Marine Biology (1997) 129: 97–102

A. L. Allcock · A. S. Brierley · J. P. Thorpe · P. G. Rodhouse

Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turqueti*

Received: 7 March 1997 / Accepted: 27 March 1997

Abstract Samples of the Antarctic octopus *Pareledone turqueti* were taken from three locations on the Scotia Ridge in the Southern Ocean. The genetic homogeneity of these populations was investigated using isozyme electrophoresis. Whilst panmixia appeared to be maintained around South Georgia ($F_{ST} = 0$) gene flow between this island and Shag Rocks, an island only 150 km away but separated by great depths, was extremely limited ($F_{ST} = 0.74$). These results are examined with respect to the discontinuous distribution of *P. turqueti* throughout Antarctica. An estimate of effective population size was also calculated ($N_e = 3600$).

Introduction

Pareledone turqueti (Joubin 1905) is a circum-Antarctic octopus (Dell 1972) (Fig. 1) which has been recorded at depths of 25 to 1116 m (Voss 1988). It is extremely abundant around the islands of the Scotia Ridge, a sea floor rise in the Atlantic sector of the Southern Ocean (Fig. 1), where it provides a component of the diet of, for example, southern elephant seals, *Mirounga leonina* (Rodhouse et al. 1992), black-browed albatross, *Diomedea melanophris* (e.g. Rodhouse 1990), and blue-eyed shags, *Phalacrocorax atriceps* (Wanless et al. 1992), and is therefore of considerable ecological importance. Despite this it has received little scientific attention until recently and hence knowledge of its biology is limited. Initial investigations have been morphologically based (Daly and Rodhouse 1994), but, as yet, there has been no research into population dynamics – a field that has attracted increasing interest amongst cephalopod biologists in recent years (Brierley et al. 1995; Boyle and von Boletzky 1996).

In octopodids, fertilisation takes place internally following a direct mating encounter and adult migration is often limited (e.g. Van Heukelem 1973; Kayes 1974; Ambrose 1982; Mather et al. 1985), so the geographic extent of genetic homogeneity within species should correlate with the degree of paralarval dispersal. As in many species of octopodid, however, the paralarvae of *Pareledone turqueti* have not been identified and the form they take is uncertain. Octopodid paralarvae may be either benthic or planktonic, with paralarval type apparently related to the size of the egg capsule (Hochberg et al. 1992). Eggs over 10 mm capsule length commonly produce demersal, crawl-away young whereas smaller eggs give rise to planktonic hatchlings. In *P. turqueti*, egg capsules appear to reach a maximum length of 12 to 13 mm (A. L. Allcock personal observation) suggesting the hatchlings may be benthic in habit. It is unlikely that these crawl-away juveniles can survive in greater depths than the adults, and the bathymetry of the Southern Ocean (where small islands are separated by great depths) will therefore provide many large barriers to dispersal. The population structure of *P. turqueti* within the Southern Ocean is therefore likely to be extremely heterogeneous.

Isozyme electrophoresis is among the most cost-efficient methods of investigating genetic phenomena at the molecular level (Murphy et al. 1990) and is therefore a valuable tool in stock assessment. It has been widely applied to squid biology and has revealed many cases of population heterogeneity (Garthwaite et al. 1989; Brierley et al. 1993b) and highlighted the frequent occurrence of cryptic speciation (Smith et al. 1987; Carvalho et al. 1992; Brierley et al. 1993a). Genetic variability in squid has also been shown to be generally remarkably low (Brierley et al. 1993a). Surprisingly the technique has rarely been applied to octopodids (although see Levy et al. 1985).

Communicated by O. Kinne, Oldendorf/Luhe

A.L. Allcock (✉) · J.P. Thorpe
Department of Environmental and Evolutionary Biology,
The University of Liverpool, Port Erin Marine Laboratory,
Port Erin, Isle of Man IM9 6JA, British Isles

A.S. Brierley · P.G. Rodhouse
British Antarctic Survey, Natural Environment Research Council,
High Cross, Madingley Road, Cambridge CB3 0ET, UK

