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ORIGINAL PAPER

Predation on cephalopods by Weddell seals, *Leptonychotes weddellii*, at Hope Bay, Antarctic Peninsula

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Abstract Cephalopods play a key role in marine environments as food resources for top predators such as marine mammals and seabirds. However, detailed information on their trophic relationships with Antarctic seals is scarce. The aim of the present study was to examine the cephalopod portion of the diet of adult and subadult Weddell seals, *Leptonychotes weddellii*, at Hope Bay, Antarctic Peninsula, through the analysis of scats collected during three consecutive summers (2003, 2004 and 2005). Cephalopods occurred in almost 45% of the 217 samples collected during the whole period of study. A total of 662 beaks (358 upper and 304 lower) were removed from scats containing cephalopod remains ($n = 93$). Octopods were largely dominant in comparison with teuthoids constituting in numerical abundance over 95% of the cephalopod prey. The octopod *Pareledone turqueti* was the most frequent and dominant prey species representing, respectively, 57.9 and 71.1% in numbers and biomass of cephalopods consumed. Species belonging to the group of papillated *Pareledone* were second in importance. The results were compared with information from previous dietary studies of *L. weddellii* at other localities of Antarctica. Based on the examination of the cephalopod prey taxa identified in this study, it is suggested that during the study period Weddell seal individuals foraged mainly on benthic prey resources close to the coast, in inshore waters where octopods were dominant in comparison with pelagic squid.

Keywords *Leptonychotes* · Cephalopods · Diet · Weddell seals · Antarctic Peninsula

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Introduction

The investigation of the feeding habits of seals is essential for the interpretation of their ecological role as top predators in marine ecosystems. The Weddell seal, *Leptonychotes weddellii,* is an important high level predator that forages in Antarctic coastal ecosystems. This species' ability to dive below 700 m allows it to forage in both benthic and pelagic habitats over the Antarctic continental shelf (Testa 1994; Lake et al. 2003). To date, most dietary studies of Weddell seals, mainly based on scat or stomach content analysis but also on stable isotope techniques, have indicated that fish, cephalopods and crustaceans are their dominant prey taxa. The relative contribution of each of these food items to the overall diet of seals is highly variable both temporally and spatially (Dearborn 1965; Plötz 1986; Green and Burton 1987; Plötz et al. 1991; Castellini et al. 1992; Casaux et al. 1997; Burns et al. 1998; Lake et al. 2003; Zhao et al. 2004; Casaux et al. 2006, among others).

However, detailed information on the cephalopod component of the diet of Weddell seals is scarce and, in fact, restricted to two studies performed at two different localities on the Scotia Arc (Lipinski and Woyciechowski 1981;

