

# Cephalopods in marine predator diet assessments: why identifying upper and lower beaks is important

José C. Xavier<sup>1,2\*</sup>, Richard A. Phillips<sup>2</sup>, and Yves Cherel<sup>3</sup>

<sup>1</sup>Department of Life Sciences, Institute of Marine Research, University of Coimbra, 3001-401 Coimbra, Portugal

<sup>2</sup>British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

<sup>3</sup>Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS, BP 14, 79360 Villiers-en-Bois, France

\*Corresponding Author: tel: +351 936728419; fax: +351 239823603; e-mail: [jccx@cantab.net](mailto:jccx@cantab.net).

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Cephalopods are components of the diet of many predators worldwide. They are identified mainly using their chitinized upper and lower beaks, but because it has been assumed that the number of upper and lower beaks would be the same in predator diet samples, more effort has been put into creating keys for the lower beaks, which are more easily identifiable from morphology. A test is made of whether the number of upper and lower beaks differs in diet samples collected from a major cephalopod predator, the wandering albatross (*Diomedea exulans*), potential biases in the estimation of predator diets are assessed, and upper:lower beak ratios in published studies of other seabirds, seals, whales, and fish from different parts of the world reviewed. The ratio of upper to lower beaks in diet samples from wandering albatrosses varied greatly in a single year (from 69.6% more lower beaks to 59% more upper beaks), and between years (from 0.5 to 32.1% more upper beaks), and biases were greater for certain cephalopod species, resulting in underestimation of their relative importance. Future studies need to consider using both upper and lower beaks to improve the assessment of the contribution of different cephalopods to predator diets.

**Keywords:** cephalopod beaks, marine ecosystems, top predator diets, trophic interactions.

## Introduction

Cephalopods are a key component of marine foodwebs worldwide (Boyle and Rodhouse, 2005; Hunsicker *et al.*, 2010). Most knowledge of cephalopods, particularly those from oceanic waters, still originates largely from analysis of stomach contents collected from their predators (Clarke, 1996), because methods for direct sampling at sea are inefficient (Clarke, 1977; Rodhouse, 1990; Xavier *et al.*, 2007a). Cephalopods are found in the diet of many species, including whales, seals, seabirds, sharks, and other fish, and are often a key component (Perrin *et al.*, 1973; Clarke, 1980; Guerra *et al.*, 1993; Klages, 1996; Smale, 1996; Cherel and Klages, 1998; Boyle and Rodhouse, 2005; Xavier and Cherel, 2009). Identification of cephalopods in diet samples is generally based on their beaks (hard, chitinous structures that resist digestion), because the flesh is often partially or totally digested. Indeed, since the 1950s, a lot of effort has been put into improving identification methods and determining the original size of the animal based on beak measurements (Akimushkin, 1955; Beteshava and Akimushkin, 1955; Clarke, 1962a, b, 1966, 1980, 1986; Mangold and Fioroni, 1966; Wolff, 1984; Kubodera and Furuhashi, 1987; Smale *et al.*, 1993; Lu and Ickeringill, 2002; Xavier *et al.*, 2007a; Xavier and Cherel, 2009). The work has been basic in revealing the ecological importance of cephalopods in marine ecosystems, particularly in obtaining reliable estimates of their consumption, and as an indirect means of assessing cephalopod distribution and

abundance to compare with information obtained from research cruises and commercial fishing (Clarke, 1983; Boyle, 1996; Xavier *et al.*, 2006, 2007b).

Although cephalopods possess both an upper and a lower beak, generally only the latter is used for identification (Clarke, 1986; Cherel *et al.*, 2000, 2004; Delord *et al.*, 2010; Richoux *et al.*, 2010), because the lower beak shows far greater morphological variation between species. Consequently, it is difficult and in some cases almost impossible to differentiate histioteuthid and ommastrephid cephalopods from upper beaks alone. The problem is even greater when beaks are eroded or broken, which explains why many more upper than lower beaks likely remain unidentified in diet studies (YC, pers. obs.).

