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Diet and feeding ecology of Cory's shearwater *Calonectris diomedea* in the Azores, north-east Atlantic

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ABSTRACT: Cory's shearwater *Calonectris diomedea* is the most abundant pelagic seabird in the Azores archipelago. We examined their diet in March and August. Fish were present in more than 90% of the samples analysed, but only included 5 species. Two small pelagic species, boarfish *Capros aper* and trumpet fish *Macrorhamphosus* sp., were the most common prey, accounting for more than 85% of the food items consumed in March and August. Due to their small size (<120 mm) these 2 species only represented about 40% of the diet by weight. Conversely, sauries (*Scomberesox saurus* and *Nanychthys simulans*) represented an important proportion of the diet by weight (25%), despite being consumed in smaller numbers (<5%). Horse mackerel *Trachurus picturatus* and chub mackerel *Scomber japonicus* were consumed in low number and together accounted for 10% of the diet by weight. Twelve cephalopod species occurred in the diet, most having a mesopelagic distribution. It is suggested that these prey are made available to shearwaters when they are driven to the surface by underwater predators. Surprisingly, no deep water fish were detected in Cory's shearwater diet, despite being known to be available to other diurnal surface-feeding seabirds in this area. The diet of shearwaters in the Azores is discussed in relation to available information on the prey consumed by other coexisting marine predators. We suggest that Cory's shearwater provides useful and novel information on abundance and distribution of small pelagic fish in this region.

KEY WORDS: Feeding ecology · Pelagic fish · Cephalopod · Seabird

INTRODUCTION

Several studies have demonstrated that seabirds can be used to sample the marine environment (e.g. Ashmole 1971, Furness & Greenwood 1993, Cherel & Weimerskirch 1995, Croxall & Prince 1996, Furness & Camphuysen 1997) and special attention has been devoted to examining the response of seabirds to changing food availability (Hamer et al. 1991, Uttley et al. 1994, Ainley et al. 1995, Phillips et al. 1996). There have been attempts to establish relationships linking avian response to food availability at sea (Montevecchi 1993, Uttley et al. 1994, Phillips et al. 1996). However, modelling such causal relationships requires detailed information on both the biology of seabirds and that of their prey, which is still not available in some regions. The lack of adequate biological data is particularly obvious in areas where there are no fishery interests in exploring local stocks, such as many sub-tropical oceanic waters exhibiting low biological productivity (Montevecchi 1993). This is the case in the pelagic waters surrounding the Azores archipelago (36–39° N, 25–31° W), in the north-east Atlantic, for which there is still a paucity of both oceanographic information and data describing food webs (see Santos et al. 1995 for a review). Recent studies have described the diet of some seabirds in the archipelago (Granadeiro et al. 1995, Monteiro et al. 1996a, Ramos et al. in press a, b). However, most of the seabird species so far examined

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feed relatively close to breeding colonies and exhibit predominantly coastal feeding behaviour, hence information on seabird prey in oceanic waters is still scarce.

Cory's shearwater *Calonectris diomedea* is a pelagic seabird, breeding in the sub-tropical north-east Atlantic (Cramp & Simmons 1977). The Azores archipelago holds over 70% of the breeding numbers of the Atlantic subspecies *C. diomedea borealis*, currently estimated as 100000 pairs (Hagemeijer & Blair 1997). Despite being the most abundant seabird in this region, to date there is no quantitative information on its diet at the breeding grounds. Published results mainly report opportunistic observations of feeding behaviour of birds (e.g. Martin 1986), or make a general description of main prey items. Furness (1994) presented a quantitative assessment of squid consumption in the north-east Atlantic, presenting data on the importance of squid in the diet of Cory's shearwater. However, no reference was made to which species of squid are consumed, and these remain totally unknown (review in Croxall & Prince 1996).

Cory's shearwaters can forage over extensive areas (e.g. Mougin & Jouanin 1997) and their abundance suggests that they are important consumers of fish and squid in the pelagic ecosystem (e.g. Prince & Morgan 1987, Warham 1996). They are generalist surface feeders, and so their diets are likely to reflect short-term variability in food availability. They therefore represent suitable sampling units for the pelagic organisms which constitute their diet. Hence, the study of their diet will add considerable insight into their role in marine food webs, while providing information on the ecological processes which control energy transfer to top predators. In this study we examine the relative importance of cephalopod and fish prey in the diet of Cory's shearwater in the Azores during the breeding season and we estimate the mass of fish consumed annually by this species in this region. We interpret this information in light of current knowledge of the birds' behaviour, as well as that of their prey and co-existing predators.

