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Comparative morphology of two sympatric *Pareledone* species from South Georgia

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Abstract: Morphometric data were collected for 410 specimens of *Pareledone turqueti* and *P. polymorpha* caught around South Georgia. The two species differ in beak morphology and in the male hectocotylus. The species have similar appearances although there is a small but significant difference in the mantle length/body mass relationship for females, with *P. polymorpha* having a relatively longer mantle. There is no significant difference in the arm length/body mass relationship between species or sexes ($p > 0.05$), except in the case of arm IV of females. There is an interspecific significant difference between sucker number on arms I and II of males, arms I–IV of females, and between hood length and mass of the buccal mass ($p < 0.05$), with *P. turqueti* having relatively lower sucker numbers, a longer hood length and greater buccal mass mass. The beak of *P. turqueti* is similar to that of *Eledone* spp. but *P. polymorpha* has a small, fine beak with the rostral tip ending in an elongated, sharp point. Differences in beak and buccal mass suggest that these sympatric species occupy distinct trophic niches and that the differing morphology of the male hectocotylus is a factor in reproductive isolation.

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Key words: *Pareledone* spp., South Georgia, sympatry, beaks, hectocotylus

Introduction

On the South Georgia shelf, two closely related species of octopodids, *Pareledone turqueti* (Joubin 1905) and *P. polymorpha* (Robson 1930), occur together. The two species are distinguishable by their beak morphology and by the hectocotylised third right arm tip of the males. Few data exist on the ecology of *Pareledone*, as literature is restricted to descriptions of preserved specimens and records of geographical distribution (Massy 1916, Berry 1917, Robson 1932), or to accounts of gonad size (Kuehl 1988). Dell (1972) recognized *P. turqueti* as circum-Antarctic, and there is one recorded specimen from Rio de Janeiro (Dell 1959), the only reported instance of this species north of the Antarctic Polar Front. The full distribution of *P. polymorpha* is not known. Kuehl (1988) recorded *P. polymorpha* as slightly more abundant than *P. turqueti* during a trawl survey on the shelf around the South Shetland Islands. The occurrence of these two closely related benthic species in the same area suggests that they occupy discrete trophic niches and have divergent reproductive cycles. This hypothesis is supported by the markedly different beak morphology and relative buccal mass size of the two species, along with comparatively higher numbers of arm suckers in *P. polymorpha*. This study quantifies some morphological similarities and differences between these two sympatric species, and examines the possibility that their specialised anatomies are related to different trophic niches, enabling them to avoid direct competition through ecological separation.

Materials and methods

Between 6–29 January 1987, seven Aggasiz trawls by RRS *John Biscoe* in Cumberland East Bay, South Georgia (Fig. 1) collected 67 specimens of *Pareledone* which were preserved and stored in *c.* 5% formalin on capture. Voight (1991) validated the use of preserved specimens for morphology studies using a number of octopus collections. Bottom depths for the trawls ranged from 131–265 m and the haul duration varied from 10–35 minutes. The samples were identified as the species *P. turqueti*, comprising 29 males and 19 females, and *P. polymorpha* comprising 11 males and eight females. Measurements of total body mass (BM), dorsal mantle length (ML), arm length (AL) and sucker number (SN) for the four arms on the right side, beak hood length (HL), and buccal mass mass (BMM) were taken for all specimens, and ligula and calamus lengths recorded for males. ML, AL, HL, and ligula and calamus lengths were recorded in mm, and BM and BMM in g. These standard parameters for describing cephalopod anatomy were selected from Roper & Voss (1983).

The beaks of each species were described in detail after Clarke (1986). Cephalopod beaks are useful in dietary studies due to their resistance to digestion, and tendency to collect in the stomach of predators, and the lower beak is usually described as it has more distinguishing features. The funnel organ of a subsample was also examined for W or VV shapes (Robson 1932).

Trawls by the MV *Falklands Protector* on the shelf around South Georgia (Fig. 1) between 4–9 February 1989 collected a sample of *Pareledone* spp. for size frequency analysis (n=343).

