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A study on octopodids from the eastern Weddell Sea, Antarctica

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Abstract A comprehensive study of octopodids in the Weddell Sea was conducted during cruise ANT XIII/3 of RV “Polarstern”. The study yielded eight species of incirrate octopodids, three of which were undescribed. There appeared to be no differences in octopodid species assemblage in the two sampling areas (Kapp Norvegia and south of Drescher Inlet), supporting the theory that there is a single macrobenthic assemblage on the eastern shelf of the Weddell Sea. Six of the octopodid species belonged to the genus *Pareledone*, illustrating the extensive radiation of this endemic genus within the Southern Ocean. The fragmented nature of suitable habitats and disturbance caused by glaciation cycles are proposed as mechanisms for this radiation. Comparative data illustrate that both the number of octopodid species present and their abundance are greater at higher latitudes than close to the Antarctic Polar Frontal Zone.

Introduction

Although 16 species of octopodids are described from the Southern Ocean (Table 1), they have received little

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scientific attention that is not taxonomic in nature. Indeed, because of confusion in the taxonomy, it has been almost impossible to make the accurate identifications necessary for ecological, physiological and behavioural studies. In addition, research has been concentrated in particular areas of the Southern Ocean: the eastern sector of Antarctica near Prydz Bay, the Antarctic Peninsula and the Scotia Sea. The Scotia Sea is defined as the body of water bounded by the Scotia Ridge and the extension of the Shackleton Fracture Zone to the southern tip of South America (Locarnini et al. 1993). It is separated from the Weddell Sea by the Weddell-Scotia Confluence whose waters lack the prominent subsurface temperature and salinity maxima that characterise the Circumpolar Deep Water found on either side (Whitworth et al. 1994). Prior to the present study, there were few records of octopodids in the Weddell Sea, and identification was hampered by poor preservation (Voß 1988).

Off South Georgia, an island on the Scotia Arc just south of the Antarctic Polar Frontal Zone (APFZ), octopodid beaks are present in the stomach contents of, for example, southern elephant seals, *Mirounga leonina* Linnaeus 1758 (Rodhouse et al. 1992), black-browed albatrosses, *Diomedea melanophris* (Temmink 1928), Rodhouse 1990) and blue-eyed shags, *Phalacrocorax atriceps nivalis* Falla 1937 (Wanless et al. 1992). Although these beaks were not identified to species level, they suggest that octopodids may be of ecological importance to some of the large Antarctic predators. Should the Weddell Sea cephalopod fauna prove to be abundant and diverse, then an important component of the ecosystem has, up until now, been overlooked.

The dominant genera in other shallow-water areas of the Southern Ocean appear to be *Pareledone* and *Megaleledone* (Allcock et al. 1997; Kuehl 1988; Lu and Stranks 1994). Both genera are found only south of the APFZ. Specimens that have been recorded farther north, [e.g. *Pareledone turqueti* (Joubin 1905) recorded off Brazil by the Terra Nova Expedition; Massy 1916] appear to have been misidentified. A taxonomic review

Table 1 Octopodidae currently described from the Southern Ocean

Subfamily	Genus	Species	Junior synonym	Weddell Sea records		
Eledoninae	<i>Pareledone</i>	<i>charcoti</i> (Joubin 1905)	<i>aurorae</i> (Berry 1917)	Voß 1988, present study		
		<i>harrissoni</i> (Berry 1917)	<i>antarctica</i> (Thiele 1920)	Voß 1988, present study		
		<i>turqueti</i> (Joubin 1905)				
		<i>pyrdzensis</i> Lu and Stranks 1994				
		<i>framensis</i> Lu and Stranks 1994				
		<i>adeliana</i> (Berry 1917)	<i>umitakae</i> Taki 1961			
		<i>polymorpha</i> (Robson 1930)		Voß 1988, present study		
		<i>senoi</i> Taki 1961		Present study		
		Graneledoninae	<i>Graneledone</i>	<i>setebos</i> Robson 1932		
				<i>antarctica</i> Voss 1976		
<i>Bentheledone</i>	<i>albida</i> (Berry 1917)					
	<i>rotunda</i> (Hoyle 1885)					
<i>Thaumeledone</i>	<i>gunteri</i> Robson 1930					
	<i>brevis</i> (Hoyle 1885)					
Bathypolypodinae	<i>Benthoctopus</i>	<i>levis</i> (Hoyle 1885)		Present study		
		<i>thielei</i> Robson 1932				

of *Pareledone* was published by Lu and Stranks (1994) following extensive fishing in eastern Antarctic waters. Of the 12 *Pareledone* species that have been described, 3 have been synonymised (Table 1). Two others, *Pareledone carlgreni* (Thore 1945) and *Pareledone nigra* (Hoyle 1910) (neither of which is found in the Southern Ocean), are being removed from the genus (C.F.E. Roper, personal communication). Seven valid species remain.