METHODS

Fieldwork was conducted in the Azores archipelago (37–40° N, 25–32° W; see Santos et al. 1995 for a description of the archipelago) from 12 to 27 March 1994 and from 28 July to 17 August 1994 (hereafter referred to as March and August, respectively). These dates correspond to the pre-laying and chick rearing periods, respectively (Zino 1971, Granadeiro 1991). On both occasions we collected diet samples in the central group (Graciosa: Baixo and Praia islets) and eastern group (Santa Maria: Vila islet). In August the western group was also visited (Corvo; Fig. 1).

Cory's shearwaters were captured by hand at their breeding grounds and marked with a metal ring. It was not possible to determine the breeding status of all birds. While in March birds were captured inside and outside burrows, the majority of birds sampled in August were captured when entering burrows to feed chicks.

Diet samples were obtained under licence, by stomach flushing with salt water, by means of a device similar to that used by Wilson (1984) in penguins. Birds were immediately released after being sampled. We did not undertake quantitative validation experiments to assess the effectiveness of the method (e.g. Gales 1987) because excessive disturbance could disrupt breeding (Warham 1990, Granadeiro 1991). Nonetheless, a few trials conducted prior to this study showed

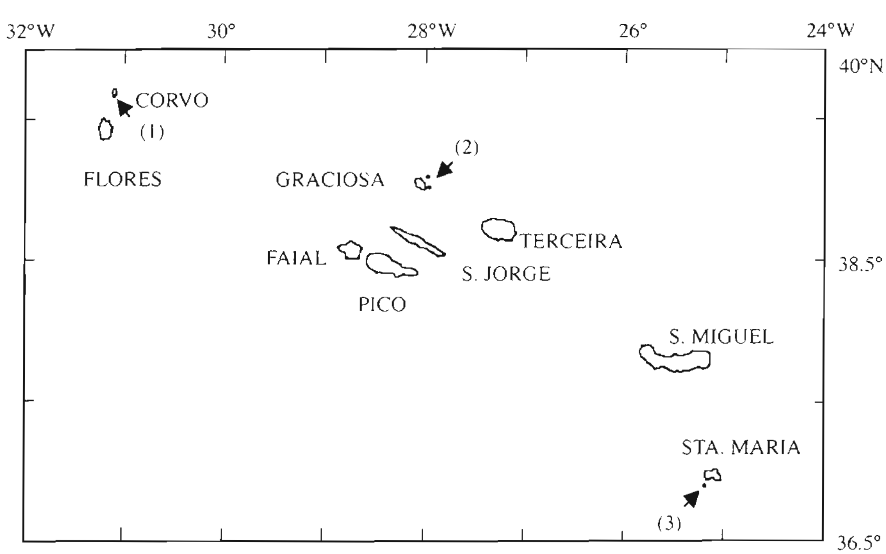

Fig. 1. The Azores archipelago, with the study colonies marked by arrows: (1) Corvo, (2) Graciosa (Baixo and Praia Islets), (3) Santa Maria (Vila Islet)

that no additional hard remains were obtained when the birds were subjected to a multiple flushing procedure, and therefore no bird was flushed twice. We sampled any individual only once. Some birds had empty stomachs and these were not considered in this study. About 90% of birds caught during the first hour after dark contained food, but this proportion decreased to about 10% of birds caught towards the end of the night, so sampling concentrated on birds arriving early in the night. Food samples were preserved in 70% alcohol, after excess salt water had been discarded. Less than 5% contained noticeable amounts of stomach oil, and we did not quantify this fraction in this study.

Samples were examined under a binocular microscope and all diagnostic structures were stored dry (fish: otoliths, scales and bones) or in 70% alcohol (cephalopod: beaks, gladii and muscular masses; exoskeletons of crustacea) for later identification. Hard remains were identified using available keys (Nolf 1985, Clarke 1986, Härkönen 1986, Watt et al. 1997) and reference collections of fish bones and otoliths, and squid beaks. For each sample the minimum number of individuals present was determined by the largest number of similar sized/shaped paired structures (fish: otoliths, jaws, cleitra; cephalopods: upper or lower mandibles) or from the number of unpaired remains (fish: spines, vomeric teeth, diagnostic vertebrae; cephalopods: gladii).

Cephalopods were identified from hard structures (beaks and gladii). Beaks can accumulate in the stomach of seabirds (Furness et al. 1984). To avoid overestimating their importance we counted only undigested beaks and muscle masses. Identification was made to the lowest possible taxon, using reference material and available keys (Clarke 1986, Pérez-Gandaras 1986), and cephalopod nomenclature followed Guerra (1992).