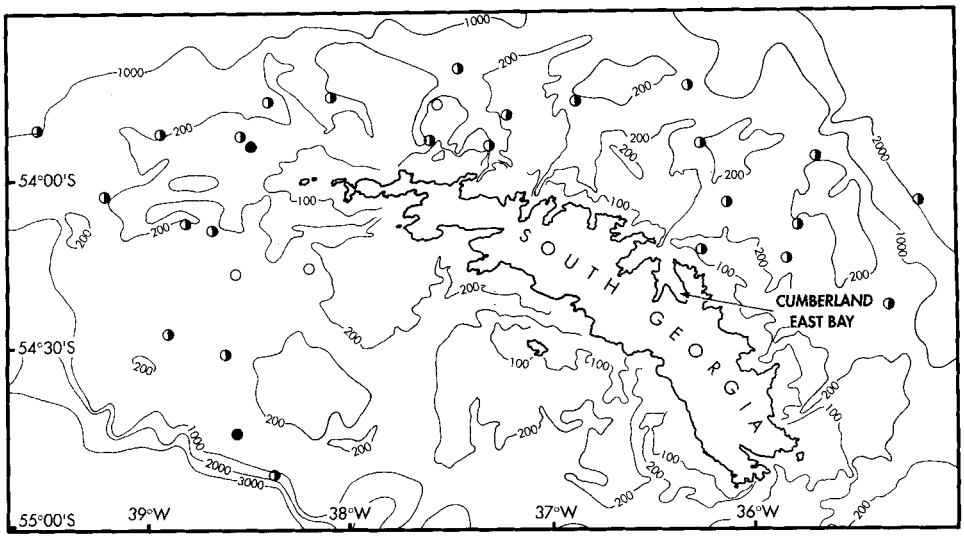

Fig. 1. Map of South Georgia, showing stations where *Pareledone turqueti* and *P. polymorpha* were caught. (Half-filled circles indicate stations where both species were caught, filled circles where only *P. turqueti* was caught and open circles where only *P. polymorpha* was caught).

The sample comprised 119 male and 108 female *P. turqueti*, 52 male and 64 female *P. polymorpha*, and one female *P. charcoti* (Joubin 1905), and was frozen immediately on capture for return to the UK. Sex, species, total body mass and dorsal mantle length were recorded from this sample. Additional species differences in skin colour, body consistency and muscularity were noted.

Statistical analyses were performed using the Minitab software package (Ryan *et al.* 1985), and all data presented in graphical form were $\log_e$ transformed. The preservation process of the sample for morphological analysis meant that some mantle shapes were slightly distorted, so body mass, rather than mantle length, was used as the independent variable throughout to derive allometric relationships.

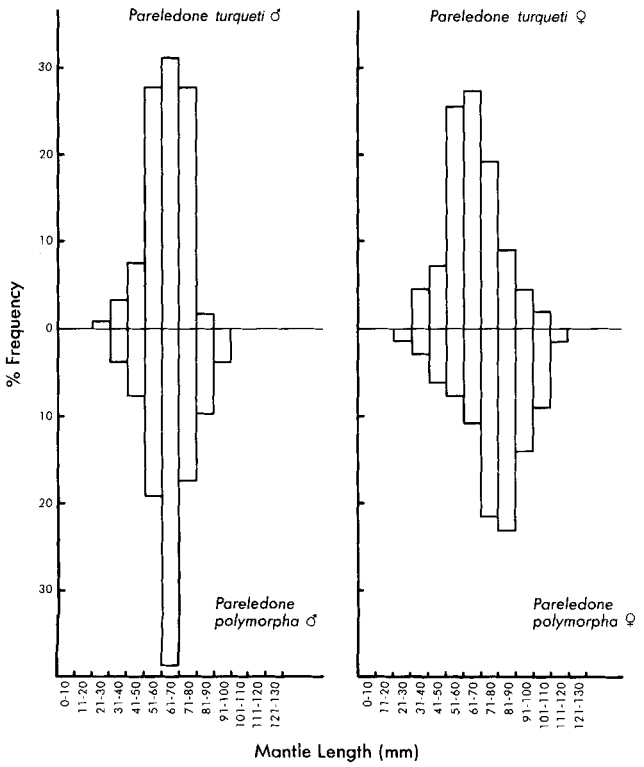

Fig. 2. Size frequency distribution of *Pareledone turqueti* and *P. polymorpha*, (n = 343).