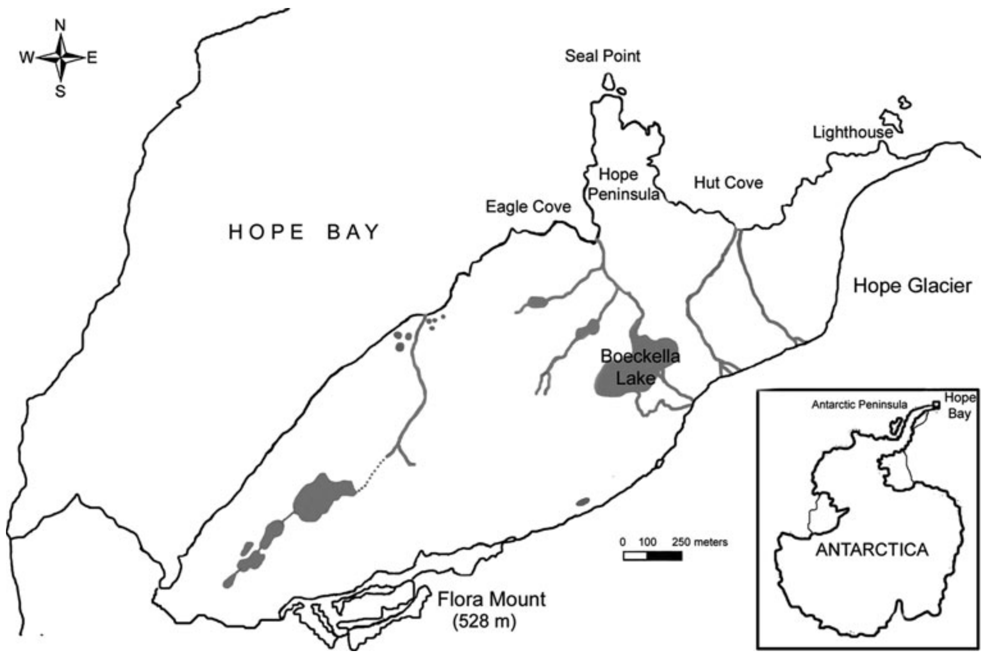

Fig. 1 Sampling area at Hut Cove, Hope Bay, Antarctic Peninsula

Clarke and MacLeod 1982). It is widely acknowledged that cephalopods play a key role in global marine ecosystems since they occupy a wide range of habitats, are voracious predators and, in turn, constitute an important food item of top predators such as marine mammals and birds (Clarke 1996). Notwithstanding, information on their biology is mostly scarce and restricted to a few commercially exploited species, mainly shelf-living families. This poor understanding of cephalopod ecology is due in part to a paucity of scientific surveys, the difficulties associated with catching oceanic species and their complicated life cycles and distribution patterns (Piatkowski et al. 2001; Cherel and Hobson 2005).

Thus, the aims of the present study were to examine the cephalopod prey of adult and subadult Weddell seals at Hope Bay, Antarctic Peninsula, during three consecutive summer seasons, to assess the contribution of this prey taxon to the overall diet of seals and to detect whether or not there was interannual variation in the sizes of the different prey species.

Materials and methods

In total, 217 scats were collected along the coasts of Hut Cove, Hope Bay (63°24′S, 57°00′W), Antarctic Peninsula, next to the Argentine scientific station Esperanza, from mid-February to mid-March of three consecutive years ($n = 51$ in 2003, $n = 87$ in 2004 and $n = 79$ in 2005) (Fig. 1). The collection was carried out around groups of up to 20 adult and/or subadult seals of both sexes. Scats were kept frozen at −20° and then washed in the laboratory through a series of sieves of different mesh size (range, 0.5–2.5 mm.). The different prey remains were sorted under a stereoscopical microscope into three main prey taxa: fish, cephalopods and crustaceans.

Cephalopods were mostly represented by mandibles (beaks) and, in minor proportions, by eye lenses and pens. Beaks were identified to the lowest possible taxonomic level by comparison with a reference collection deposited at the Instituto Antártico Argentino and using appropriate published literature (Lipinski and Woyciechowski 1981; Clarke 1986; Xavier and Cherel 2009). Squid lower beak rostral lengths (LRL) and octopus lower beak hood lengths (LHL) were measured using digital vernier callipers to the nearest 0.01 mm, and from these measurements, the dorsal mantle length (ML) and wet mass were estimated using allometric equations from Rodhouse et al. (1992), Gröger et al. (2000) and Xavier and Cherel (2009). Furthermore, in order to detect interannual differences in the size frequency distribution of the main cephalopod species preyed on by seals, a nested Anova test was performed.

Results

Over the study period as a whole, the two main prey taxa were fish and cephalopods which occurred, respectively, in an average of 94.5 and 45.6% of scats containing food remains, the presence of crustaceans being of minor importance (7.8%). There were no significant differences between years in the frequency of occurrence of these three main taxa (x^2_4: 4.19, $P = 0.38$) (Fig. 2). A total of 662 beaks (358 upper and 304 lower) were removed from 75 of the 93