Pareledone framensis (Lu and Stranks 1994), *Pareledone pyrdzensis* (Lu and Stranks 1994), *Pareledone harrissoni* (Berry 1917) and *Pareledone adelianna* (Berry 1917) appear to be restricted to eastern Antarctica. *Pareledone turqueti* and *Pareledone polymorpha* (Robson 1930) are likewise thought to be restricted to western Antarctica, whilst *Pareledone charcoti* (Joubin 1905) is thought to be the only circumpolar species (Lu and Stranks 1994).

The other prominent octopodid species in shallow Antarctic waters, *Megaleledone senoi* (Taki 1961), is distributed in the Indo-Atlantic sector of the Southern Ocean. Although additional species are recognised from the area (Table 1), these are restricted to deeper waters and their taxonomy is, in many cases, still extremely confused. The aim of this paper is to present basic ecological data on species composition and abundance in shallower waters (< 1,000 m) in the Weddell Sea.

Materials and methods

Octopods were collected during the ANT XIII/3 cruise of RV "Polarstern" to the Weddell Sea in February 1996. The sampling programme was planned with the knowledge that most of the faunal components of the area were familiar (Arntz and Gutt 1997), and investigations concentrated on two main areas, using a variety of gear types. A combination of up to 17 different gear types was launched at 33 stations (see Arntz and Gutt 1997 for full details). The gear types included three trawl nets that yielded octopods: a standard Agassiz trawl (AGT); a benthopelagic net (BPN); and a bottom trawl (GSN). The GSN was a commercial-scale 47-m headline bottom trawl with an effective mouth opening of 22.5 m by 3 m and a cod-end mesh size of 20 mm. It was the same net as that used 10 months later in a sampling programme off the

Antarctic Peninsula (ANT XIV/2), and hence comparison between these two data sets was facilitated.

Octopods were collected regardless of the gear that yielded them. They were identified to species and measured. Catch per unit effort (CPUE) was calculated as the number of octopods caught in each haul divided by the duration of the trawl in minutes. The cumulative number of species captured was plotted against total trawl time to assess whether it was likely that all the species present were captured. Trawls were plotted in sequential order.