It can be assumed that predators do not selectively ingest upper or lower beaks and that their ratio should, therefore, be 1:1 in diet samples. Consequently, there is no need to duplicate effort by trying to identify both beaks (Clarke, 1986). However, beaks can remain in the stomachs of predators for up to several months, which can affect the upper and lower beaks differently (Ashmole and Ashmole, 1967; Imber and Russ, 1975; Furness *et al.*, 1984; Duffy and Jackson, 1986; Jackson and Ryan, 1986; Gales and Cheal, 1992; Votier *et al.*, 2003; Xavier *et al.*, 2005). Although some studies have assessed the number of upper and lower beaks in diet samples, to date there has been no critical examination of the potential biases, e.g. with respect to different cephalopod species, and no general implications for diet studies of marine predators.

Albatrosses are known cephalopod predators (Cherel and Klages, 1998), including the wandering albatross (*Diomedea exulans*), which specializes in feeding on oceanic squid in subtropical–Antarctic waters (Xavier et al., 2003a, 2004, 2005). During breeding, wandering albatrosses consume >60 cephalopod species, fewer than five of which are common in net-haul samples (Imber, 1992). Albatross chicks are fed cephalopods, crustaceans, and fish, and before fledging, they voluntarily regurgitate a bolus (also known as a cast or pellet) of all indigestible items, including beaks, retained during a chick-rearing period that lasts up to ~9 months (Xavier et al., 2003a, 2004, 2005). Consequently, the boluses provide a unique opportunity to show that the assumption of parity in occurrence of upper and lower beaks does not always hold. Here, we test the hypothesis that the number of upper beaks equals the number of lower beaks in diet samples. The specific objectives were: (i) to assess differences in the incidence of upper and lower beaks in the diet samples of wandering albatrosses, depending on sampling methods (boluses from chicks, stomach contents from adults), on prey ingested, and on prey size; (ii) to compare the ratio of upper and lower beaks in published diet studies of seabirds, including wandering albatrosses, seals, whales, and fish carried out elsewhere; and (iii) to discuss the implications of any biases in the numbers of lower or upper beaks for diet estimation.

## Material and methods

To assess the differences in upper:lower beak ratios within and between years, beaks were obtained from boluses regurgitated voluntarily by wandering albatross chicks at Bird Island, South Georgia (54°S 38°W) close to their nests during October–January of 1989–1999, and frozen at –20°C for later analysis. Further, to assess the effect of the diet-sampling technique, stomach samples were collected from adults at Bird Island during April–October 2009 and from chicks at the Crozet Islands (46°S 51°E) in June, August, and October 1998. Stomach samples include a larger proportion of fresh material (i.e. with fresh beaks—beaks recently consumed by predators that still have flesh attached, beaks in buccal masses, or from complete or

partially completed specimens; Xavier and Cherel, 2009), although there may also be some older beaks (i.e. beaks with no transparent part and often eroded or broken) retained from previous meals, whereas boluses represent accumulated undigested hard parts only and are produced towards the end of chick rearing. Data from stomach samples were pooled for the chick-rearing period, because that period corresponds to the time during which the contents of boluses accumulate in chick stomachs. Stomach samples were collected from chicks immediately after they were fed by a parent, each chick being inverted over a bucket and its stomach massaged (Xavier et al., 2003b). To minimize disturbance, each chick was sampled only once, because the loss of one meal has negligible effects on chick growth and survival (Phillips, 2006).

For all samples of albatross, cephalopod beaks were cleaned, separated into upper and lower, and depending on the study year, identified to species level. Identification of the lower beaks followed Xavier and Cherel (2009). Beaks were checked against a reference collection held at the Centre d'Etudes Biologiques de Chizé. Chi-squared tests were used to determine whether samples conformed to a 1:1 ratio of the number of upper and lower beaks for each cephalopod species (where beak frequency >10%; Table 1) using the MINITAB statistical package.

To evaluate the implications of identifying lower beaks only, the mass of each cephalopod species for which there were more upper than lower beaks was calculated. As upper beaks were not measured, a minimum, an average, and a maximum contribution by mass to the diet was calculated, based on the measurements of lower beaks converted to mass using the species-specific allometric equations published by Xavier and Cherel (2009).