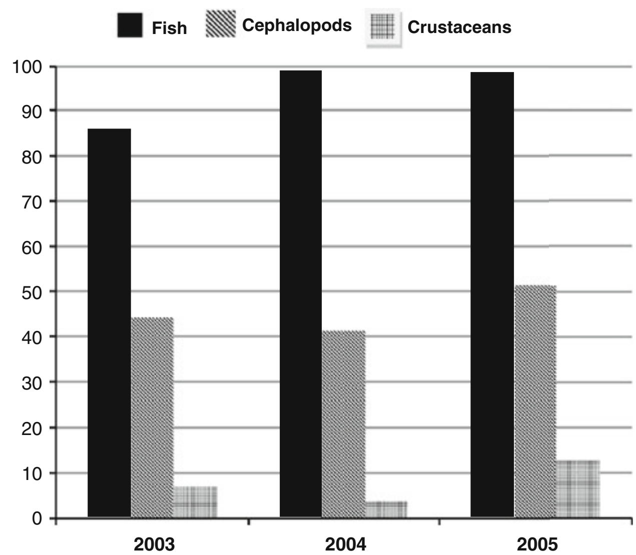

Fig. 2 Frequency of occurrence of fish, cephalopods and crustaceans found in Weddell seal scats, during three consecutive years at Hope Bay, Antarctica

faecal samples that contained cephalopod remains. Of these, 79 beaks (34 lower and 45 upper) were removed from the 19 scats collected in 2003 at a rate of 4.2 beaks per scat, 245 beaks (113 lower, 132 upper) from the 34 scats collected in 2004 at a rate of 7.2 beaks per scat and 338 beaks (181 upper, 157 lower) from the 40 scats collected in 2005 at a rate of 8.2 beaks per scat. The maximum number of beaks in a given sample was 54 (25 upper, 29 lower) representing 2286.7 g wet mass, and the maximum number of cephalopod taxa identified in a sample was four. Pens and eye lenses were also removed from these scats but in minor proportions.

Octopods were largely dominant in comparison with teuthoids throughout the total period of study, constituting in numerical abundance over 95% of the cephalopod prey of seals. The octopod *Pareledone turqueti* was the most frequent and dominant prey species occurring in 65.7% of samples and representing, respectively, 57.9 and 71.1% in terms of numbers and biomass of cephalopods consumed. Species belonging to the group of papillated *Pareledone* (see Allcock 2005) were second in importance, occurring in 49.2% of samples and representing almost 25% in numbers. Species in this group are morphologically very similar and cannot currently be separated to species on beak morphology. Papillated *Pareledone* together with *Adelieledone polymorpha* constituted 27.5% by mass of the cephalopod prey. The presence of teuthoids was negligible, and these were only represented by the Antarctic glacial squid, *Psychroteuthis glacialis* (Table 1). The LHL of the different octopod prey species ranged from 1.6 to 7.8 mm, which represented specimens of 33.6–121.4 mm ML and 14.0–367.3 g wet mass, while the LRL of the squid *P. glacialis* ranged from 3.0 to 4.5 mm representing specimens of 85.9–184.2 mm ML and 18.2–117.9 g wet mass (Table 2). The estimated dorsal mantle length (ML) frequency distributions of the different cephalopod species preyed on by Weddell seals during the total period of study are shown in Fig. 3. There were only significant interannual differences in the mean sizes (ML) of *P. turqueti* specimens preyed upon by seals (mean 79.3 ± 16.4 in 2003; mean 74.8 ± 19.2 in 2004; mean 83.9 ± 16.2 in 2005) (nested Anova $P < 0.001$), the difference lying between the 2004 and 2005 season (Tukey HSD post hoc comparison of means $P < 0.01$).

Discussion

The present study indicates that, in terms of frequency of occurrence, cephalopods constituted an important prey item, after fish, in the diet of Weddell seals at Hope Bay. Furthermore, octopods constituted the bulk of the cephalopod diet, being represented by one species group and two species (papillated *Pareledone* species group, *P. turqueti*, *A. polymorpha*). According to previous dietary studies at several localities of the Southern Ocean, the relative contribution of cephalopods to the diet of this phocid seal seems

Table 1 Taxonomic composition of the cephalopod prey of Weddell seals, *Leptonychotes weddellii*, at Hope Bay during three consecutive years expressed as the frequency of occurrence (f), percent frequency of occurrence (%f), number of otoliths (n), percentage of the total number (%n), mass (m) and percentage of total mass (%m)