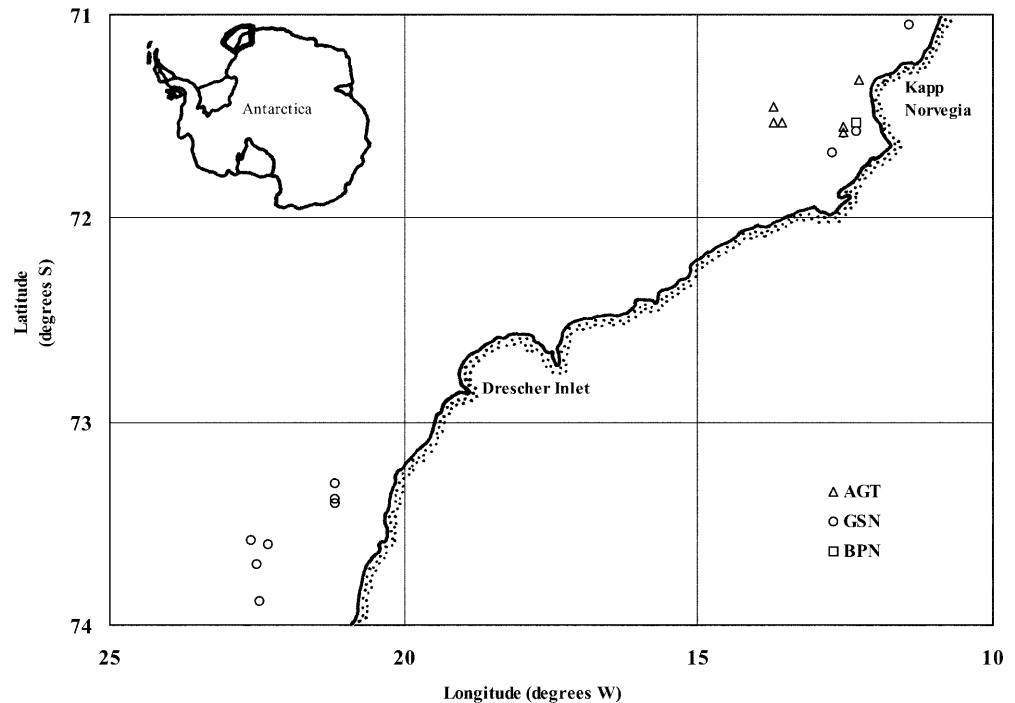
Multi-dimensional scaling (MDS) using the PRIMER statistical package (Clarke and Warwick 1994) was performed to assess whether the depth bands chosen were appropriate. Similarities between the compositions of a pair of samples (*i* and *l*) were calculated using the Bray-Curtis coefficient, S_{il} , where $S_{il} = 100 * (1 - (\sum |y_{ij} - y_{lj}| / (\sum y_{ij} + \sum y_{lj})))$ and where y_{ij} and y_{lj} are the counts for species *j* in samples *i* and *l*, respectively and *n* is the total number of species recorded. The Bray-Curtis coefficient is equal to 100 if the samples are identical, but equal to zero if there are no species in common. Joint absences do not affect the similarity between samples. Given a similarity matrix defined by Bray-Curtis coefficients, we used the subroutine ANOSIM to test if communities were different. This procedure compares the average rank similarity within predefined groups with the average similarity between groups. Values close to 1 indicate that there is some discrimination between the groups. The significance of the between-group to within-group comparison can be tested using a randomisation test (Clarke and Warwick 1994). This test arbitrarily assigns samples to the predefined groups and generates a test statistic distribution, which indicates whether the measured discrimination statistic is likely to have risen by chance alone.

Results

The sampling programme yielded 446 octopods: 294 from off Kapp Norvegia and 152 from southwest of the Drescher Inlet (Fig. 1). A total of 84 specimens were caught in a single benthopelagic net that unintentionally touched the sea floor; 22 specimens were caught in a total of 5 Agassiz trawls, and 1 specimen was caught in each of the epibenthic sled and multibox corer. The remaining specimens (338) were taken in a series of 10 bottom trawls, the majority of which were in the more southerly sampling area (Table 2).

A single cirrate species, *Cirroctopus glacialis* (Robson 1930), and eight species of incirrate octopods were

Fig. 1 Sampling locations in the Weddell Sea during cruise ANT XIII/3 of RV "Polarstern"



identified from the catches. Six species belonged to the endemic genus *Pareledone* (*Pareledone turqueti*, *Pareledone charcoti*, *Pareledone polymorpha* and three undescribed species); one species belonged to the endemic monotypic genus *Megaleledone* and one belonged to the taxonomically confused genus *Benthoctopus*.

No major differences in community assemblage between the two main sampling areas were obvious. All the species were found in both areas with the exception of *Benthoctopus* cf. *levis*. The genus *Benthoctopus* is generally associated with increased bottom depth and the species' apparent absence from Kapp Norvegia may be an artifact caused by lack of fishing at appropriate depths.

Because it is well known that community composition is affected by depth (Brey and Clarke 1993), the trawls were split into arbitrary depth bands in an attempt to eliminate this confounding factor from the data (Table 3). Trawls that spanned the boundary between two depth ranges were assigned to the deeper band. The necessity for grouping data into broad ranges is further illustrated by the fact that three of the eight species appear to be restricted in their distribution to two of the

three depth bands, while a fourth (*Pareledone* sp. B) is restricted to a single depth band.

The catch data were root transformed and an MDS plot (Fig. 2) was generated. The discrete groupings of the components of the three depth bands suggest that these bands are appropriate, as does the ANOSIM statistic $R=0.808$. The latter equates to a probability of there being a difference in community composition between the depth bands of $P=0.001$, which is significant.

Three of the ten bottom trawls were located at the more northerly sampling area off Kapp Norvegia, and these are indicated by filled-in symbols on the MDS plot (Fig. 2). The wide dispersal of these points on the MDS plot supports the suggestion that there is no difference in community assemblage between Kapp Norvegia and the more southerly sampling area. Furthermore, when an ANOSIM statistic was calculated to examine any differences that might exist between these two areas, the value of $R=0.190$ was not significant ($P=0.167$). A significant result would be unlikely considering the lack of replication at each depth and location.