A search for published papers, using the ISI Web of Knowledge (<http://wok.mimas.ac.uk/>) and Google scholar (<http://scholar.google.com/>), on the cephalopod component of the diet of marine predators was conducted to determine the range of upper and lower beaks found in such studies. We were particularly interested in the diet of key cephalopod predators, including seabirds, seals, whales, and fish.

**Table 1.** Number of upper and lower beaks and estimated mass of cephalopod species identified in boluses ( $n = 33$ ) from wandering albatross chicks and from stomach contents (using only old material) collected at the Crozet Islands in 1998.

Species	n							Estimated mass (g)			$\chi^2$ test	
	F	FU	FL	U	L	U–L%	Minimum	Mean	Maximum	d.f.	$\chi^2$ value	p-value
<i>Batoteuthis skolops</i>	30	28	28	138	111	10.8	416 (0.1)	945 (0.1)	1 584 (0.2)	29	17.05	n.s.
<i>Martialia hyadesi</i>	30	28	28	196	168	7.7	8 082 (1.7)	15 452 (2.4)	28 056 (3.8)	29	9.93	n.s.
<i>Moroteuthis ingens</i>	33	32	32	173	159	4.2	7 332 (5.8)	27 400 (5.9)	71 014 (5.9)	32	11.23	n.s.
<i>Histioteuthis atlantica/corpuscula</i>	33	27	32	182	169	3.7	959 (1.5)	3 837 (1.5)	7 395 (1.5)	32	21.69	n.s.
<i>Chiroteuthis veranyi</i>	16	14	14	20	19	2.6	83 (0.1)	131 (0.1)	190 (0.1)	15	4.71	n.s.
<i>Kondakovia longimana</i>	33	33	33	1 280	1 314	–1.3	–	–	–	32	3.13	n.s.
<i>Moroteuthis knipovitchi</i>	31	30	31	128	133	–1.9	–	–	–	30	6.98	n.s.
<i>Taonius</i> sp. B (Voss)	19	16	18	61	64	–2.4	–	–	–	18	0.86	n.s.
<i>Mastigoteuthis</i> A (Clarke)	20	20	18	31	33	–3.1	–	–	–	19	4.28	n.s.
<i>Galiteuthis glacialis</i>	33	33	32	316	344	–4.2	–	–	–	32	20.02	n.s.
<i>Alluroteuthis antarcticus</i>	29	27	28	83	95	–6.7	–	–	–	28	10.64	n.s.
<i>Taonius</i> sp. (Clarke)	17	17	17	34	39	–6.8	–	–	–	16	5.91	n.s.
<i>Gonatus antarcticus</i>	21	20	19	51	59	–7.3	–	–	–	20	6.43	n.s.
<i>Cycloteuthis akimushkini</i>	20	17	19	31	38	–10.1	–	–	–	19	5.19	n.s.
<i>Histioteuthis eltaninae</i>	33	32	33	732	991	–15.0	–	–	–	32	20.23	n.s.
<i>Histioteuthis miranda</i>	17	9	17	15	32	–36.2	–	–	–	16	9.59	n.s.
All species	33	33	33	3 471	3 768	–4.1	16 872	47 766	108 240	32	43.46	<0.01

n denotes the number of beaks, F the frequency of upper and lower beaks combined, FU the frequency of occurrence of upper beaks (U), FL the frequency of occurrence of lower beaks (L), d.f. the degrees of freedom, and n.s. means not significant. Values in parenthesis of the mean mass estimates are the percentage of the mass that would increase according to estimates using minimum, mean or maximum estimates.

## Results

Upper beaks were more numerous than lower beaks, significantly different from a 1:1 ratio of upper and lower beaks, in individual

**Table 2.** Variations within a single year in the number of upper and lower cephalopod beaks in boluses from wandering albatrosses collected at Bird Island, South Georgia in 1999 ( $N$  is the number of the sample, and  $n$  the number of beaks).