Prey taxon	2003						2004						2005					
	f	%f	n	%n	m	%m	f	%f	n	%n	m	%m	f	%f	n	%n	m	%m
Octopods																		
Papillated *Pareledone*	9	60	15	44.1	931.6	35.5	9	42.9	34	30.1	2,643.1	29.0	15	48.4	26	16.6	2,000.0	11.2
Pareledone turqueti	7	46.7	10	29.4	1,100.0	41.9	14	66.7	54	47.8	5,305.2	58.1	23	74.2	112	71.3	14,653.3	82.1
Adelieledone polymorpha	4	26.7	4	11.8	258.2	9.8	10	47.6	25	22.1	1,181.0	12.9	10	32.3	18	11.5	1,134.2	6.4
Teuthoids																		
Psychroteuthis glacialis	2	13.3	5	14.7	332.4	12.7							1	3.2	1	0.6	57.7	0.3

Table 2 Number of lower beaks and estimated size and wet mass of octopod and squid ingested by *L. weddellii* at Hope Bay

Prey species	Season	N	LHL/LRL			ML		
			Mean ± SD	Median	Range	Mean ± SD	Median	Range
P. turqueti	2003	10	4.6 ± 1.2	4.6	3.3–6.6	79.3 ± 16.4	78.9	61.2–105.3
	2004	54	4.3 ± 1.4	3.6	2.1–6.8	74.8 ± 19.2	66.2	45.7–108.1
	2005	112	5.0 ± 1.2	5	2.2–7.8	86.9 ± 16.2	84.7	46.6-121.4
Papillated *Pareledone*	2003	15	3.4 ± 1.1	2.8	2.4–5.5	38.0 ± 9.2	33.1	29.4–55.6
	2004	34	3.8 ± 1.5	3.3	1.9–7.1	41.4 ± 12.5	37	24.7–68.8
	2005	26	3.9 ± 1.1	3.8	1.6–7.0	41.9 ± 9.5	41.3	22.8–68.0
A. polymorpha	2003	4	2.6 ± 0.5	2.7	1.9–2.9	57.0 ± 11.9	60.6	40.6-66.1
	2004	25	2.3 ± 0.4	2.3	1.6–3.5	50.4 ± 10.6	51.5	33.6–79.6
	2005	18	2.5 ± 0.5	2.4	1.8–3.5	55.9 ± 11.8	54.1	36.6–80.9
P. glacialis	2003	5	3.9 ± 0.6	3.9	3.0–4.5	141.1 ± 40.5	144.5	85.9–184.2
	2004	0						
	2005	1	3.9			141.9		

ML Mantle length, *LRL* lower rostral length, *LHL* lower hood length

to be highly variable. For instance, Bertram (1940), based on the analysis of stomach contents from 367 killed specimens on the coast of Graham Land, indicated that cephalopods and fish were the main constituents of the diet of adult Weddell seals, being equally represented in stomachs. At McMurdo Sound, Dearborn (1965) found that cephalopods, mostly represented by octopod remains, occurred in 17% of 36 seal stomachs while fish were the dominant prey, occurring in almost all samples (97%). Similarly and for the same locality, Testa et al. (1985) found that cephalopod remains occurred in 17.9% while fish were present in over 90% of the 28 stomach samples examined. In East Antarctica, Green and Burton (1987) reported that cephalopods were present in an average of 10% of 845 faeces collected throughout one year at Davis, in 25% of 20 stomachs collected at McMurdo Sound and in 44.4 and 100% of 18 scats and 5 stomach samples, respectively, from the Mawson area, with a clear dominance of octopods. In contrast, Burns et al. (1998) found that cephalopods, mostly represented by teuthoids, tentatively identified as Brachioteuthidae sp., occurred in less than 10% of 197 Weddell seal scats at McMurdo Sound. Lake et al. (2003) studying the temporal and spatial variation in the diet of *L. weddellii* at four localities of East Antarctica (Commonwealth Bay, Larsemann Hills, Mawson and Vestfold hills) concluded, in agreement with Green and Burton (1987), that cephalopods constituted an important food item of seals at Mawson. This taxon occurred in 56% of 201 scats and contributed 82% by mass to the overall diet, being mainly represented by octopods and in minor proportion by the squid *P. glacialis.*

In the southern and eastern Weddell Sea, Plötz (1986) indicated that cephalopods were a minor constituent of the diet of Weddell seals, with octopods and teuthoids occurring, respectively, in 14.3 and 23.8% of 21 stomachs examined. Moreover, for this same area, Plötz et al. (1991) reported that cephalopods constituted only 3.6% of the total number of prey items of seals.

