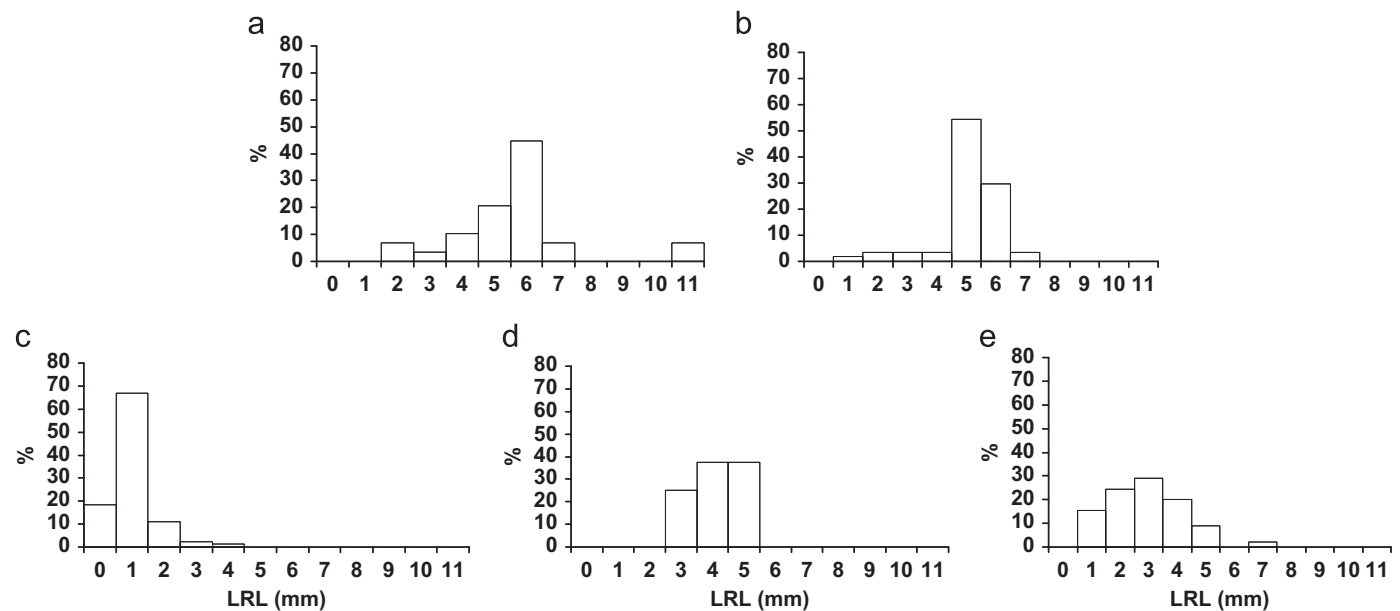


Fig. 9. Lower rostral length distributions of (a) *Gonatus steenstrupi*; (b) *Taonius pavo*; (c) *Ommastrephes bartramii*; (d) *Teuthowenia* sp. and (e) *Histioteuthis* A in the diet of Cory's shearwaters.

Table 9
Comparison of the mean mantle length (ML, mm) of different cephalopod families in the stomachs of Cory's shearwaters (this study), sperm whales (Clarke, 2006), swordfish (Clarke et al., 1995) and blue sharks (Clarke et al., 1996).