Results

Cumberland East Bay and the position of hauls around South Georgia are shown in Fig. 1. In the combined 1987 and 1989 collections 67% of the catch was composed of *P. turqueti*, and 33% of *P. polymorpha*, with a single *P. charcoti* specimen. The size range of *P. turqueti* was 22–107 mm ML and 8–211 g BM and the size range of *P. polymorpha* 16–113 mm ML and 4–274 g BM. The *P. charcoti* was 50 mm ML and 133 g BM.

The size frequency distribution of the 1989 collection is shown in Fig. 2. *T*-tests assessed significance of difference between distributions. There is no significant difference between the mean ML of male (63.6 ± 11.5) and female (66.8 ± 15.2) *P. turqueti* ($t = 1.75, p > 0.05$). The mean ML of *P. polymorpha* females (78.3 ± 19.3) is significantly larger ($t = 4.17, p < 0.001$) than the males (65.9 ± 12.5). Comparison between the males of both species shows no significant difference (t = 1.14, $p > 0.05$). The *P. polymorpha* females have a significantly larger mean ML than the *P. turqueti* females (t = 4.09, $p < 0.001$).

Comparative external morphology.

The superficial impression of skin colour among the frozen sample was that both species are mid-grey/brown in colour, with pale ventral mantle and arm surfaces. However, close inspection reveals that colour differed slightly, with *P. polymorpha* having a pink tinged skin and a pale blue broken border around the lateral edge between the dorsal and

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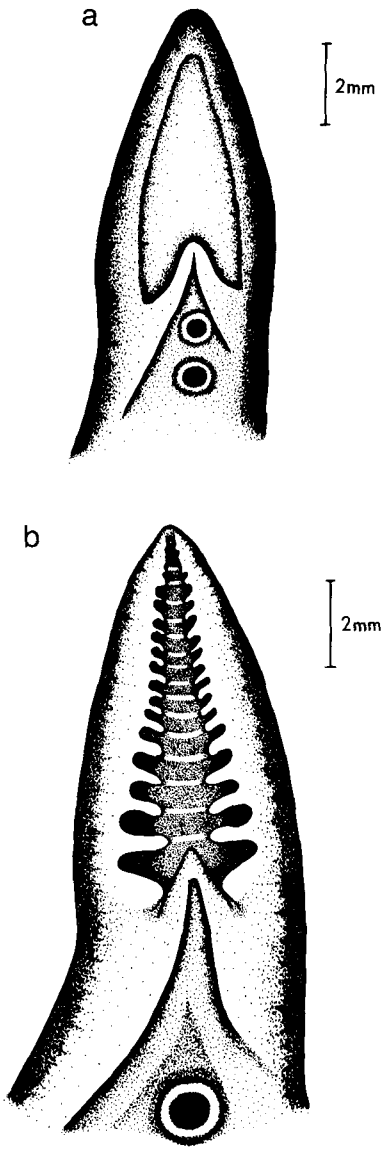

Fig. 3. The hectocotylus tip of *Pareledone turqueti* and *P. polymorpha*. **a** = *P. turqueti*, **b** = *P. polymorpha*.

ventral mantle surfaces. *P. turqueti* is grey/brown, and lacks the defined border around the mantle edge. *P. turqueti* specimens were muscular, and resistant to abrasion, as specimens were rarely damaged. *P. polymorpha* is delicate and less muscular and many specimens were badly damaged by abrasion during trawls, with extensive loss of skin and suckers. The funnel organs of the preserved specimens showed some morphology but it was not clearly present in all specimens. Of the 17 *P. polymorpha* examined, 12 could be interpreted as W shapes, two had unrecognizable patterns, and three had no patterns. Of 36 *P. turqueti* funnels examined, all had varying patterns of ridges, four of which could be described as VV shaped, with the remaining 32 having no definite form. VV or W shapes were not apparent in the funnel organ of frozen/defrosted specimens.