In the Scotia Arc, several dietary studies of *L. weddellii* have indicated a relatively greater contribution of cephalopods to their overall diet in comparison with those reports coming from the Weddell Sea area and East Antarctica.

At Nelson Island, Casaux et al. (1997) reported that the cephalopod diet of Weddell seals was mainly represented by octopods that were present in almost 50% of samples analysed (41 faeces and 5 vomits) and contributed 23% and over 60% in terms of numbers and mass, respectively. The presence of squid (*P. glacialis*) was negligible. At Laurie Island, South Orkney Islands, Casaux et al. (2009) analysed the diet of Weddell seals during two periods (May 1999–January 2000 and September–December 2001). Although octopods were present in over 60% of the scats collected ($n = 44$ in 1999 and $n = 22$ in 2001), their contribution in numbers and mass differed widely between the collection periods (15%, 1999/2000 vs. 0.1%, 2001 and 46.6%, 1999/2000 vs. 8.8%, 2001, respectively). As reported from Nelson Island, the presence of squid, also represented by *P. glacialis,* was negligible.

At King George Island, Lipinski and Woyciechowski (1981) examined the stomach contents of 12 Weddell seals caught in Admiralty Bay, indicating that cephalopods, mainly represented by octopods, were as important as fish in the diet of seals, occurring in over 90% of the samples analysed. The main prey species were identified as *Megaleledone senoi* (now *M. setebos*), *P. turqueti* and *P. charcoti* (which probably actually comprised several species in the papillated *Pareledone* complex).