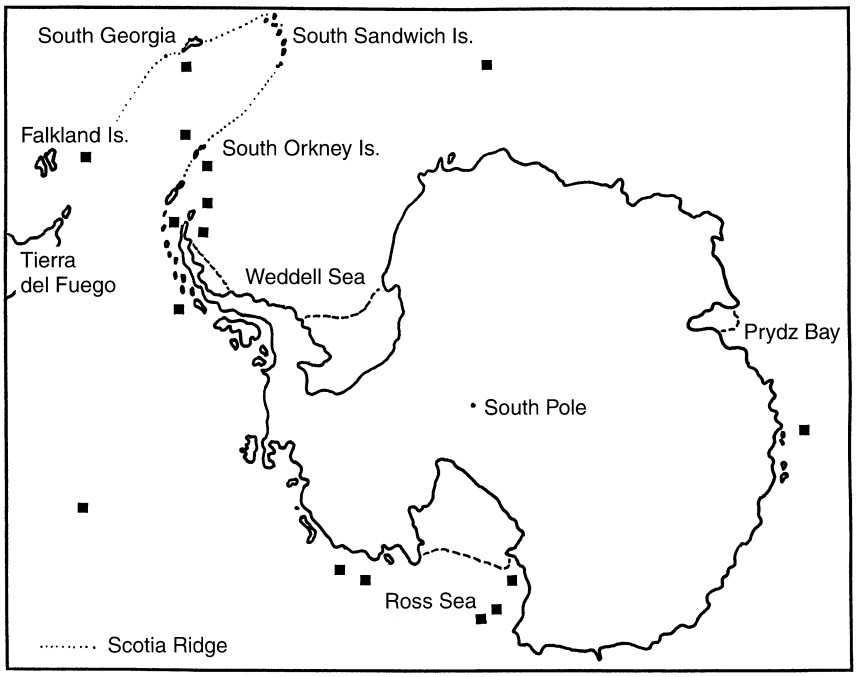

Fig. 1 Map of Antarctic region showing previous capture locations (■) of *Pareledone turqueti* (adapted from Voss 1988)

In the present study isozyme electrophoresis was applied to *Pareledone turqueti* specimens collected from Shag Rocks and from South Georgia, adjacent islands on the Scotia Ridge. These locations are separated by less than 150 km of sea (Fig. 2), of which approximately 30 km is deeper than 1000 m (close to the maximum recorded depth of *P. turqueti*), reaching a maximum depth of approximately 1750 m. This putative barrier is small relative to most of those encountered across the distribution of *P. turqueti* and, if there is marked heterogeneity across this barrier, it is likely that across the entire Southern Ocean *P. turqueti* will also be extremely genetically heterogeneous.

Materials and methods

Field sampling

The study area was surveyed by the Falkland Islands fishery patrol vessel M.V. "Cordella" over the period 6 January to 8 February 1994. During this time bottom trawls of 30 min duration were conducted at 82 random sites in three areas: Shag Rocks (SR), North-West South Georgia (NWSG) and South-East South Georgia (SESG) (Fig. 2) using an FP120 commercial trawl with a net mesh of 160 mm in the upper wings decreasing to 40 mm in the cod end liner. The *Pareledone turqueti* in the catch were hand sorted at sea and tissue samples from the dorsal mantle were dissected and stored frozen at −20 °C.