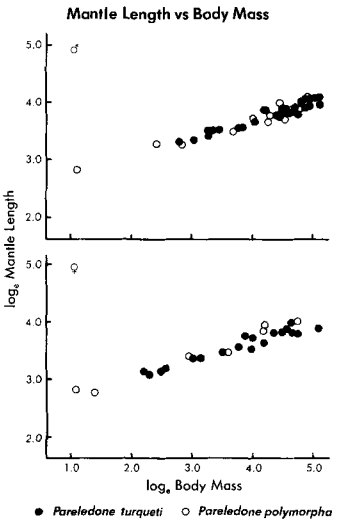

Fig. 4. Relationship between mantle length and body mass for *Pareledone turqueti* and *P. polymorpha*.

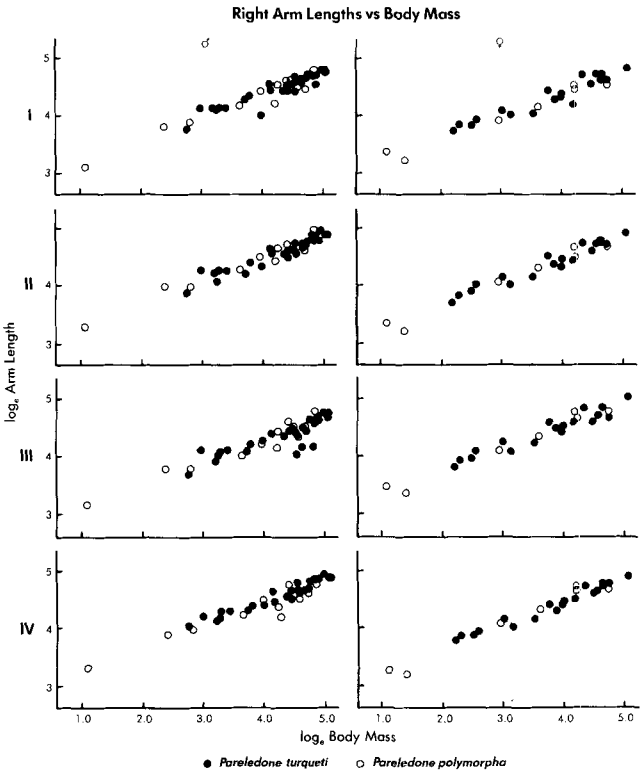

Fig. 5. Relationship between arm length and body mass for *Pareledone turqueti* and *P. polymorpha*.

The tip of the hectocotylised arm of males is morphologically distinct for each species (Fig. 3). *P. turqueti* has a smooth ligula depression and *P. polymorpha* has a ligula with transverse ridges. In *P. polymorpha* the ligula is 13.1% of the length of right arm III and the calamus 51.1% of the ligula. For *P. turqueti* the mean values are 7.9% of the arm length

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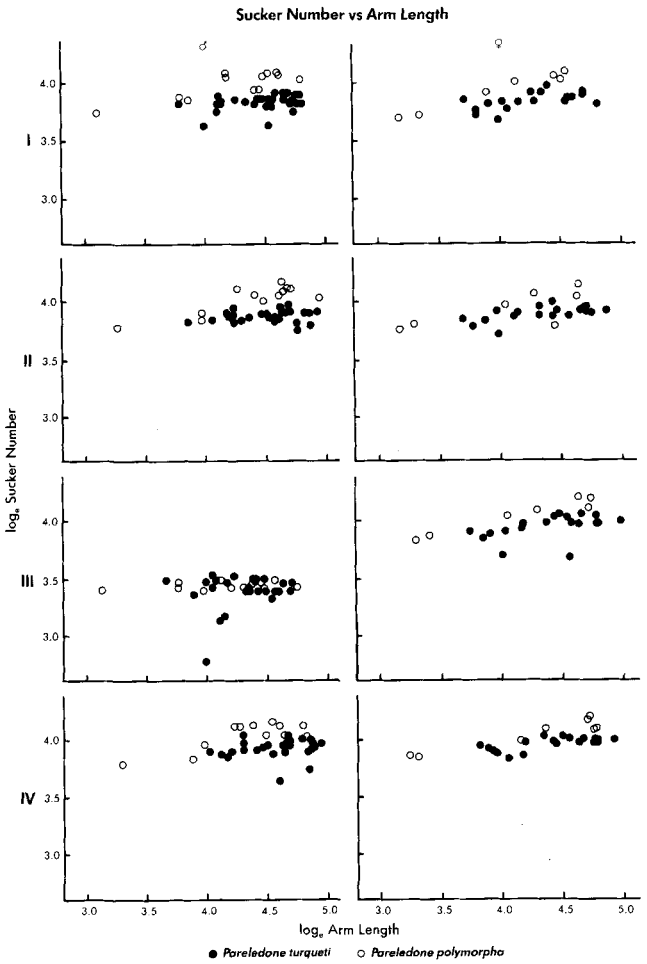