Cephalopod Family	Cory's shearwater	Sperm whale*	Swordfish	Blue shark
Histioteuthidae				
<i>Histioteuthis A</i>	61.3 (10.8–141.9)	111	68 (52–83)	69.6 (31.5–107.8)
<i>Histioteuthis B</i>	38.8 (24.2–46–4)	59	41 (30–46)	31.9 (8.6–61.9)
Ommastrephidae				
<i>Todarodes sagittatus</i>	92.6 (77.5–121.7)	484	168 (136–229)	–
<i>Ommastrephes bartramii</i>	116.2 (77.6–143.8)	486	245 (160–378)	–
Cranchiidae				
<i>Taonius pavo</i>	331.6 (172.0–411.6)	412	313 (282–344)	315.9 (233.4–350.1)
Brachioteuthidae	113.3 (76.6–110.8)	–	66 (53–79)	–
Gonatidae	215.5 (179.5–261.0)	149	–	–
Chiroteuthidae	72.1 (65.2–97.3)	154.5	129 (75–175)	130.9 (87.2–192.4)
Mastigoteuthidae	110.7 (76.7–158)	170.5	94 (94–94)	139.0 (18.6–204.7)
Onychoteuthidae	149.5 (136–166)	166	180 (124–337)	–
Octopoteuthidae	76.7 (68.9–84.5)	325	–	–
Joubiniteuthidae	53 (53–53)	–	–	54.6 (45.6–70.1)
Pyroteuthidae	54.4 (54.4–54.4)	–	39 (39–39)	–

* The range of ML is not available for sperm whales.

requirement (DER) of about 1204 kJ d^{-1} for FMR and about 366.8 kJ d^{-1} for BMR (see Section 2). Overall Cory's shearwaters prey on fish weighing on average 43 g and cephalopods weighing on average 76 g. Considering annual consumption, and based on the numerical frequencies of fish and cephalopod presented in Fig. 8, throughout the year the Azorean population of Cory's shearwaters would consume about 54.5 t of cephalopod and 18.1 t of fish in a year like 1998; on the other hand, in years like 2000 when the diet is composed mainly of fish, birds would consume about 9.6 t of cephalopods and 41.1 t of fish.

4. Discussion

The large diversity of fish and cephalopods found in this study, as well as the detection of spatio-temporal differences in diet, strongly suggest that Cory's shearwaters are opportunistic feeders. Inter-annual variations in Cory's shearwater diet were already known to occur (Granadeiro et al., 1998; Xavier et al., 2011). However our study is the first to demonstrate spatial variation as well as variation across the breeding cycle for a given year.

4.1. Prey distribution

Our study greatly increased the number of prey species observed in Cory's shearwater diet. 37 species of oceanic cephalopods were present including three octopods. Of those, most have a mesopelagic distribution and would not be expected to occur at the sea surface, on the basis of present knowledge from net captures (Clarke, 2006). In 1999, we found 11 specimens of *Helicocranchia joubini* in the stomachs of Cory's shearwaters; this is a rare cranchiidae that has hardly been seen again since its original description by Voss, 1962. 83% of the cephalopod species caught have photophores and could be targeted at dusk and dawn. Among cephalopods, the families Histioteuthidae, Ommastrephidae and Cranchiidae were the most common in the diet of Cory's shearwaters, occurring in all the sampled years. A previous study on Cory's shearwater diet conducted in the Azores, Madeira and the Canary islands between 1977 and 1981 also found Histioteuthidae and Ommastrephidae to be the most abundant cephalopod families (Den Hartog and Clarke, 1996). Cranchiidae and Histioteuthidae have been found to be important in the diet

of other Procellariiformes such as the grey-faced petrel *Pterodroma macroptera* (Imber 1973) and Providence petrel *Pterodroma solandri* (Bester et al., 2010).