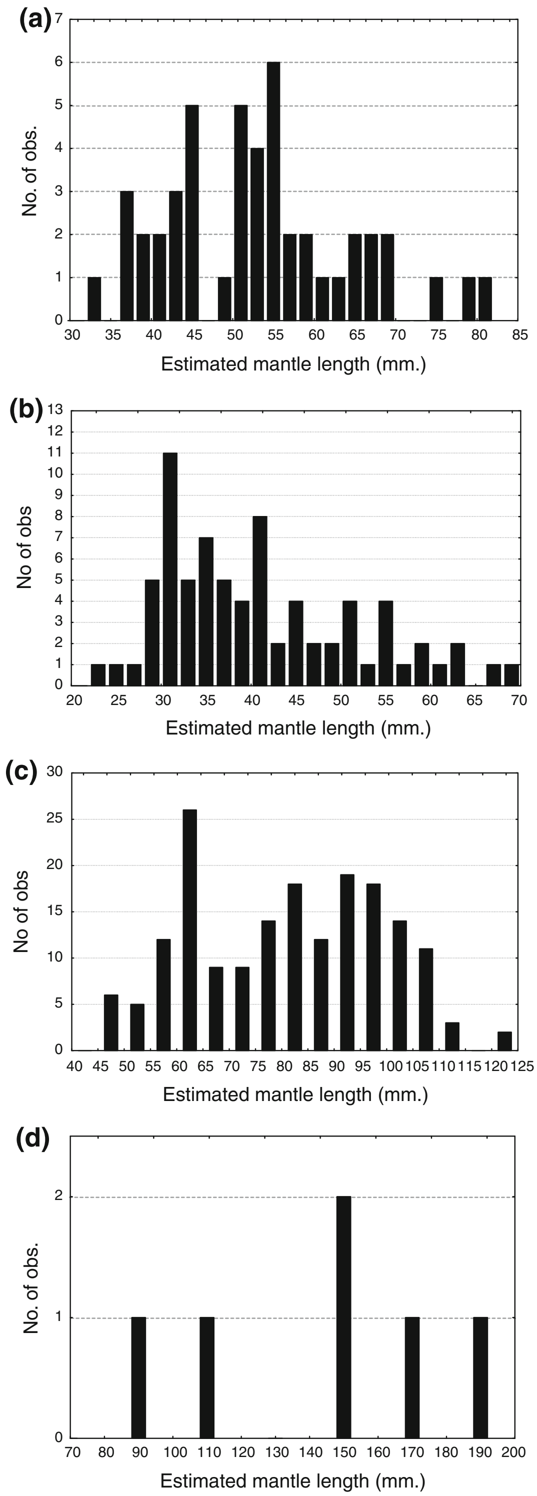

Fig. 3 Estimated mantle length frequency distribution of **a** *A. polymorpha*, **b** papillated *Pareledone,* **c** *Pareledone turqueti* and **d** *Psychroteuthis glacialis* preyed upon by Weddell seals at Hope Bay during the whole study period

Clarke and MacLeod (1982) based on the examination of the stomach contents of eight Weddell seals killed at Deception Island reported that cephalopod remains occurred in all samples. However, and unlike other studies, teuthoids made a substantial contribution to their diet with *Moroteuthis knipovitchi* and *P. glacialis* constituting together 60% in terms of numerical abundance followed by octopods (identified as *Pareledone* sp. but which may also have included *M. setebos,* see Allcock et al. 2003a, b), which represented 33.6% in numbers. Furthermore, *M. knipovitchi* and *Pareledone* sp. represented together almost 70% by mass of the cephalopod diet of the seals.

The only previous dietary study of *L. weddellii* carried out in the Antarctic Peninsula comes from Danco Coast where a total of 144 scats were collected from January to March of 1998 ($n = 105$) and 2000 ($n = 39$) (Casaux et al. 2006). In comparison with our study, the contribution of cephalopods was of lesser importance both in numbers (<5%) and in mass (<10%), but teuthoids (*P. glacialis)* were more frequent than octopods (*Pareledone* sp.) (average frequency of occurrence 35 vs. 17%).

As previously stated, almost all studies performed in different areas of Antarctica have reported that fish followed by cephalopods were the most important prey of Weddell seals. Moreover, when analysing the cephalopod portion of the diet, with few exceptions, there was a general predominance of octopods to teuthoids. It is worth mentioning that in a great proportion of these studies, the identification of both octopod and squid beaks was tentative or restricted to the genus or even to a higher taxonomic level (e.g. Clarke and MacLeod 1982; Plötz et al. 1991; Burns et al. 1998; Lake et al. 2003; Casaux et al. 2006, 2009).

In the present study, a total of three cephalopod species and one species group were identified: this included two octopod species and one species group and one squid species (Table 1). The only squid prey found in this study, *P. glacialis,* is an endemic species with a circumpolar distribution, extending to the Antarctic continent (Gröger et al. 2000) This species is considered one of the most abundant in high Antarctic areas, extending as far north as South Georgia but not beyond the Antarctic Polar Front (Collins and Rodhouse 2006). As do many other Antarctic squids, *P. glacialis* individuals undergo an ontogenetic descent with juvenile forms found at shallower depths close to the surface and adults living at deeper depths, probably near the bottom at the shelf break (Filippova and Pakhomov 1994; Collins et al. 2004). The contribution of this squid species to the diet of seals in terms of numerical abundance was low, and its size frequency distribution showed that seals ingested both juvenile and adult forms (Fig. 3).

In regard to the octopod prey of seals, these were mainly represented by three taxa. Two of them (one species and one species group) belong to the most speciose, abundant and widespread genus of the Southern Ocean, i.e. *Pareledone* that, in common with the endemic notothenioid fish families (e.g. Channichthyidae and Artedidraconidae), has undergone extensive radiation, probably as a consequence of the isolated areas of shelf associated with different island groups (Allcock et al. 2001; Collins and Rodhouse 2006). It is worth emphasizing that, until recently, all papillated specimens of *Pareledone* from the Antarctic Peninsula area were ascribed to the species *P. charcoti*. However, a re-examination of the papillated-type material of *Pareledone,* coupled with extensive fishing over several years off the Antarctic Peninsula, has led to the identification of eight new species of papillated *Pareledone* from the Antarctic Peninsula region (Allcock 2005; Allcock et al. 2007). These are distinguished by subtle taxonomic characters, such as the morphology and placement of their papillae, whereas traditional features such as beak morphology fail to separate them as they all show a strong resemblance to *P. charcoti* (Allcock 2005). Most papillated *Pareledone* species occur on bottoms less than 400 m deep, but at least one species is found on bottoms below 800 m (Allcock 2005), so the seals may be foraging on different members of this species group at different depths. The other dominant octopod prey species of Weddell seals at Hope Bay was *P. turqueti.* This species is extremely abundant around the islands of the Scotia Ridge and in West Antarctic, where it is regularly caught in bottom trawl surveys, its bathymetric range extending from 25 to 1,100 m (Kuehl 1988; Yau et al. 2002; Collins et al. 2004; Allcock 2005). In regard to the third octopod species identified, *A. polymorpha,* this is commonly distributed in West Antarctic and has been caught at depths between 15 and 860 m (Allcock et al. 2003a, b).