Fig. 6. Relationship between sucker number and arm length for *Pareledone turqueti* and *P. polymorpha.*

and the calamus 36.0% of the ligula.

The ML, AL, HL and BMM plotted against BM for both species are shown in Figs 4, 5, 8 respectively. Fig. 6 shows the relationship between SN and AL. Analysis of covariance (ANCOVA) was used to test for interspecific differences in these relationships and results are summarized in Table I. The relationship between ML and BM (Fig. 4) shows that the two species and both sexes appear similar in their overall proportions. There was no significant difference between the slopes for males or females, or in the intercepts for the males (Table I). However, the intercepts for the ML/BM relationship were significantly different in females, with *P. polymorpha* having a slightly larger ML when the effect of BM was removed. The relationship between AL and BM (Fig. 5) shows no significant difference in the slopes or intercepts for any male arms or arms I–III of females (Table I). Arm IV in the females shows a small but significant difference between the slopes for the species. In the relationship between SN and AL (Fig. 6), there was a significant difference in the slopes of arms I and II for males and arm I for females (Table I). Sucker numbers on arms III and IV for males were not significantly different. Sucker numbers on arms II–IV

Table I. Summary of results on analysis of covariance (ANCOVA) between body mass (BM) and mantle length (ML), arm length (AL), hood length (HL) and buccal mass mass (BMM), and AL and sucker number (SN) in *Pareledone turqueti* and *Pareledone polymorpha.* (Significance level $p < 0.05$, NS = not significant).

Comparison	Slope (F)	$p<$	Intercept (F)	$p<$
Males				
ML v BM	0.50	NS	-0.63	NS
AL I v BM	-0.97	NS	-0.70	NS
AL II v BM	-0.95	NS	-0.50	NS
AL III v BM	0.02	NS	-0.90	NS
AL IV v BM	-1.00	NS	3.55	NS
SN v AL I	5.83	0.025	40.38	0.001*
SN v AL II	12.12	0.01	56.00	0.001*
SN v AL III	-0.22	NS	0.25	NS
SN v AL IV	2.25	NS	3.00	NS
Females				
ML v BM	0.34	NS	5.36	0.05
AL I v BM	-0.94	NS	0.41	NS
AL II v BM	0.28	NS	-0.82	NS
AL III v BM	-0.95	NS	-0.58	NS
AL IV v BM	4.72	0.05	-1.05	NS*
SN v AL I	6.67	0.025	21.67	0.001*
SN v AL II	0.17	NS	6.25	0.025
SN v AL III	0.28	NS	11.23	0.01
SN v AL IV	3.40	NS	23.63	0.001
Combined sexes				
HL v BM	5.83	0.025	321.17	0.001*
BMM v BM	3.56	NS	235.62	0.001

*Where a significant difference is seen between the slopes of the comparison, the analysis for a significant difference in intercept assumes a common slope.

for females were not significantly different in slopes but the difference between intercepts was significant (Table I), indicating a higher number of suckers for a given arm length in *P. polymorpha.*

Feeding structures

The lower beaks of both species are illustrated in Fig. 7. In the following description the term 'normal' refers to the beak shape characteristic of the subfamilies Octopodinae, Eledoninae and Bathypolypodinae (Clarke 1986).