Cory's shearwaters have been observed diving down to $\sim 20 \text{ m}$ (Daniel Goetz, pers. comm., Bried and Lambardi unpubl. data). Of the cephalopod species present in their diet, only *Helicocranchia pfefferi*, *Leachia cyclura*, *Onykia caribbaea*, *Onychoteuthis banksi*, *Abraliopsis* sp. and *Brachioteuthis riisei* would be expected to be available at those depths. *Valbyteuthis danae*, *Grimalditeuthis bonplandi*, *Joubiniteuthis portieri* and *Neoteuthis theilei* have all been caught only rarely by nets (possibly < 10 – 20 times; Clarke, 2006) and their occurrence in the diet shows how inefficient net sampling is, particularly close to the surface. The occurrence of these species was rather low and may result from scavenging of individuals found floating. Cephalopod species which would not be expected to come within hundreds of metres of the sea surface (on the basis of our present knowledge from net captures) are *Mastigoteuthis magna*, *Chiroteuthis* spp., *Valbyteuthis* sp., *Grimalditeuthis bonplandi*, *Joubiniteuthis portieri*, *Octopoteuthis* sp., *Neoteuthis theilei* and *Haliphron atlanticus*. The other species consumed by Cory's shearwaters (*Taonius pavo*, *Teuthowenia megalops*, *Galiteuthis armata*, *Histioteuthis bonnellii* and *Gonatus steenstrupii*) are of a size which makes their closeness to the surface unlikely. One explanation to account for some of these occurrences may be that cetaceans eat the same species and vomit their beaks, with some attached flesh, at the surface. The regular occurrence of heads of *H. atlanticus* floating on the sea surface in the Azores adds credence to this view and might explain the consumption of some of the larger species which are also eaten by sperm whales. The very fluid and gelatinous tissue of *H. atlanticus* has defied most efforts to estimate weight or, in most cases, to even collect complete specimens (the IRLs of *H. atlanticus* found in the diet of Cory's shearwaters varied between 1.5 and 5.5 mm). These are very large, measuring over 2 m long and it is impossible that a bird could swallow one whole. The densest and most nutritious morsel of these cephalopods is probably the buccal muscle around the beaks and it is likely that that is the reason for *H. atlanticus* beaks occurring in Cory's shearwater stomach contents. Rather than including the total weight for the Haliphron it would seem better to include a figure for the buccal mass weight (ca 150 g). Even so, this shows that the species contribution is not inconsiderable. All other beaks represent specimens which could probably be attacked and consumed by a Cory's shearwater given their estimated mantle length.

All the cephalopods found in this study are oceanic, in line with the results of Magalhães et al. (2008) and Paiva et al. (2010a), who found that Azorean Cory's shearwaters feed in oceanic areas and not off the Portuguese and African coastal shelves. Otherwise they would probably consume *Loligo* sp., as well as *Sepia* sp. and benthic octopods. In the northeast Atlantic *Gonatus steenstrupi* has only been found at latitudes comprised between 46° and 60°N (Clarke, 2006) and therefore its presence in the stomachs of Cory's shearwaters indicates that the birds feed north of the Azores. This is also in accordance with results from Magalhães et al. (2008) who found that the Cory's shearwaters from the Azores can forage up to 1800 km north of their breeding colonies. *Gonatus steenstrupi* is particularly nutritious as its liver contains oil similar to squalene for buoyancy.

4.2. Comparison with other predators

Cory's shearwater diet showed a large diversity of cephalopods; 18 families were present in their stomachs, a number slightly higher than for sperm whales (16; Clarke, 2006), swordfish (17; Clarke et al., 1995) blue sharks (16; Clarke et al., 1996) and net captures (16; Clarke, 2006) and more than twice the number present in Bulwer's petrels (5; Neves et al., 2011) and Barolo shearwater (6; Neves et al., 2012) stomach contents (Fig. 10). There is a clear dietary segregation among Azorean breeding Procellariiformes regarding cephalopod consumption with Cory's shearwater relying on several families while the smaller Bulwer's petrel and Barolo shearwater mainly consume a few species (Neves et al., 2011, 2012). Histioteluthidae and Cranchiidae were the only families present in the diet of these three seabirds (Fig. 10) and Cranchiidae was the only family consumed by all the different predators (Table 8).

The size distribution of the beaks of *Taonius pavo* (Fig. 9b) with a peak at 5–6 mm and an average of 5.5 mm, is similar to what was found for swordfish (Clarke et al. 1995) and blue sharks (Clarke et al., 1996), but Cory's shearwaters prey on a larger range of sizes (Table 9). The size distribution of the beaks of *Teuthowenia* sp.