$N$	Upper (U)		Lower (L)		U–L%
	$n$	Percentage	$n$	Percentage	
1	196	79.7	50	20.3	59.3
2	51	73.9	18	26.1	47.8
3	134	73.6	48	26.4	47.3
4	67	72.0	26	28.0	44.1
5	35	70.0	15	30.0	40.0
6	138	69.3	61	30.7	38.7
7	136	69.0	61	31.0	38.1
8	159	68.5	73	31.5	37.1
9	188	68.4	87	31.6	36.7
10	107	68.2	50	31.8	36.3
11	172	68.0	81	32.0	36.0
12	180	67.7	86	32.3	35.3
13	195	67.2	95	32.8	34.5
14	121	67.2	59	32.8	34.4
15	235	67.0	116	33.0	33.9
16	232	66.9	115	33.1	33.7
17	265	66.8	132	33.2	33.5
18	308	66.7	154	33.3	33.3
19	34	66.7	17	33.3	33.3
20	121	66.1	62	33.9	32.2
21	407	66.0	210	34.0	31.9
22	328	65.9	170	34.1	31.7
23	215	65.7	112	34.3	31.5
24	189	65.6	99	34.4	31.3
25	84	65.1	45	34.9	30.2
26	84	65.1	45	34.9	30.2
27	50	64.9	27	35.1	29.9
28	203	64.0	114	36.0	28.1
29	82	62.6	49	37.4	25.2
30	67	61.5	42	38.5	22.9
31	43	61.4	27	38.6	22.9
32	35	59.3	24	40.7	18.6
33	30	29.7	71	70.3	–40.6
34	12	15.2	67	84.8	–69.6

boluses collected from wandering albatrosses in 1999 ( $n = 34$  samples;  $\chi^2_{33} = 188.8$ ,  $p < 0.01$ ). Upper beaks represented  $64.6 \pm 2.0\%$  of the total number of beaks (range of upper beaks: 15.2–66.1%; Tables 2 and 3). Of 11 years, 45% had significant differences between the number of upper and lower beaks (Table 3). Comparing boluses collected in all years, the number of upper beaks was always, and significantly, higher than the number of lower beaks (range 50.2–79.7% of the total, mean  $54.4 \pm 1.4\%$ ;  $\chi^2_{264} = 974.0$ ,  $p < 0.01$ ; Tables 2 and 3), whereas in stomach samples collected from adult wandering albatrosses in 2010, the number of upper and lower beaks was similar ( $\chi^2_{27} = 10.4$ ,  $p = 0.99$ ; Table 4). When just comparing the lower beak size from stomach contents [range of lower rostral length, LRL, of lower beaks from wandering albatrosses in 2010: 2.7–17.6 mm; mean  $7.4 \pm 3.5$  (s.d.)] and boluses [range of LRL of lower beaks from wandering albatrosses in 1999: 2.3–24 mm; mean  $7.0 \pm 3.5$  (s.d.)], no differences were significant ( $t$ -test = 1.24,  $p = 0.22$ ).

When assessing the number of upper and lower beaks identified to species level, for 8 of 16 species, the number of lower vs. upper beaks differed by <5% in boluses and stomach contents collected from the Crozet Islands (Table 1). When combining all upper and lower beaks from all species, there was a significant difference from a 1:1 ratio of upper and lower beaks, with lower beaks more abundant ( $\chi^2_{15} = 43.5$ ,  $p < 0.01$ ; Table 1). However, when assessing differences in 1:1 ratio at species level, there were no differences, even for the species that had the greatest difference between the number of upper and lower beaks; *Histioteuthis miranda* had 36.2% more lower than upper beaks (Table 1). Moreover, upper beaks of *H. miranda* were only present in 53% of the samples, but lower beaks in all samples (Table 1). For two species, *Batoteuthis skolops* and *Martialia hyadesi*, samples contained more upper than lower beaks (10.8 and 7.7% more upper beaks, respectively; Table 1). In contrast, the bias was towards lower beaks in *Histioteuthis eltaninae*, *H. miranda*, and *Cycloteuthis akimushkini* (range 10.1–36.2% more lower beaks; Table 1), where the range in size of the beaks included the range of size in the diet of wandering albatrosses [i.e. small *H. eltaninae* beaks (LRL range 2.8–4.2 mm), mid-size *H. miranda* beaks (LRL range 6.3–7.7 mm), and large *C. akimushkini* beaks (LRL range 8.0–17.6 mm); all lower beaks LRL range 2.8–17.6 mm). Despite this, the ratio of upper to lower beaks for each of these species was not significantly different from unity (Table 1).