Some food samples were relatively well digested, but most remains were still covered by some muscle tissue. In these situations, vertebrae and squid beaks were generally not eroded by physical and chemical erosion. In contrast, very few otoliths could be found, because fish heads were nearly completely digested or were totally absent. The few otoliths found generally showed evidence of chemical abrasion and were used to identify, but not to estimate size or weight of, prey.

In order to reconstruct the original dimensions and weight of fish, we used species-specific regression equations relating vertebrae size with fish size and wet weight (J. Granadeiro & M. A. Silva unpubl. data). These equations were derived from size of vertebrae that could be uniquely identified even if the skeleton was totally disarticulated. Therefore size and weight estimates were obtained only when these characteristic vertebrae showed no signs of erosion. The 2 species of Atlantic saury, *Scomberesox saurus* and *Nanichthys simulans*, both occurring in the Azores (Whitehead et al. 1986), could not be distinguished from vertebral features and were pooled (= saury). We did not have equations relating bone size with saury dimension or weight, and hence we used vertebrae measurements obtained from only 2 specimens in our reference collection. We estimated size of sauries in food samples by linear interpolation using measurements of these 2 specimens, and weight was computed from log-transformed values of weight in relation to vertebral size.

The weight of cephalopods was estimated from measurements of rostral length of well-preserved beaks, following equations given in Pérez-Gandaras (1986) and Clarke (1986). A specimen with an estimated weight of 589 g (*Histioteuthis dolfleini*) was not considered in the computations of average weight, because most probably it was not consumed as a whole prey item. Crustacea were detected by remains of their exoskeletons, flesh being generally absent. A weight of 2 g was attributed to each crustacean, based on the average weight of *Pasiphaea* spp. caught off the Portuguese coast during 19 research cruises (2.0 ± 0.1 g), carried out between 1990 and 1997 (A. Silva pers. comm.). This procedure was unlikely to produce serious bias in the computations, because Crustacea represent a negligible proportion of Cory's shearwater diet.

All vertebrae and squid beaks were measured to the nearest 0.02 mm, using a binocular microscope fitted with an eye-piece graticule. In order to obtain the weight contribution of each species in the diet of shearwaters, we multiplied the number of specimens by the species-specific weight, obtained at each site during each period. Unidentified cephalopods were considered to occur according to the frequency distribution obtained from identified remains. Their contribution by weight was calculated by multiplying the number of individuals thought to belong to a given species by the corresponding estimated weight. When weight estimates were not available for a given species, we calculated a weighted average Family-specific weight. Since we could not measure beaks of Alloposidae and Mastigoteuthidae specimens, these were assigned an arbitrary weight corresponding to the average of all cephalopod specimens (72 g).

In order to estimate fish consumption by Cory's shearwater in the Azores, we multiplied the number of individuals of this species thought to occur in the region by their estimated daily energy requirements (DER) and by the proportion of fish found in their diet. Estimated DER was converted to energy intake needs by dividing this amount by energy assimilation efficiency, taken as 80% (Furness 1994, Warham 1996). The Azorean shearwater population was estimated as 70 000 breeding pairs (Hagemeijer & Blair 1997) and pre-breeding age birds were considered to correspond to 70% of the number of breeders (Furness 1994, Warham 1996), giving a total of about 238000 adults. We did not include consumption by chicks since this represents only about 5 to 10% that of adult birds (Mougin et al. 1996). In the absence of direct measures of energy expenditure, we estimated DER from published relationships between field metabolic rates (FMR, kJ d^{-1}) and bird weight (W, g) in Procellariiformes: $FMR = 22.34\,W^{0.575}$ (Warham 1996). Species-specific calorific values were not available for most prey items and these are likely to exhibit large variations due to a variety of factors (e.g. Hislop et al. 1991). For the purpose of this crude assessment, we adopted an average value of 6 kJ g^{-1} wet weight, based on values obtained on several fish species (Warham et al. 1976, Clarke & Prince 1980, Hislop et al. 1991). This assumption is likely to produce small errors, compared to those arising due to the imprecision in the shearwater population estimates.