The *P. turqueti* beak described and illustrated was from a female specimen with a ML of 97 mm and a BM of 187 g, and the *P. polymorpha* beak from a female with a ML of 80 mm and a BM of 134 g. Specimens of both species were at a late stage of sexual maturity.

The general shape and relative length of the hood are the most prominent differences between the species. The hood of *P. turqueti* was 5.05 mm long and darkened from the rostral tip back 4.27 mm with a narrow white/translucent border along the posterior edge. The chitin is dark over most of the beak, the hood, rostrum and crest being coloured black, and the wings and lateral walls dark brown. The wings and lateral walls have a

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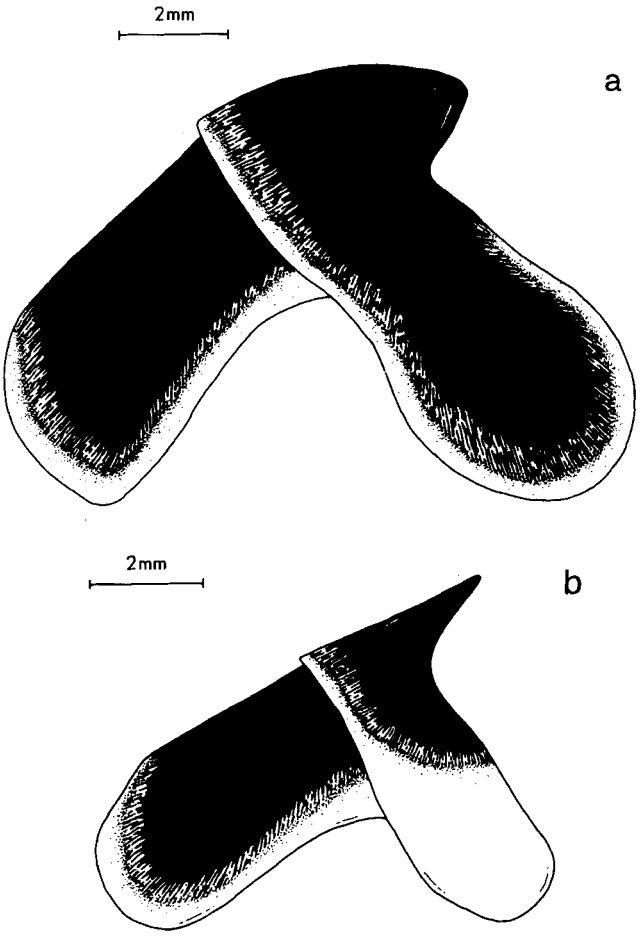

Fig. 7. The lower beak of *Pareledone turqueti* and *P. polymorpha*. **a** = *P. turqueti*, 97 mm ML, 187 g BM. **b** = *P. polymorpha*, 80 mm ML, 134 g BM.

narrow white border around the periphery. The hood of *P. polymorpha* was 3.37 mm long and darkened from the rostral tip back to *c.* 3.09 mm, gradually becoming transparent at the posterior edge. The chitin is black around the hood and rostrum and brown chitin extends a short way down the wings, just past the free biting edge of the beak. The main part of the wings are white/translucent. The lateral walls are brown and have a narrow white border around the edges. The *P. turqueti* beak has a prominent rostrum, a curved rostral edge and the hood is a 'normal' distance from the crest. The *P. polymorpha* beak has a less prominent rostrum, a straight rostral edge and the hood lies close to the crest. The hood-wing structure is 'normal' relative to the lateral wall in *P. turqueti*, and is fairly narrow in *P. polymorpha*. The rostrum protrudes a 'normal' distance forward in *P. turqueti* and a top view of the beak shows a marked V-indentation between the lateral walls, from the posterior corners to the crest. The *P. polymorpha* beak has a rostrum which protrudes forward a long distance and the top view shows a slight V-indentation between the lateral walls, although some specimens have a slightly more square-shaped indentation. The

Table II. Comparison of ratios of beak dimensions of *Parelodone turqueti* and *P. polymorpha*, parameters a–f from Clarke (1986), a = rostral edge, b = wing length, c = height, d = base length, e = wing width, f = crest length and g = hood length.