**Table 3.** Variation between years in the number of upper and lower cephalopods in boluses of wandering albatrosses collected at Bird Island, South Georgia, during the years 1989–1999 ( $N$  is the number of samples analysed,  $n$  the number of beaks, d.f. the degrees of freedom, and n.s. means not significant).

Year	$N$	Upper (U)		Lower (L)		U–L%	$\chi^2$ test		
		$n$	Percentage	$n$	Percentage		d.f.	$\chi^2$ -value	$p$ -value
1989	30	2 587	52.4	2 350	47.6	4.8	29	64.03	<0.01
1990	24	879	50.4	865	49.6	0.8	23	23.66	n.s.
1991	22	1 321	52.0	1 219	48.0	4.0	21	16.37	n.s.
1992	21	1 366	51.6	1 280	48.4	3.3	20	26.34	n.s.
1993	31	1 990	55.9	1 571	44.1	11.8	30	67.47	<0.01
1994	16	973	55.0	795	45.0	10.1	15	35.52	<0.01
1995	24	1 302	56.4	1 006	43.6	12.8	23	35.94	<0.05
1996	21	1 176	56.6	902	43.4	13.2	20	19.34	n.s.
1997	27	1 534	50.2	1 520	49.8	0.5	26	35.65	n.s.
1998	19	1 421	51.7	1 329	48.3	3.3	18	26.89	n.s.
1999	34	4 903	66.1	2 518	33.9	32.1	33	188.77	<0.01

**Table 4.** Number of upper and lower beaks in stomach samples collected from adult wandering albatrosses at Bird Island, South Georgia, during the months May–October 2009 (*N* is the number of the sample, and *n* the number of beaks).

<i>N</i>	Upper (U)		Lower (L)		U–L%
	<i>n</i>	Percentage	<i>n</i>	Percentage	
1	2	100.0	0	0.0	100.0
2	7	58.3	5	41.7	16.7
3	7	58.3	5	41.7	16.7
4	7	58.3	5	41.7	16.7
5	17	53.1	15	46.9	6.3
6	8	50.0	8	50.0	0.0
7	8	50.0	8	50.0	0.0
8	8	50.0	8	50.0	0.0
9	8	50.0	8	50.0	0.0
10	3	50.0	3	50.0	0.0
11	3	50.0	3	50.0	0.0
12	1	50.0	1	50.0	0.0
13	9	50.0	9	50.0	0.0
14	9	50.0	9	50.0	0.0
15	4	50.0	4	50.0	0.0
16	15	46.9	17	53.1	–6.3
17	15	46.9	17	53.1	–6.3
18	15	46.9	17	53.1	–6.3
19	15	46.9	17	53.1	–6.3
20	8	42.1	11	57.9	–15.8
21	8	42.1	11	57.9	–15.8
22	5	38.5	8	61.5	–23.1
23	5	38.5	8	61.5	–23.1
24	7	36.8	12	63.2	–26.3
25	2	28.6	5	71.4	–42.9
26	1	25.0	3	75.0	–50.0
27	0	0.0	1	100.0	–100.0
28	0	0.0	1	100.0	–100.0

### Diet reconstruction

There were more upper than lower beaks recorded for five species (*B. skolops*, *M. hyadesi*, *Moroteuthis ingens*, *Histioteuthis atlantica/bonnelli* *corpuscula*, and *Chiroteuthis veranyi*; Table 1). Based on the number of upper rather than lower beaks for these species, their contribution to the diet of wandering albatrosses would increase by 16 872–108 240 g (Table 1). From the species that showed greater variation, the estimated contribution by mass of *M. hyadesi* doubled, with values from +1.7 to +3.8% (Table 1).