The grouping into depth bands allowed the data to be compared with those from a more extensive sampling programme off the Antarctic Peninsula (Allcock 1997; Piatkowski et al. 1998) which used the same commercial bottom trawl. At the two shallower depths, the Antarctic Peninsula appears more speciose than the Weddell Sea (Fig. 3). Five species were captured in the Weddell Sea at 200–400 m depth compared with 10 species off the Antarctic Peninsula. Seven species were captured in the Weddell Sea at 400–600 m depth compared with 11 species off the Antarctic Peninsula. In the deeper band (600–800 m) both curves are similar in shape, suggesting that at

Table 2 Number of gear deployments in each area. Figures in parentheses indicate how many deployments captured octopodids

Gear	Off Kapp Norvegia	South of Drescher Inlet
Bottom trawl	3 (3)	7 (7)
Agassiz trawl	10 (5)	1 (0)
Benthopelagic trawl	1 (1)	3 (0)
Epibenthic sled	5 (1)	0 (0)
Multibox corer	31 (1)	3 (0)

Table 3 Numbers of each species of octopodid caught during each of ten trawls with a commercial bottom trawl in the Weddell Sea

Depth band	200–400 m			400–600 m				600–1000 m			Total
	227–232	242–246	333–338	428–446	457–459	465–468	462–481	574–604	620–640	850–859	
<i>Pareledone charcoti</i>	35	8	8	6	2	1	33	2	1	2	98
<i>Pareledone</i> sp. A	10	19	1			1	2				33
<i>Pareledone</i> sp. B				6	2	3	5				16
<i>Pareledone turqueti</i>	16	17	9	4	2	5	8		2		63
<i>Pareledone</i> sp. C				10	2	8	2	1	7	2	32
<i>Pareledone polymorpha</i>	10		5	4	3	6	52				80
<i>Megaleledone senoi</i>	2	3			1		5	3			14
<i>Benthoctopus cf. levis</i>										2	2
Total number of specimens	73	47	23	30	12	24	107	6	10	6	338
Trawl duration (mins)	16	15	15	16	15	16	26	14	15	15	163

these depths the Weddell Sea and the Antarctic Peninsula may support a similar number of octopodid species, although further survey work is required in the Weddell Sea to verify this.

The overall abundance of octopodids in the Weddell Sea and off the Antarctic Peninsula (in terms of catch per unit effort to standardise for different trawl durations) was also compared for each depth band using *t*-tests. No significant differences ($P < 0.05$) in CPUE between the Weddell Sea and the Antarctic Peninsula were found at any of the depth ranges (Fig. 4). Multiple *t*-testing was used in preference to ANOVA to avoid the problems inherent in an unbalanced design, as we were not interested in the interaction term. Whilst multiple hypothesis testing increases the probability of a type I error, the latter effect is only important when the null hypothesis is rejected. Levene's test for equality of variances was insignificant in each case and therefore equal variances were assumed throughout.

Size-frequency analysis showed that the most abundant size class was 21–30 mm mantle length (Fig. 5).

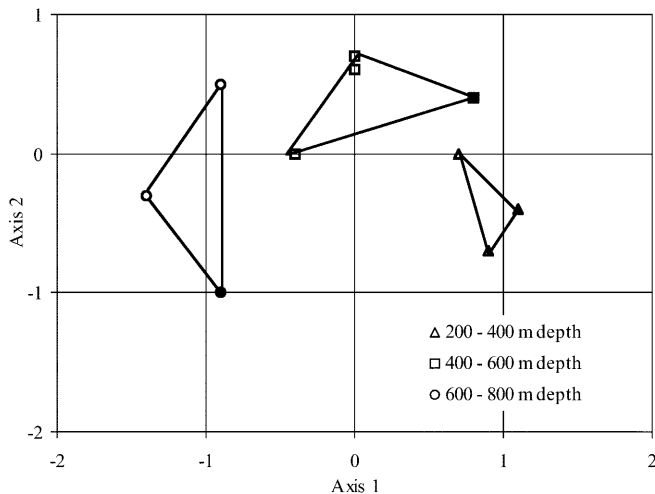


Fig. 2 MDS plot for ten GSN hauls taken at three depth bands in the Weddell Sea. Filled symbols represent hauls from the region off Kapp Norvegia. Unfilled symbols represent hauls from the area south of the Drescher Inlet

Discussion

Of the eight incirrate octopod species captured in the Weddell Sea, seven were from genera endemic to the Southern Ocean and, of the six species of *Pareledone*, at least two of the undescribed species may be endemic to the Weddell Sea. *Megaleledone senoi* has been reported from both eastern Antarctica (Lu and Stranks 1994) and from the Antarctic Peninsula (Kubodera and Okutani 1994; Piatkowski et al. 1998) so its presence in the Weddell Sea is not unexpected. It is possible that this species may be circumpolar although its presence in the Ross Sea is yet to be confirmed.