(Fig. 9d) peaks at 4–6 mm lower to what was found for sperm whales (Clarke et al., 1993).

The species, distribution and abundance of squids in the subtropical mid-North Atlantic are difficult to assess by conventional oceanographic means (Clarke, 2006) and as seen by our study the sampling of cephalopods can be complemented with samples collected from Cory's shearwater. Two families present in Cory's shearwaters stomachs, but not in those of other predators or in nets; were Neotheluthidae and Tremoctopodidae (Table 8). Cory's shearwaters cover a much smaller proportion of the ocean than sperm whales, swordfish and blue sharks, as well as scientific nets as these birds do not dive very deep (maximum diving depth = 9.8 ± 2.4 m; Paiva et al., 2010b), nevertheless they are efficient samplers of oceanic cephalopods. While the sizes of some cephalopods such as those from Cranchiidae, Histioteluthidae, Joubinoteuthidae and Onychoteuthidae families are similar in the stomachs of Cory's shearwaters and other predators (Table 9), others such as the Ommastrephidae family are smaller in Cory's shearwaters stomachs (mean = 92 mm) than in sperm whale stomachs (mean = 485 mm; Clarke et al., 1993) and swordfish stomachs (mean = 207 mm; Clarke et al., 1995). So it is certain that Ommastrephidae are not made available for the birds by cetacean regurgitations. In the northeast Atlantic, *Todarodes sagittatus* is mainly caught between 400 and 700 m and the shallowest individual was caught at 52 m (Lordan et al., 2001); however our study shows that this species is available in the upper 20 m of the water column. All the *T. sagittatus* found in Cory's shearwater stomachs were juveniles; this cephalopod reaching maturity at sizes > 280 mm (Lordan et al., 2001) but most of the individuals consumed by Cory's shearwaters were below 120 mm.

Lanternfishes have been described previously from the diets of Azorean Laridae (Hamer et al., 1994), Sternidae (Ramos et al., 1998; Granadeiro et al., 2002) and small Procellariidae (Neves et al., 2011) but our study is the first to detect them in the diet of Cory's shearwater. It is possible that some of the deep-water fishes found in Cory's shearwaters diet can be driven to the