There is still some debate about the taxonomic status of trumpet fish in relation to a possible separation of the forms *Macrorhamphosus scolopax* and *M. gracilis* (Brêthes 1979). Therefore in this study, trumpet fish are referred to as *Macrorhamphosus* sp. Dietary information is presented in terms of frequency of occurrence (% of samples with a given prey item), numerical importance (number of specimens of each prey type, expressed as % of all prey found) and proportion by weight (weight contribution of a given species, as % of total weight). Statistical procedures followed Zar (1996). Throughout this paper, we present means ± standard deviation.

RESULTS

Frequency of occurrence and numerical importance of prey

All fish remains found in food samples could be attributed to 5 species/genera (Table 1). Fish was the most important prey type in terms of both occurrence (90.6% in March, 96.2% in August; Table 1) and number (91.9% in March, 95.7% in August; Table 2). There was no significant difference between the 2 periods in the proportion of samples containing fish (Yates-corrected $\chi^2 = 1.19$, $p = 0.3$, df = 1).

Table 1. Frequency of occurrence (%) of fish species, cephalopods and Crustacea in food samples of Cory's shearwaters *Calonectris diomedea* in the Azores

Taxon	March			August				Total
	Graciosa	Sta Maria	Total	Corvo	Graciosa	Sta Maria	Total	
Saury	–	29.8	26.4	13.8	19.0	11.4	15.1	18.9
Trumpet fish	16.7	44.7	41.5	27.6	31.0	82.9	47.2	45.3
Boarfish	50.0	19.1	22.6	69.0	88.1	8.6	56.6	45.3
Horse mackerel	16.7	–	1.9	13.8	28.6	22.9	22.6	15.7
Chub mackerel	–	2.1	1.9	6.9	2.4	5.7	4.7	3.8
Crustacea	–	12.8	11.3	–	4.8	2.9	2.8	5.7
Cephalopoda	50.0	21.3	24.5	17.2	19.0	37.1	24.5	24.5
No. of samples	6	47	53	29	42	35	106	159

Table 2. Numerical frequency (%) of fish species, cephalopods and Crustacea in food samples of Cory's shearwaters *Calonectris diomedea* in the Azores

Taxon	March			August				Total
	Graciosa	Sta Maria	Total	Corvo	Graciosa	Sta Maria	Total	
Saury	–	9.6	8.8	3.3	3.0	3.6	3.3	4.7
Trumpet fish	33.3	67.0	64.2	15.0	14.0	77.8	39.8	46.0
Boarfish	47.6	15.5	18.1	70.8	74.4	7.2	46.8	39.5
Horse mackerel	4.8	–	0.4	5.0	4.7	5.2	5.0	3.8
Chub mackerel	–	0.4	0.4	1.7	0.3	1.0	0.8	0.7
Crustacea	–	2.5	2.3	–	0.6	0.3	0.4	0.9
Cephalopoda	14.3	5.0	5.8	4.2	3.0	4.9	3.9	4.4
No. of prey items	21	239	260	120	336	307	763	1023

In August, boarfish *Capros aper* and trumpet fish dominated the diet in terms of occurrence (Table 1) and numbers (Table 2). Taken together these species were present in more than 85% of the samples and also represented more than 85% of all prey found in this period (Table 2). Boarfish occurred less frequently in diet samples in March as compared to those collected in August (Yates-corrected χ^2 = 15.11, $p <$ 0.0001, df = 1) and its numerical importance was also lower. In August, trumpet fish were significantly more frequent (in occurrence) in Santa Maria than in Graciosa and Corvo (χ^2 = 26.8, p = 0.0001, df = 2), while the converse was true for boarfish, which was relatively uncommon in Santa Maria (χ^2 = 51.6, $p <$ 0.0001, df = 2). There is some suggestion of a similar geographical pattern in March, but the spring sample sizes were too small to enable meaningful statistical analysis.

All cephalopods identified belonged to the Order Teuthoidea, Sub-order Oegopsida, except for 1 specimen identified as *Halyphron atlanticus* (syn. *Alloposus mollis*), which belongs to the Order Octopoda, Sub-order Incirrata (Table 3). In both periods slightly eroded structures or muscle were found on about 25% of the samples and their numerical importance varied between 3.0 and 14.3% (Table 3). Histioteuthidae was the most represented Family (3 species, 41.4% by number), followed by Cranchidae (5 species, 27.6% by number) and Gonatidae (1 species, 17.2% by number). All species are mesopelagic, some also presenting epipelagic (especially juvenile forms) or bathypelagic distribution (Table 3). It is worth highlighting that severely eroded squid beaks (usually the tips of lower and upper mandibles) were found in 60.4 and 52.7% of the samples analysed in March and August, respectively, and if considered (see 'Methods') would have represented ca 10% of all prey found.