Only the genus *Benthoctopus* is non-endemic. *Benthoctopus* has two representatives in the Southern Ocean: *B. levis* (Hoyle 1885) described from off Heard Island, and *B. thielei* (Robson 1932) described from the shores of Kerguelen. Both descriptions are poor, and even the diagnosis of the genus is unclear (Grimpe 1921; Robson 1927). *Benthoctopus* specimens were also reported from Elephant Island, South Shetlands (Kuehl 1988) but these were not identified to species level. A recent cruise to the Antarctic Peninsula yielded specimens also diagnosed as *Benthoctopus cf. levis* (Piatkowski et al. 1998).

The endemic Antarctic genus *Pareledone* not only accounted for six of the species captured but also for over 95% of the specimens collected by the GSN. A survey of eastern Antarctica by Lu and Stranks (1994) yielded two new species of this genus whilst a survey of the Antarctic Peninsula by RV "Polarstern" in 1996 also yielded several undescribed species of *Pareledone* (Piatkowski et al. 1998). It is evident that this genus has undergone widespread radiation in the Southern Ocean. Like many families of endemic fishes (e.g. Artedidraconidae, Bathydraconidae, Channichthyidae), *Pareledone* was probably associated in its earlier history with the waters of the Antarctic Plate prior to the formation of the Southern Ocean. The genus dominates the octopodid fauna and has probably had little competition from other octopodid genera during its radiation, as all other octopodids in the Southern Ocean are associated with deeper water.

Fig. 3 Total number of species present at each depth band in the Weddell Sea and off the Antarctic Peninsula. Plots of cumulative number of species captured against trawl time. Trawls plotted sequentially

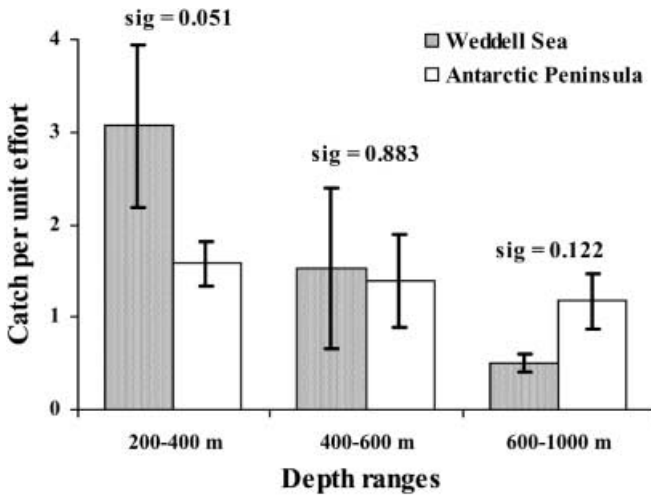
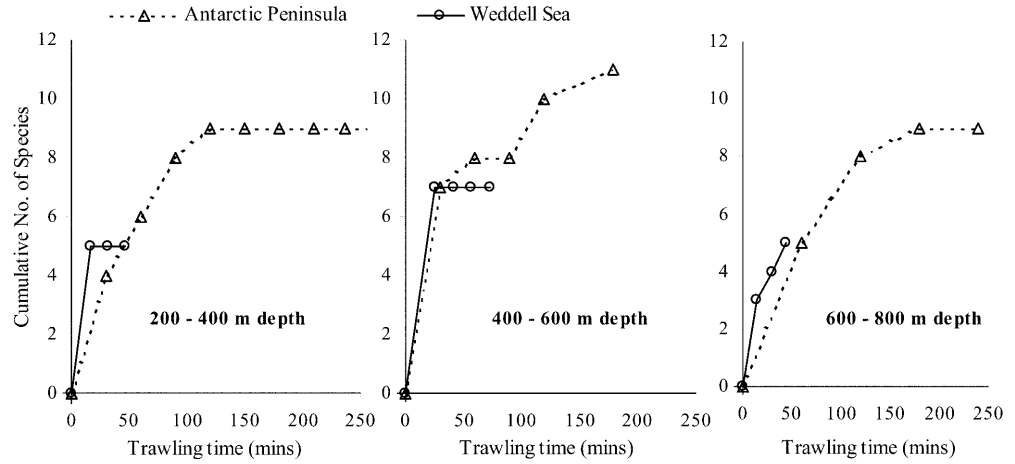