Ratio	*P. turqueti*	*P. polymorpha*
wing length/rostral edge (b/a)	5.30	2.27
height/base length (c/d)	0.83	0.78
base length/wing width (d/e)	2.41	2.65
crest length/hood length (f/g)	1.91	2.40
base length/crest length (d/f)	1.98	0.95

wing or jaw angle of *P. turqueti* is close to right-angled and in cross-section the crest is narrow. The wing angle of *P. polymorpha* is obtuse and in cross-section the crest is broad. Large *P. turqueti* beaks often have a small indentation in the rostral tip, probably due to wear, which is not apparent in smaller specimens which have rounded rostra. The rostral tip of *P. polymorpha* beaks are sharp and pointed, and have a characteristic slight upturn, which is more pronounced in smaller individuals.

Ratios describing beak dimensions, after Clarke (1986), are shown in Table II. The ratios aid discrimination between some species. The wing length/rostral edge (b/a) ratio in most Octopodidae is > 4 (Clarke 1986). In *P. turqueti* b/a = 5.30, but for *P. polymorpha* b/a = 2.27. The base length/crest length ratio (d/f) is larger in *P. turqueti* (Table II), indicating that it has a proportionately longer base and shorter crest. Ratios height/base length (c/d), base length/wing width (d/e) and crest length/hood length (f/g) are not notably different between the species.

The relationship between HL and BM for each species is shown in Fig.8a. There is a significant difference between the slopes and intercepts (Table I) indicating different relationships, with a relatively longer HL in *P. turqueti*. Fig.8b shows the relationship between BMM and BM. There is no significant difference between slopes but there is a significant difference between the intercepts (Table I).

Discussion

The two *Pareledone* species from the South Georgia shelf are superficially similar, although the *P. polymorpha* females are larger than the males (Fig. 2) and have a slightly longer ML relative to *P. turqueti* females (Table I). The AL to BM relationships are very similar, with only the fourth arm of females showing any significant difference between species. Identification of *Pareledone* species has relied on characteristics such as the hectocotylus (Dell 1959, Nesis 1987) which is only useful in males, and in the funnel organ morphology (Massy 1916, Berry 1917). This study found some patterns in the funnels of both species, but interpretation of the shapes formed is ambiguous in some cases. No funnel organ shapes were apparent in three *P. polymorpha* funnels, indicating the unreliability of the funnel organ as a means of supporting identification. The *P. turqueti* funnel organs often had narrow ridges on the inner surface but the patterns formed could not be