All these aforementioned cephalopod species are benthic, and information on their diet indicates that polychaetes, amphipods, bivalves and gastropods are among their commonest prey (Piatkowski et al. 2003; Collins and Rodhouse 2006). This would suggest that the occurrence of the above-mentioned prey taxa in stomach contents or scats of Weddell seals would represent secondary prey items, i.e. that they were previously ingested by octopods. However, Daly and Rodhouse (1994) based on the analysis of the beak shape of *A. polymorpha*, which is more delicate and fine in relation to other octopod beak types, surmised that this species could be more specialized to exploit an atypical resource probably in the water column and might also indicate an adaptation to a life style hunting off the bottom.

The size frequency distribution of the three octopod taxa throughout the whole period of study was normal only in *A. polymorpha* (Shapiro–Wilk test $P = 0.2$) but not in *Pareledone* spp. (Shapiro–Wilk test $P < 0.01$) (Fig. 3). Furthermore, according to these distributions, seals ingested both mature and immature forms of the three octopod taxa. Moreover, for *P. turqueti,* an increase with time was observed in the modes of the estimated dorsal mantle length of specimens ingested, probably reflecting the growth of the main classes preyed upon (Fig. 4).

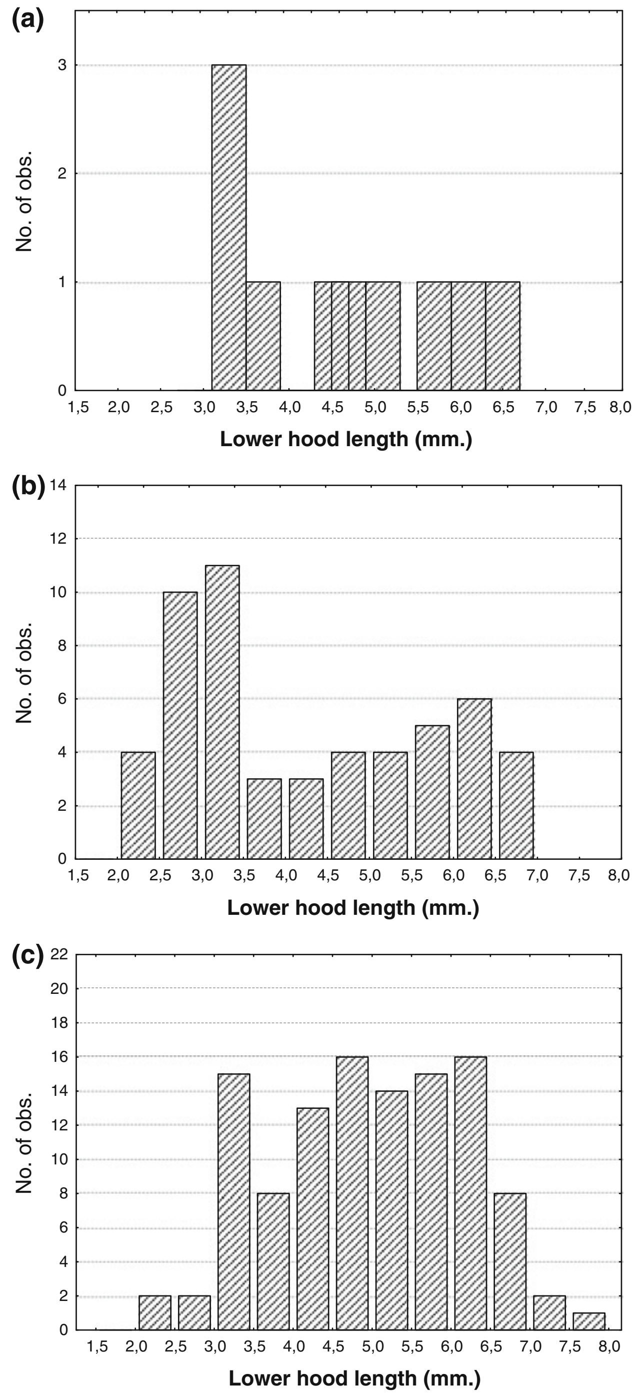

Fig. 4 Lower beak size frequency distribution of *P. turqueti* in **a** 2003 **b** 2004 and **c** 2005

When comparing the beak size of *P. glacialis* specimens found in this study with those reported by Clarke and MacLeod (1982) at Deception Island, we found that the size range was narrower and the modal size class lower (Table 3).

Table 3 Lower rostral length (LRL, mm.) and lower hood length (LHL) of *P. glacialis* and octopodid species eaten by Weddell seals at different localities of the Southern Ocean

Locality	*Psychroteuthis glacialis* (LRL)		Octopodidae spp. (LHL)	
	Range	Mode	Range	Mode
Deception Island[a]	2.7–7.1	4.5–6.0	2.5–12.0	–
King George Island[b]	–	–	3.8–15.5	7.5–8.0
Hope Bay[c]	3.0–4.5	3.5–4.0	1.6–7.8	3.0–3.5

[a] Clarke and MacLeod 1982

[b] Lipinski and Woyciechowski 1981

[c] This study

In the case of octopodids, and regarding all species combined, their beak size (LHL) range was also narrower and the maximum size lower in comparison with those caught by Weddell seals at Deception Island and King George Island (Lipinski and Woyciechowski 1981; Clarke and Macleod 1982) (Table 3).