Crustacea were represented by few individuals (Table 1). Six specimens were classified as Decapoda: Natantia. From these, 3 were identified as *Pasiphaea* sp. Their relatively large size (ca 5 cm) and low state of digestion suggests that they were not taken by fish or squid species found in samples.

Size of prey and their contribution by weight

Table 4 shows the estimated size and weight of prey fish, obtained from 760 measurements of fish vertebrae. The means presented in Table 4 were calculated

Table 3. Cephalopod species identified in Cory's shearwater *Calonectris diomedea* diet in the Azores in March and August, and corresponding vertical distribution (E, epipelagic; M, mesopelagic; B, bathypelagic; following Clarke 1986, Guerra 1992). Weight (mean ± SD, sample size in parentheses) was estimated from beak measurements (for explanation, see 'Methods')

Family Genus/species	Vertical distribution	Depth (m)	No. of individuals March	No. of individuals August	Total (%)	Estimated weight (g)
Ommastraphidae						
Ommastrephes sp.	E, M	0–1500	1	–	2.2	3.7 ± 0.7 (2)
Gonatidae						
Gonatus steenstrupii	M	0–1000	4	1	11.1	166.0 ± 136.1 (5)
Histioteuthidae						
Histioteuthis sp.	M	–	2	–	4.4	–
H. reversa	M	0–1800	–	6	13.3	36.6 (1)
H. dofleini[a]	M	0–700/800	3	–	6.7	140.3 ± 54.8 (2)
H. maleagroteuthis	M	100–700	–	1	2.2	–
Mastigoteuthidae						
Mastigoteuthis sp.	M, B		–	2	4.4	–
Cranchidae						
Cranchia scabra		0–200	–	1	2.2	–
Leachia sp.	M, B	0–2000	–	4	8.9	5.3 (1)
Taonius pavo	M, B	0–2000	1	–	2.2	80.5 (1)
Teuthowenia sp.	E, M	0–1500	1	–	2.2	–
Galiteuthis sp.	M, B	500–2000	–	1	2.2	–
Alloposidae						
Halyphron atlanticus	E, M	0–3000	–	1	2.2	–
Unidentified	–	–	3	13	35.6	–
Total			15	30		

[a]One individual with an estimated weight of 589 g was excluded from computation of mean weight

Table 4. Standard length (boarfish and trumpet fish, in mm) and total length (all other species, in mm) and weight (g) of fish preyed upon by Cory's shearwater *Calonectris diomedea* in the Azores, in March and August, and statistical comparison between months. Mean values (±SD, sample size in parenthesis, range below) were estimated from vertebrae measurements, and were calculated as averages per food sample (for explanation, see text)

Taxon	Vertebrae used in estimations	Fish length (mm) March	Fish length (mm) August	Fish weight (g) March	Fish weight (g) August	Mann-Whitney *U*-test
Saury	1st caudal	376.0 ± 12.9 (6) 365.1–397.0	355.3 ± 30.7 (6) 312.5–406.6	69.8 ± 9.31 (6) 62.0–85.0	57.8 ± 19.4 (6) 34.5–93.0	$U = 6$, $p < 0.05$
Trumpet fish	4th, 5th, 1st caudal	87.4 ± 5.5 (17) 71.9–95.4	82.8 ± 11.2 (26) 68.2–115.8	4.7 ± 0.7 (17) 2.8–5.9	4.2 ± 1.8 (26) 2.4–9.8	$Z = 2.81$, $p < 0.01$
Boarfish	5th, 1st caudal	61.2 ± 5.3 (6) 57.5–71.4	54.5 ± 4.9 (30) 49.0–70.8	8.9 ± 2.3 (6) 7.5–13.4	6.5 ± 1.9 (30) 4.6–13.4	$Z = 3.01$, $p < 0.01$
Horse mackerel	1st caudal	–	139.1 ± 13.2 (9) 119.9–157.3	–	22.3 ± 6.2 (9) 14.2–30.9	–
Chub mackerel	1st caudal	191.4 (1) –	237.3 ± 68.8 (2) 188.7–286.0	39.6 (1) –	110.1 ± 102.7 (2) 37.0–187.7	–

Table 5. Importance by weight (%) of fish, cephalopods and Crustacea in the diet of Cory's shearwater *Calonectris diomedea* at each colony, in March and August