### Upper:lower beak ratios in other studies

In the few studies published on the number of upper and lower beaks in the stomach contents of other marine predators (<10% of more than 100 publications on papers on diets that included cephalopods), the ratio varies widely (Table 5). This study showed more upper beaks than lower beaks, with the greatest biases in boluses from grey-headed *Thalassarche chrysostoma* and wandering albatrosses (36.5 and 32.3% more upper than lower beaks, respectively; Table 5). The opposite also applied, with some studies recording more lower beaks, by as much as 64.9% in gentoo penguins (*Pygoscelis papua*; Libertelli et al., 2004). Many studies analysed old material, particularly the stomach contents of beached whales, in which beaks may have been retained for a considerable time, or did not discriminate between old and fresh material. In contrast, diet studies of fish and, to a certain extent, seabirds were generally of fresh material only (Table 5). The type

of diet sample, therefore, had a major bearing on upper:lower beak ratios, with biases greater in boluses collected from albatrosses and in stomach contents that contained beaks accumulated over long periods. Beak ratios in scats of seals and penguins also tended to be strongly biased (Table 5).

### Discussion

To our knowledge, this is the first study to review critically the differences in the number of upper and lower cephalopod beaks in the diets of a broad suite of marine predators. The ratio of upper to lower beaks in the diet of wandering albatrosses can vary considerably within samples from a single year, between years, and between diet-sampling methods, but there was no evidence across cephalopod species. Upper:lower beak ratios also vary greatly in the diet of other predators, including penguins, seals, whales, and fish. The results emphasize the need for workers to report the number of upper and lower beaks in their studies and to consider the implications of identifying one or both beak types when evaluating the cephalopod component of the diets of predators.

The biases in the ratio of the number of upper and lower beaks in diets can be in either direction and can be associated with the method used to assess the diet. In wandering albatrosses, cephalopod diet has been assessed from both whole stomach contents and boluses (Xavier et al., 2003a). Stomach contents include mostly freshly ingested cephalopods with flesh attached, but may also contain old beaks accumulated over days or even months. Boluses contain only old cephalopod beaks delivered by both parent birds during the preceding winter, up to ~9 months (Prince and Morgan, 1987), so upper and lower beaks can be eroded (Xavier et al., 2003a). For example, cephalopod species with smaller beaks can be digested entirely or become sufficiently eroded that they pass through the gut (Ashmole and Ashmole, 1967; Imber, 1973; Rodhouse et al., 1987; Xavier et al., 2003a), which may result in a bias towards larger species and species with bigger beaks. However, in this study, we did not find differences between the sizes of lower beaks from stomach contents and boluses, but there may be such differences in other predators.

Another potential source of bias between beak numbers is that upper and lower beaks are morphologically different and may be affected differently in predator stomachs. Small beaks often accumulate within the rostrum of large upper beaks. This may lead to a bias towards upper beaks, which are generally smaller and therefore more likely to be protected in that manner. It also highlights the need for workers to check inside the rostrum of large upper beaks. It is also possible that high gut temperatures cause lower beaks to flatten, resulting in the wings touching and abrading (Xavier et al., 2005) and their consequent underrepresentation in predator diets (Rodhouse et al., 1987). *Gonatus antarcticus* and *Taonius* sp. B (Voss) are two good examples of species whose lower beaks do change shape in this way. However, our study shows that there was no consistent difference between the number of upper and lower beaks of these species in diet samples (Table 1), suggesting that beaks that change shape are not necessarily subject to greater erosion (Table 1). Further work needs to explore which cephalopod beaks can change shape and identify those more likely to be affected.

Although the ratio of upper and lower beaks for all cephalopod species was not statistically different from unity, the results of this study show a strong bias towards lower beaks for *H. eltaninae* and *H. miranda* in diet samples from wandering albatrosses



**Table 5.** The number of upper and lower beaks recorded in diet studies of seabirds, seals, whales, and fish in relation to sampling methodology (*N* is the number of samples analysed, and *n* the number of beaks).