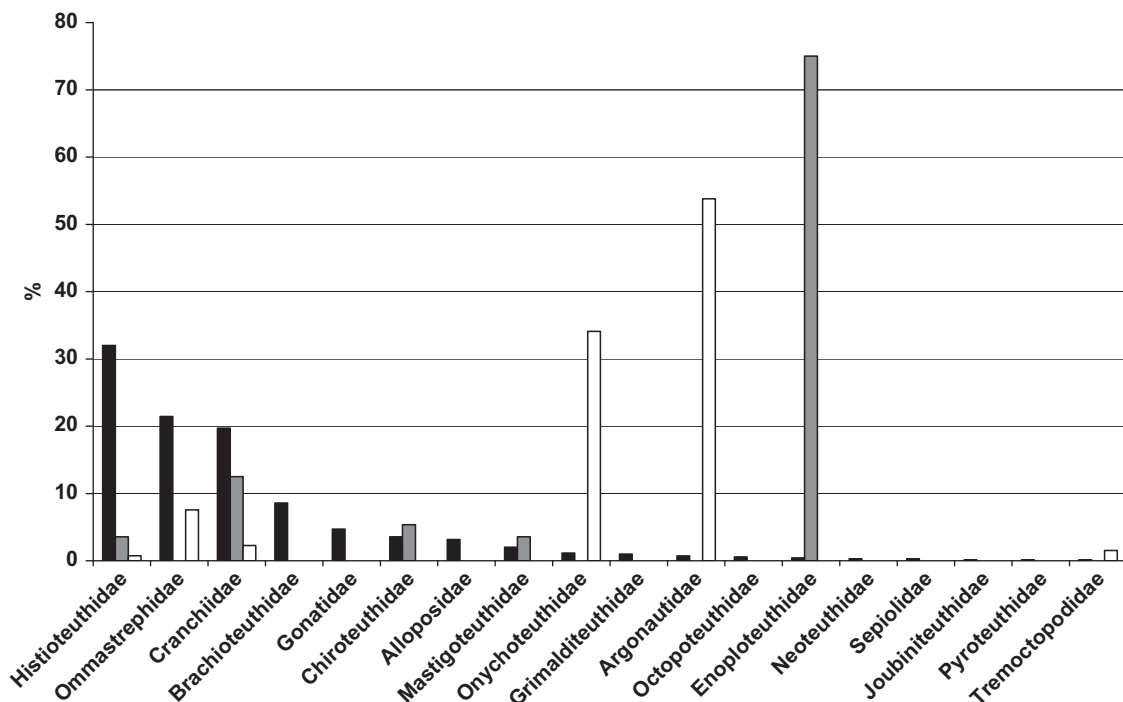


Fig. 10. Relative numbers of the different cephalopod families in the stomachs of Cory's shearwaters (black columns), Bulwer's petrels (grey columns) and Barolo shearwaters (white columns). Data on Bulwer's petrels from Neves et al. (2011) and from Barolo shearwaters from Neves et al. (2012).

surface by subsurface predators such as tuna and dolphins. However Cory's shearwaters also prey on mesopelagic squid (our study, Hartog and Clarke, 1996; Granadeiro et al., 1998; Xavier et al., 2011) and shrimp, namely *Parapasiphae sulcatifrons*, which is known to occur between 438 and 5340 m Udekem d'Acoz et al. (2001) and it is very unlikely that these organisms would come to the surface driven by tuna and dolphins. One of the fish present in the diet of Cory's shearwater, *Diaphus adenomus*, was detected for the first time in the Azores region. The presence of mesopelagic prey in the diet of both coastal feeders like terns and oceanic feeders like Cory's shearwater and Bulwer's petrel, as well as the fact they occur in birds from different colonies and islands and in different years, suggests that the availability of mesopelagic prey at the surface is a common phenomenon in the area.

4.3. Comparison with previous studies on Cory's shearwater diet

Blue jack mackerel was the main prey of Cory's shearwaters in 2002 (this study), in 2005 (Xavier et al., 2011) and in 2006 and 2007 (Paiva et al., 2010b), but was absent from the diet in 1999 and 2000 (this study) and occurred in only 3.8% by number in 1994 (Granadeiro et al., 1998). The commercial fleet captures of blue jack mackerel in the Azores in 1999 and 2000 were at their lowest level (João Gil pers. comm.) and this might help to explain the absence of this species in the diet of Cory's shearwater during those years. The breeding success of Cory's shearwaters on Vila islet, a mammal-free colony, has varied dramatically over the last 15 years (37.9 to 74.5%, in 2003 and 1994, respectively; Monteiro et al., 1996; Joël Bried, pers. comm.). It is possible that part of this variation is linked to fluctuations in food availability. In 2002 and 2005, years when blue jack mackerel formed a large proportion of the diet (this study, Xavier et al., 2011, respectively), the breeding success of Cory's shearwaters was high on Vila islet (64.6 and 62.9%, respectively; Joël Bried, pers. comm.), but unfortunately we do not have data for breeding success in 1999 and 2000 when blue jack mackerel was absent from Cory's shearwater diet. To better understand the effects of food availability we need to simultaneously collect data on diet and breeding success.

Our study provides a baseline to monitor changes in the cephalopod community in the northeastern Atlantic, especially in the current context of global climate change (Hughes, 2000), and highlights the potential role of seabirds as indicators of these changes (see also e.g., Shealer, 2002; Pinaud et al., 2005). We recommend studying seabird diet in the Azores on a regular basis.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2012.08.003>.

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