Taxon	March			August				Total
	Graciosa	Sta Maria	Total	Corvo	Graciosa	Sta Maria	Total	
Saury	–	39.7	35.7	18.6	18.0	18.0	18.1	24.9
Trumpet fish	7.0	19.1	17.9	7.3	7.6	30.8	16.8	17.2
Boarfish	15.8	7.4	8.3	37.1	49.4	4.2	29.4	21.2
Horse mackerel	5.0	–	0.5	14.4	9.9	13.7	12.2	7.7
Chub mackerel	–	1.0	0.9	4.9	1.2	10.7	5.6	3.8
Crustacea	–	0.3	0.3	–	0.1	0.1	0.1	0.2
Cephalopoda	72.2	32.5	36.5	17.7	13.7	22.5	17.9	25.1
Total weight of prey (g)	461	4096	4558	1214	3138	2867	7220	11778

from average size/weight of each species in each food sample, to account for potential problems arising due to the effects of pseudoreplication (Hurlbert 1984). There were small but significant differences in size and weight of prey captured in both periods (Table 4). The statistical significance of the comparisons and the magnitude and 'direction' of the differences remained unaffected when tests were applied to all measurements obtained from food samples, suggesting that there was no inverse relationship between size and number of fish in our samples.

Estimated weights of cephalopod species are presented in Table 3. Overall, fish contributed about 75% weight and cephalopods 25% (Table 5). Cephalopods were the most important prey in March, followed by saury (35.7%) and trumpet fish (17.9%). In August, fish prey were proportionally more important (82.0% in weight), with boarfish contributing 29.4%, followed by saury, trumpet fish and horse mackerel *Trachurus picturatus*.

Estimates of fish consumption by Cory's shearwaters

Adult Cory's shearwaters in the Azores weigh about 900 g (Granadeiro 1993), yielding an estimated DER of about 1116 kJ d^{-1} (see 'Methods'). During 270 d, roughly corresponding to their period at the breeding grounds (Zino 1971, Granadeiro 1991), Cory's shearwaters would consume about 11200 t of fish.

DISCUSSION

Diet of Cory's shearwaters

Cory's shearwater is a surface-seizing predator, apparently unable to capture prey deeper than 2 m (Haney 1986, Monteiro et al. 1996a), in contrast with other shearwaters better adapted to diving (Warham 1990). Previous observations of the feeding behaviour of Cory's shearwater have suggested fish and squid to be the main prey (Martin 1986, Monteiro et al. 1996a), either caught alive or through scavenging (Abrams 1983, Sara 1993) occasionally in association with underwater predators such as marine mammals and tuna (Martin 1986).

Our data indicate a predominately fish diet of Cory's shearwater in the Azores, involving few species. Small shoaling fish, mainly trumpet fish and boarfish, were the most frequent prey, presumably caught as they shoaled in large numbers close to the surface. These prey fish mainly include 1 year-class (as assessed by their average size, following Brêthes 1979), extremely abundant in the area roughly delimited by the Azores archipelago, the south of Portugal and the Canary islands (Ehrich 1975). However, due to their small size, their contribution by weight is not as high as that of saury.

Small pelagic fish also formed the basis of the diet of most diurnal feeding seabirds in the Azores. Taken together, boarfish and trumpet fish represented more than 60% of the prey found in pellets or delivered to chicks of the common tern *Sterna hirundo* (Granadeiro et al. 1995), roseate tern *Sterna dougalli* (Ramos et al. in press a) and Cory's shearwater (this study). Boarfish and trumpet fish were also present in about 70% of the yellow-legged gull *Larus cachinnans* pellets containing fish (Ramos et al. in press b). There are no estimates of the importance by weight of these 2 fish prey in the diet of any seabird in the Azores, but given their comparatively higher frequency (Ramos et al. in press a, b) they certainly represent a major contribution to their diet by weight.

The importance of boarfish in the diet of Cory's shearwater is somewhat surprising as this species is seldom consumed by seabirds in the Mediterranean, despite being discarded in large numbers during trawling activities (Oro & Ruiz 1997). Experimental fish discards in the Mediterranean also support the view that boarfish is not a preferred prey (Sara 1993), because most seabirds select prey such as European anchovy *Engraulis encrasicolus*, horse mackerel and blue whiting *Micromesistius poutassou*, which are easier to handle and swallow (Sara 1993).

In August, boarfish and trumpet fish exhibited a significant geographical variation in their importance in shearwater diet (Table 1). The former species was found more frequently and contributed more by weight in Corvo and Graciosa, being less common in Santa Maria, while trumpet fish showed the reverse pattern. The proportionally larger importance of trumpet fish in the eastern group is also documented in common terns in the Azores (Granadeiro et al. 1995), which is consistent with the hypothesis that these differences reflect genuine variation in the availability of such prey.