Fig. 4 The non-significant differences in catch per unit effort between the Weddell Sea and the Antarctic Peninsula at each depth band. Error bars represent 1 standard error of the mean

Radiation of octopodid genera in this way is most unusual. Of the 23 genera that are currently recognised in the family Octopodidae (Sweeney and Roper 1998), 8 are monotypic, and a further 5 comprise only 2 species each. When the three new species from this survey are included in the genus *Pareledone*, only two octopodid genera are more speciose. These are *Octopus* and *Benthoctopus*, both of which are considered to be taxonomically confused, and are likely to be split into several less speciose genera. Why then has *Pareledone* shown a degree of radiation that appears to be untypical of its family?

There are two factors that may be pertinent. Firstly, the habitat occupied by *Pareledone* in the Southern Ocean is extremely fragmented. As well as inhabiting the shelf and upper slope of the Antarctic continent, *Pareledone* is also present on the shelf and slope areas provided by the numerous islands in the vicinity of the Antarctic Peninsula and the Scotia Arc. Many of these islands are separated by tracts of ocean where the depth

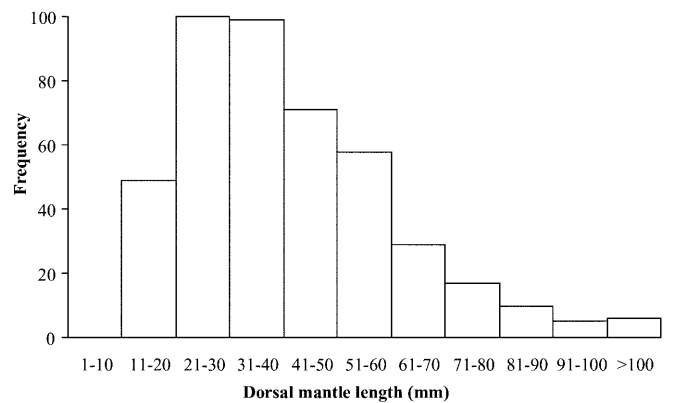


Fig. 5 Size-frequency analysis of octopodids captured during cruise ANT XIII/3 of RV "Polarstern" to the Weddell Sea

of the seafloor far exceeds that which may be colonised by *Pareledone*, and many populations of *Pareledone* are therefore isolated. The ovaries of mature females of *Pareledone* contain eggs up to 20 mm in length (A.L. Allcock, unpublished data). Eggs of such large size give rise to benthic, crawl-away young (Hochberg et al. 1992). Since fertilisation is internal and adult movement is probably limited, the lack of a planktonic stage may have severe consequences for dispersal and hence the maintenance of genetic panmixia. Indeed, populations of *Pareledone turqueti* from South Georgia and Shag Rocks show wide genetic divergence (Allcock et al. 1997) even though these islands of the Scotia Arc are separated by only 90 miles of ocean. Nonetheless, some genetic exchange must take place and, at some point, octopodids crossed these barriers and colonised the islands of the Scotia Arc. Rafting, particularly of small juveniles, is the most likely explanation for this. There is extensive literature on organisms rafting on floating and submerged drift algae (Holmquist 1994; Johannesson 1988; Worcester 1994), including long-distance dispersal in the Southern Ocean (Helmuth et al. 1994).

The second factor that may be pertinent to the radiation of *Pareledone* is the glacial nature of Antarctica. It

is possible that the early *Pareledone* underwent vicariant speciation due to events on a geological time scale, such as warming in the Pliocene, which led to the formation of interglacial fjords (Webb 1990). These fjords may have provided environments where populations of *Pareledone* flourished. Such populations would also be isolated because of the limited dispersal capabilities of the benthic hatchlings, and conditions would be ideal for allopatric speciation. Although this situation is hypothetical, it is true that high levels of diversity are often found in regions that are climatically stable over years or hundreds of years, but are geologically or climatically unstable on a time scale of 10^5 – 10^6 years (Cook 1991). The glaciation cycles of Antarctica appear to fulfil these criteria. A superficially similar radiation is seen in the shallow-water octopuses of the Philippines (another fragmented habitat), where more than 20 species are recognised (Norman and Sweeney 1997). This is one of the highest octopodid diversities in the world. Although 18 of these are currently placed in the genus *Octopus*, they comprise 5 “species groups”, which are likely to be split into genera at a later date. Until the taxonomic revision of *Octopus* is complete, it is not possible to determine whether this radiation is comparable.