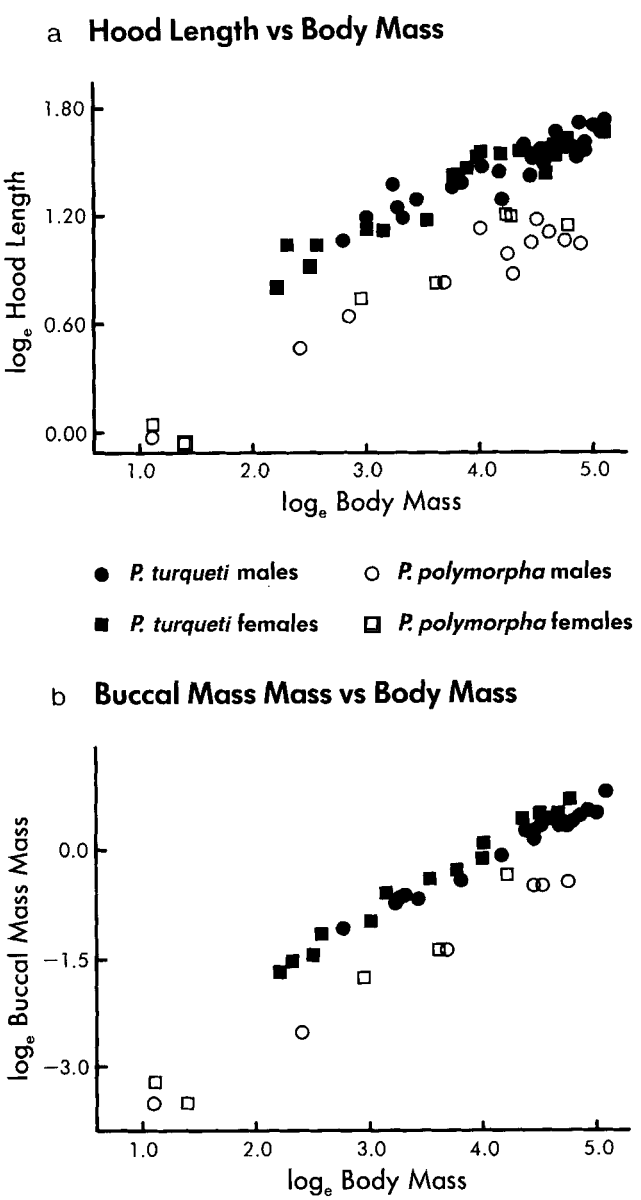

Fig. 8. a. Relationship between hood length and body mass for *Pareledone turqueti* and *P. polymorpha*. **b.** Relationship between buccal mass mass and body mass for *P. turqueti* and *P. polymorpha*.

easily defined.

Inter-breeding between these similar species is prevented by reproductive mechanisms. Genetic isolation is apparently assured by the differing relative size and shape of the hectocotylus, which is approximately 50% larger in *P. polymorpha* than in *P. turqueti*. There also appeared to be sexual dimorphism in *P. polymorpha*, with the modal ML of females 20 mm longer than males (Fig. 2). Sexual dimorphism was not apparent in *P. turqueti*. The body mass of a female octopus tends to be proportional to the number of eggs she lays (Mangold 1987).

As there was no significant interspecific difference in the relationship between AL and BM in all cases except arm IV of females, the relatively higher number of suckers along arms I–IV in females and arms I and II in males of *P. polymorpha* (Table I) means the suckers may be closer together or have a smaller diameter. Numerous small or closely packed arm suckers may be an adaptation to manipulate small prey items. In males arm III on the right side forms the hectocotylus and is usually the shortest and has fewest suckers.

The beak of *P. turqueti* is similar in overall shape to *Eledone cirrhosa* (Lamarck) and to *Octopus vulgaris* (Cuvier) which are illustrated in Clarke (1986), and is a common beak form among octopods. The beak of *P. polymorpha* is comparatively small and fine (Fig. 7), and is similar to the beak of *P. adelieana* (Berry 1917) and *P. umitakae* (Taki 1961). Throughout different animal groups, such specialization of mouthparts among closely related species indicates trophic niche separation (Giller 1984). Cephalopod diets are not well known but existing information indicates that they have similar, varied diets, consisting mainly of benthic molluscs, crustacea and fish with polychaetes, chaetognaths and siphonophores taken by some species (Bidder 1966, Nixon 1987). Beak shape suggests that the diet of *P. turqueti* has similar components to other octopus species with a 'normal' beak. The beak of *P. polymorpha* is more delicate and fine, and is unlike any other octopod beak illustrated in Clarke (1986). This species beak is possibly specialized to exploit an atypical resource, possibly in the water column. The delicacy of *P. polymorpha*, indicated by the less muscular body, higher number of small suckers and frequency of damage among trawled specimens, might also indicate adaptation to a life style hunting off the bottom. The robust body of *P. turqueti*, on the other hand, might indicate a more conventional behaviour for octopuses, hunting wholly benthic prey.

The diet of the two *Pareledone* species, identified from stomach contents, will be the subject of future research, although this approach may give biased results. A degree of external digestion takes place in the crustacean prey of *O. vulgaris* (Nixon 1984) and *E. cirrhosa* (Grisley & Boyle 1990), making it difficult to identify soft material in the stomach. Other approaches, such as experimental aquarium studies, are required to relate the anatomical adaptations, in mouthparts and sucker number, to behavioural and life cycle differences.

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