Temporal variation in diet of Cory's shearwater has never been reported and is difficult to interpret in light of current knowledge. The fact that we collected data during only 1 year precludes assessment of inter-annual consistency of such a pattern. It is not possible to ascertain the extent to which it reflects a change in prey availability, a shift in prey selection, or a change in foraging areas as breeding season progresses. Indeed, Cory's shearwaters can profit from oceanographic phenomena such as eddies, and major upwelling events associated with seamounts, known to be related to biomass enhancement (Haney 1986, Rogers 1994). However, the extent and frequency of such phenomena in Azorean waters remain largely unknown, and whether the temporal differences found in this study could correspond to varying intensity of such events in different times of the year remains a matter for speculation. Alternatively, temporal differences could be attributed to active prey selectivity. Differences in the food of adult seabirds and that provided to their chicks have been described in some seabird species (e.g. Furness & Hislop 1981, Nogales et al. 1995) and interpreted as a means for providing a better quality food to chicks. Squid was equally represented in numbers in both periods (Table 2), but its importance by weight in March was twice that recorded in August (Table 5). The decrease in the proportion of squid (which is of lower calorific value; Warham et al. 1976, Clarke & Prince 1980, Furness 1994) in the diet of shearwaters in August could therefore reflect an increase in prey selectivity as breeding season progresses, and the subject clearly deserves further investigation.

The frequency of occurrence of cephalopods in the diet of shearwaters agrees with previous data from the Azores presented by Furness (1994), which were used to estimate the amount of squid consumed in this area. This estimate was based on hard remains obtained from stomach-flushed birds, as well as post-mortem analysis of the contents from gizzards of fledglings that had died from accidents, and the vast majority of squid found were identified as ommastrephids (Furness 1994). The preponderance of this Family has also been reported by Martin (1986), but that contrasts with our findings, which suggest a considerably higher diversity of squid prey (12 species, 6 Families). Our observations highlight the possible role of seabird dietary studies as a means of sampling the marine environment (Furness & Greenwood 1993, Croxall & Prince 1996, Furness & Camphuysen 1997).

Although juvenile forms of some of the squid species represented show an epipelagic distribution (Clarke 1986), adult animals occur mainly in mesopelagic or even bathypelagic environments (see Table 3). These species undertake diel vertical migrations, ascending to the surface only at night (Imber 1973, Prince & Morgan 1987). Similarly, boarfish and trumpet fish are epipelagic while juveniles, undergoing a shift in their vertical distribution as adults, and occur mainly at 50–150 and 100–400 m, respectively (Brêthes 1979, Whitehead et al. 1986). Klomp & Furness (1992) suggested that the later arrival of shearwaters at a colony on moonlit nights could indicate enhanced prey availability or visibility, which could explain the presence of these deep water prey in our samples. However, there is little evidence for a relationship between time of arrival and nocturnal feeding at other colonies (e.g. Hamer & Hill 1993, Granadeiro et al. in press), suggesting that mesopelagic prey can be obtained during the day. Although it is likely that shearwaters feed opportunistically at night, most deep water prey are probably driven to the surface by underwater predators, such as tuna and marine mammals (Prince & Morgan 1987, Au & Pitman 1988, Croxall & Prince 1996), or by local upwelling events (Monteiro et al. 1996a, Ramos et al. in press a).

While deep water squid species were detected in diet samples, mesopelagic fishes (e.g. Myctophidae, Sterniphicidae or Gonostomatidae) were strikingly absent. These prey are thought to occur in large numbers in the area (Gjøsaeter & Kawaguchi 1980), and therefore represent a potential source of food. These species occur regularly in the diet of common terns (Granadeiro et al. 1995, Ramos et al. in press b), roseate terns (Ramos et al. in press a) and most small petrels breeding in the Azores (Monteiro et al. 1996a, Granadeiro unpubl. data). Their presence has also been reported in yellow-legged gulls (Hamer et al. 1994, Ramos et al. in press b, Granadeiro unpubl. data). Hence, deep water fishes are readily available to mainly diurnal foraging seabirds, some of which probably sample the environment in much the same way as shearwaters. Since mesopelagic fish usually possess large otoliths (Nolf 1985, Härkönen 1986) and resistant maxillae and teeth (Watt et al. 1997) it is extremely unlikely that if they were present we systematically failed to detect them in all our samples.