The total number of species captured will increase as the time devoted to trawling increases, until finally all the species susceptible to that gear in the area have been captured. However, without greater fishing effort in the Weddell Sea, we can only speculate on whether all the octopodid species present have been captured. However, the octopodid fauna of the high Antarctic does appear to be richer than that found close to or just outside the Antarctic Polar Frontal Zone. Around the Falkland Islands, to the north of the APFZ, only three species of octopodids are recorded from depths shallower than 400 m (Allcock 1997; Robson 1932), while demersal fish surveys around South Georgia have yielded only two species of *Pareledone* and only three octopodid species in total in these depths (Allcock 1997; Daly and Rodhouse 1994). The third species, *Thaumeledone gunteri* Robson 1930, is in fact a deep-water species, whose range marginally extends to this depth band; just three specimens were caught in the deepest trawl of the fish survey, which reached 394 m depth.

Although on rare occasions the Falkland Islands and South Georgia may also have suffered disturbance due to glaciation effects (for example, the last glacial maximum that occurred approximately 20,000 years ago is thought to have led to fully glacial conditions in southern South America; Quilty 1990), it is likely that the impact of glacial cycles has been much greater at higher latitudes, and perhaps this is partly responsible for the latitudinal differences seen in species richness.

The similarities in the octopodid species assemblage between Kapp Norvegia and the area southwest of the Drescher Inlet are consistent with the theory that there is a single macrobenthic assemblage in these areas, termed the “Eastern Shelf Community” (Voß 1988). The fragmented nature of habitats of shallower depths around

the Antarctic Peninsula suggests that more than one community assemblage was sampled in that area. This may explain why octopodid species richness off the Antarctic Peninsula exceeds that in the Weddell Sea. This inference is supported by the projected similarity of the actual numbers of octopodid species in the Weddell Sea and off the Antarctic Peninsula in the deepest waters sampled (600–800 m) (Fig. 3) as deep habitats off the Antarctic Peninsula are less fragmented than those in shallow waters.

Octopodid abundance also appears to be reduced around South Georgia. Eighty-two 30-min hauls by an FP 120 commercial bottom trawl yielded just 359 specimens of *Pareledone turqueti* (Allcock et al. 1997). *Pareledone turqueti* was the most abundant of the three species captured around South Georgia (Allcock 1997). The catch figures suggest an order of magnitude lower abundance compared with the Weddell Sea. This supports the view of Brey and Clarke (1993) who suggested that high standing stocks on the Antarctic shelf and slope may be the result of adaptations to low and oscillating food levels.

The standing stock in the Weddell Sea in February 1996 might actually have been higher than that suggested by catch per unit effort. The majority of individuals captured by the GSN were quite small (Fig. 5). Since the cod-end mesh size was 20 mm, it is likely that many individuals with mantle lengths less than this escaped the net. This hypothesis is supported by the size-frequency distribution (Fig. 5), which shows a considerable lack of animals below 20 mm mantle length. There is no information on the reproductive cycle of *Pareledone* although most species of octopus are semelparous brooders (Hochberg et al. 1992). We are unaware at what age these animals reach maturity and during which season spawning occurs, if indeed spawning is seasonal. The existence of all maturity stages of *Pareledone* in the catch suggests that seasonal spawning may not occur in this genus. It is, however, necessary to extend our sampling window from just a few months in the Antarctic summer if we are to gain a deeper insight into the life-cycle of these animals.

Clearly these data raise many questions and there is ample room for further study. Although Antarctic science is costly, ecological studies of the Southern Ocean octopodid fauna could be amalgamated with the extensive surveys of fish stocks at little extra cost. The commercial bottom trawls used to capture demersal fishes have proved to be by far the most efficacious gear for sampling octopodids, and the data yielded by rigorously designed fishing strategies would be of considerable scientific merit, especially for ecological studies.

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