Predator	N	Location	Sampling method	Material (fresh/old)	n		U – L%	Source
					Upper (U)	Lower (L)		
Seabirds								
Grey-headed albatross	72	South Georgia	Boluses	Old	3 538	1 615	36.5	BAS (unpublished data)
Wandering albatross	34	South Georgia	Boluses	Old	4 903	2 508	32.3	This study; Xavier <i>et al.</i> (2003a)
Yellow-nosed albatross	8	Kerguelen	Stomach contents	Old	50	35	17.6	Cherel <i>et al.</i> (2002); BAS (unpublished. data)
Black-browed albatross	120	South Georgia	Stomach contents	Mixed	891	628	17.3	Xavier <i>et al.</i> (2003b)
Grey-headed albatross	38	Kerguelen	Stomach contents	Old	1 893	1 365	16.2	Cherel <i>et al.</i> (2002); BAS (unpublished. data)
Black-browed albatross	35	Kerguelen	Stomach contents	Old	675	510	13.9	Cherel <i>et al.</i> (2002); BAS (unpublished. data)
Grey-headed albatross	120	South Georgia	Stomach contents	Mixed	2 684	2 157	10.9	Xavier <i>et al.</i> (2003b)
Gentoo penguin	55	South Georgia	Stomach contents	Fresh	8	7	6.7	Unpublished data
Black-browed albatross	114	Kerguelen	Stomach contents	Old	778	689	6.1	Cherel <i>et al.</i> (2000); BAS (unpublished data)
Magellanic penguins	16	South Brazil	Stomach contents	Fresh	262	240	4.4	Baldassin <i>et al.</i> (2010)
Wandering albatross	33	Crozet	Stomach contents	Old	3 716	3 905	–2.5	This study
Gentoo penguin	125	South Orkneys	Stomach contents	Mixed	346	1 628	–64.9	Libertelli <i>et al.</i> (2004)
Seals								
Antarctic fur seal	206	South Orkneys	Scats	Old	91	57	23.0	Daneri <i>et al.</i> (1999)
Antarctic fur seal	39	South Orkneys	Scats	Old	62	41	20.4	Libertelli <i>et al.</i> (2004)
Cape fur seal	?	Namibia	Scats	Old	1 817	1 253	18.4	Bruyn <i>et al.</i> (2003)
Southern elephant seal	11	South Orkneys	Stomach contents	Old	68	50	15.3	Clarke and MacLeod (1982a)
Weddell seal	8	South Shetland Islands	Stomach contents	Old	383	349	4.6	Clarke and MacLeod (1982b)
Australian fur seal	1 043	Tasmania	Scats/stomach contents	Old	300	301	–0.2	Hume <i>et al.</i> (2004)
Southern elephant seal	18	South Shetland Islands	Stomach contents	Old	285	303	–3.1	Daneri <i>et al.</i> (2000)
Galapagos fur seal	7	Galapagos Islands	Stomach contents	Old	184	275	–19.8	Clarke and Trillmich (1980)
Whales								
False killer whale	1	Gran Canaria, Spain	Stomach samples	Old	29	22	13.7	Hernández-García (2002)
Cuvier's beaked whale	1	UK	Stomach samples	Old	8 423	6 858	10.2	Santos <i>et al.</i> (2001)
Sperm whale	17	Azores, Portugal	Stomach samples	Old	28 534	26 654	3.4	Clarke <i>et al.</i> (1993)
Cuvier's beaked whale	1	Spain	Stomach samples	Old	693	659	2.5	Santos <i>et al.</i> (2001)
Sperm whale	36	Australia	Stomach samples	Old	52 109	49 774	2.3	Evans and Hindell (2004)
Sperm whale	?	Ecuador	Scat samples	Old	133	164	–10.4	Smith and Whitehead (2000)
Cuvier's beaked whale	1	Spain	Stomach samples	Old	525	673	–12.4	Santos <i>et al.</i> (2001)
Pilot whale	4	Argentina	Stomach samples	Old	87	118	–15.1	Clarke and Goodall (1994)
Sperm whale	14	Peru/Chile	Stomach samples	Old	595	1 057	–28.0	Clarke <i>et al.</i> (1976)
Fish								
Sleeper shark	36	Kerguelen	Stomach contents	Mixed	308	245	11.4	Cherel and Duhamel (2004)
Blue shark	26	UK	Stomach contents	Mixed	97	92	2.6	Clarke and Stevens (1974)