The reduced importance of mesopelagic prey in the diet of shearwaters is further supported by the mercury levels in their plumage and food regurgitations. Mesopelagic organisms tend to show high mercury concentrations (Monteiro et al. 1996b) and high mercury levels are also found in seabird species (mainly small petrels) which rely extensively on these prey, reflecting a causal link between diet and mercury burdens (Monteiro et al. 1996). In contrast to these species, Cory's shearwaters present an overall low mercury burden (Monteiro 1996), which is consistent with the absence of deep water fish species in their diet recorded in this study.

Fish consumption and comparison with other marine predators

Cory's shearwaters were estimated to consume about 11 000 t of fish per year in the Azores region. The scarcity of information on fish standing stocks and on natural and fisheries-induced mortality precludes any assertion about potential competition with local fisheries (Furness 1982, Montevecchi 1993). However, Cory's shearwaters in the Azores feed mainly on non-commercial species and therefore interaction with fisheries, if any, is only likely to occur in relation to horse mackerel, caught to some extent as live bait for local tuna fisheries. In the Azores, Pinho et al. (1995) estimated an annual catch of small horse mackerel of about 305 and 226 t in 1993 and 1994, respectively, and the sizes taken (80 to 230 mm fork length) are well within the range captured by shearwaters (Table 4). Assuming that horse mackerel represents 8% (by weight) of the prey taken (Table 5), Cory's shearwater would consume about 1046 t per year, almost an order of magnitude higher than that of bait catches. Horse mackerel can exhibit important inter-annual variations in abundance (Pinho et al. 1995) but the extent to which both commercial catches and natural consumption are likely to be affected is unclear. Cory's shearwater is mainly an opportunistic feeder and therefore it is unlikely that a reduction in a single prey type would significantly affect their provisioning behaviour. Nonetheless, long-term studies of shearwater diet can provide indications on relative abundance of these prey fish, possibly enabling an assessment of their availability in the Azorean pelagic food web.

The diet of Cory's shearwater in the Azores shows several similarities with prey taken by underwater predators. Boarfish was the most commonly found prey in the diet of swordfish *Xiphias gladius* in the Azores (72% occurrence, 76% by numbers), being the second most important prey by weight (Clarke et al. 1995). The estimated fork length and weight of fish taken by swordfish (70 mm and 5 g, respectively, Clarke et al. 1995) is well within the range captured by shearwaters (Table 4). Similarly, blue sharks *Prionace glauca* examined by Clarke et al. (1996) in the central group of the Azores showed a preponderance of boarfish (49% by numbers and 21% by weight) and trumpet fish (34% in numbers, 21% by weight). The size of intact fish peaked at 50 to 60 mm (Clarke et al. 1996), which is in general agreement with the size consumed by shearwaters, as obtained from fish vertebrae measurements (Table 4).

Further similarities can be seen with data obtained from commercial fisheries in the Azores. Small shoaling species are captured alive to provide bait for tuna fisheries (Pinho et al. 1995). These species include blackspot seabream *Pagellus bogaraveo* and horse mackerel, the former not reported in Cory's shearwater diet, as it mainly exhibits a coastal distribution (Whitehead et al. 1986). Bait catches are carried out at night, when individuals are attracted to the surface by intense lights from the boats, and fish are captured using purse-seine nets (Pinho et al. 1995). Modal sizes for fish captured with this gear are 140 mm (fork length) for horse mackerel and 220 mm (fork length) for chub mackerel *Scomber japonicus*, almost exactly matching our estimated measurements for shearwaters' prey (Table 4). The broad similarity in the sizes preyed upon by different predators suggests that they are sampling all available size classes, thus being potentially useful as indicators of the availability of these prey (Furness & Greenwood 1993, Furness & Camphuysen 1997).

These considerations support the notion that small pelagic prey probably occur in very large numbers in Azorean waters. At high latitudes, a single abundant prey supports a wide range of predators: krill in the southern oceans support many species of seabirds, seals and whales (e.g. Kasamatsu & Joyce 1995, Reid & Arnould 1996, Croxall et al. 1997, and references therein); capelin in the Barents Sea supports seabirds, seals and cod (review in Gjøsæter 1997). However, it is generally found that at low latitudes prey species diversity is much higher (Ashmole 1971, Croxall 1987). Yet, in the Azores, only 2 species of small fish appear to be key prey for a variety of predators. The central role of trumpet fish and boarfish in the marine food web in the Azores, and the fact that these prey can exhibit strong variation in abundance (e.g Brêthes 1979), raises the question of how adaptable predators will be to extensive changes in their availability.

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