This might be explained by the different source from which beaks were obtained, since in the present study, these were removed from scats, whereas in the other cited studies, they were extracted from stomachs. Therefore, and following Bigg and Fawcett (1985) suggestion, the accumulation or differential retention of bigger beaks in the stomach rugae or the pyloric sphincter of seals could lead to an underestimate of the sizes and number of cephalopod prey ingested since bigger specimens might not pass through the intestinal tract and therefore could not be found in scats. Future dietary studies of Weddell seals should also include, where possible, a comparative analysis of beak size and numbers removed from different sources, i.e. stomachs vs scats to corroborate or refute this suggestion. Finally, the proportionally higher abundance of octopods to teuthoids observed in the cephalopod diet of Weddell seals in this study would be in line with Green and Burton (1987) observation at Davis. These authors remarked that the seasonal inverse relationship in the proportions of teuthoids and octopods in the cephalopod diet of seals, probably reflected their movements from shallow inshore waters in spring-summer, when octopods were dominant, to deeper offshore waters as the sea ice advanced in winter, when squid became the main prey. As this study was carried out during three consecutive summer seasons, a time when the sea ice cover retreats, Weddell seal individuals probably foraged close to the coast in inshore waters where benthic octopods are dominant in comparison with pelagic squid. The examination of the cephalopod component in the diet of Weddell seals at Hope Bay, during the summer season, a time when seals rest or moult, indicated that these foraged mainly on benthic prey resources as reflected by the clear dominance of octopods in relation to teuthoids. In this sense, it is worth mentioning that preliminary analyses of the fish component of the diet of Weddell seals at this same locality have indicated a predominance of nototheniid fish as their main prey comprising over 90% by numbers followed by channichthyids in minor proportions (Daneri et al. 2007). However, monitoring the diet of this species for a longer period of time (preferentially a decade) at different seasons of the year and therefore at different stages of its annual cycle, i.e. reproductive/moulting phase, will be essential to gain adequate knowledge of its trophodynamics and its ecological role as a top predator of the Antarctic marine ecosystem in the area of the Antarctic Peninsula.

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