Continued

Table 5. Continued

Predator	N	Location	Sampling method	Material (fresh/old)	n		U–L%	Source
					Upper (U)	Lower (L)		
Patagonian toothfish	3 640	South Georgia	Stomach contents	Fresh	185	178	1.9	Xavier <i>et al.</i> (2002)
Longnose lancetfish	150	Seychelles	Stomach contents	Fresh	66	66	0.0	Potier <i>et al.</i> (2007)
Porbeagle shark	20	Kerguelen	Stomach contents	Mixed	343	346	–0.4	Cherel and Duhamel (2004)
Patagonian toothfish	?	Kerguelen	Stomach contents	Mixed	1 372	1 430	–2.1	Cherel <i>et al.</i> (2004); BAS (unpublished data)
Patagonian toothfish	?	Crozet	Stomach contents	Mixed	845	894	–2.8	Cherel <i>et al.</i> (2004); BAS (unpublished data)
Lantern shark	12	Kerguelen	Stomach contents	Mixed	14	16	–6.7	Cherel and Duhamel (2004)

BAS, British Antarctic Survey. The list is in order of the percentage difference between the number of upper and lower beaks, by taxonomic group.

(>15% lower beaks; Table 1), suggesting that the upper beaks of those species can become heavily eroded and unrecognizable, or even pass through the gut. Given the small size of the upper beak of *H. eltaninae*, this result is not surprising, but less expected for the upper beaks of *H. miranda*, which is of similar size to those of *G. antarcticus* and *H. bonnellii corpuscula/atlantica*, so might be regarded as reasonably resistant to erosion. Also, unlike upper beaks of *H. miranda*, upper beaks of *H. eltaninae* cannot be confused with those from other histioteuthids. *Histioteuthis eltaninae* is one of the most common cephalopod species consumed by wandering albatrosses and is also found in the diet of a range of other seabirds, fish, whales, and dolphins across the Southern Ocean (Cherel and Klages, 1998; Xavier *et al.*, 2003a; Xavier and Cherel, 2009). In contrast to the results for *H. eltaninae* and *H. miranda*, the bias was towards upper beaks in many other species (Table 1). Therefore, if only lower beaks are used for identification, cephalopods can be underestimated in the diets of predators. According to our results, this would underestimate the number of *B. skolops* and *M. hyadesi* consumed by 10.7 and 7.7%, respectively (Table 1). Moreover, the maximum estimated mass of cephalopods consumed by wandering albatrosses in the sample increases by >108 kg if the assessment is based on the more numerous upper beaks for the five species where there was an obvious bias (Table 1). The results here clearly show that by looking at lower beaks only, cephalopod importance in the diet of predators can be underestimated. Moreover, biases towards upper or lower beaks may extend to the studies of other predators, including other seabirds, seals, whales, and fish (Table 5). As most studies use just lower beaks for species identification (Klages, 1996; Smale, 1996; Cherel and Klages, 1998; Boyle and Rodhouse, 2005; Xavier and Cherel, 2009), the cephalopod component can be underestimated (by frequency of occurrence, by number, and by mass) when upper beaks are more frequent. Indeed, in stomach contents from predators that contained few beaks (either fresh or accumulated), it is uncommon to find pairs of beaks (Cherel *et al.*, 2004). In such cases, it is important to be able to identify (and measure) cephalopods from upper beaks.

To conclude, as the ratio of upper:lower beaks frequently differs from unity, we suggest that workers should report the number of each beak type and, in instances where there is a consistent bias (>30%), all beaks should be identified, and as many as possible lower or upper beaks used to reconstruct the cephalopod

component of the diet by mass. In samples collected from predators that tend to retain material, it is also important to separate old and fresh material during the initial sorting process (Cherel *et al.*, 2000) to derive a qualitative assessment of the extent of erosion of the material. These components can then be analysed separately, as required, and the results compared. We also propose that greater effort be assigned to describing upper beak morphology, to aid identification (the few available references are Clarke, 1962a; Imber, 1978; Wolff, 1984; Lu and Ickeringill, 2002; Xavier and Cherel, 2009), to measuring upper beaks in diets, and to developing allometric equations for estimating cephalopod mass based on both lower and upper beak measurements.

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