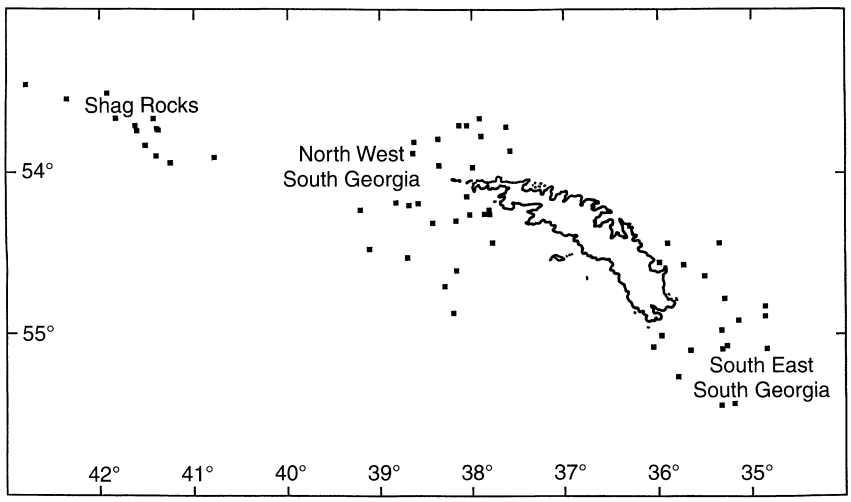

Fig. 2 Sampling locations (■) of *Pareledone turqueti*

Electrophoresis

Horizontal starch gel electrophoresis (Murphy et al. 1990) was carried out using 12.5% hydrolysed starch (Sigma S4501) gels (dimensions $180 \times 150 \times 10$ mm). Samples of mantle tissue were prepared for electrophoresis by homogenising approximately 0.1 g tissue in 100 µl of 1% Triton (Sigma X100). The resulting homogenate was incubated at 4 °C for 2 h and then frozen rapidly in liquid nitrogen. On defrosting, samples were spun in a minifuge at $12\,000 \times g$ for 4 min and the supernatant applied to the gel on 10×2 mm strips of filter paper. Gels were run at 4 °C for 18 h at 100 V and the enzymes were subsequently stained histochemically. Gel banding patterns were scored immediately after the completion of staining and genotypes were assigned accordingly.

Data analysis

Genotypes and allele frequencies were analysed using the computer programs BIOSYS-1 (Release 1.7) (Swofford and Selander 1981) and FSTAT (Release 1.2) (Goudet 1994). The fixation index, f (Weir and Cockerham 1984), was calculated for each population and tested for significant deviation from zero at the 95% confidence level using the normal approximation to the χ^2-distribution (i.e., if $f\sqrt{n} > 1.96$ then H_0 is rejected, where n is the number of individuals in the population sample and the null hypothesis is $H_0: f = 0$). An estimate of F_{ST}, θ (Weir and Cockerham 1984), was calculated across all populations. A pairwise matrix of θ was also constructed to indicate between which samples, if any, population subdivision occurred (Slatkin 1993; Goudet 1994). Genetic identity, I (Nei 1978), was calculated for pairwise comparisons of samples and clustered using UPGMA (unweighted pair group mean analysis) (Sneath and Sokal 1973). The effective number of migrants between populations (N_em) was estimated from $4N_em = (1/\theta) - 1$ (Cockerham and Weir 1993) and m, the maximum estimate of migration rate between populations, was calculated from $I = m/(m+v)$ (Nei 1987), where v is the mutation rate [approximated at 2×10^{-6} (Nei 1975; Mukai and Cockerham 1977)]. From the values of N_em and m an estimate of N_e, the effective population size (Wright 1931), was also calculated.

Results

Initially 54 enzymes were screened using a range of buffering regimes. This led to the resolution of ten enzymes on two buffer systems (Table 1). Two of the resolved loci were polymorphic and allele frequencies at these loci are given in Table 2. Mean observed heterozygosity per locus (H) was estimated as $H = 0.024$. The fixation index, f, was not found to differ significantly from zero in any of the samples (Table 3) and it was assumed therefore that each sample was drawn from a single breeding unit not deviating significantly from Hardy–Weinberg equilibrium.

The estimate of F_{ST}, θ, calculated across all populations was found to be 0.544.

Cluster analysis of Nei's (1978) genetic identity (Fig. 3) supports the conclusions drawn from F-statistics and indicates that the Shag Rocks sample is genetically distinct from those from South Georgia. Because of the similarity of the two samples from South Georgia, data from these sites were pooled for subsequent analysis.

After pooling, the F_{ST} between Shag Rocks and South Georgia was calculated as $\theta = 0.74$, the effective number of migrants (N_em) between Shag Rocks and South Georgia as 0.09 and the migration rate (m) as 2.5×10^{-5}, giving an estimate for effective population size, N_e, of 3600.

Table 1 Enzymes resolved, most effective buffer system employed and number of loci detected. For stain recipes see Harris and Hopkinson (1977), except for OPDH staining see Murphy et al. (1990); for buffer recipes see Murphy et al. (1990)

Enzyme	EC No.	Buffer	No. of loci
G3PDH	1.1.1.8	Tris-borate-EDTA II	1
PEP leu-tyr	3.4.13.*		1
OPDH	1.5.1.11		1
SOD	1.15.1.1		1
AAT	2.6.1.1		1
ICD	1.1.1.42	Tris-citrate III	1
MDH	1.1.1.37		2
MDHP	1.1.1.40		1
MPI	5.3.1.8		1
G6PDH	1.1.1.49		1

Table 2 *Pareledone turqueti*. Allele frequencies at two polymorphic loci in three samples

Locus, allele	Sample location		
	Shag Rocks	North-West South Georgia	South-East South Georgia
*G3PDH**			
(*n*)	(46)	(230)	(83)
**a*	0.478	0.935	0.940
**b*	0.522	0.065	0.048
**c*	0.000	0.000	0.012
*ICD**			
(*n*)	(46)	(230)	(83)
**a*	0.185	0.954	0.946
**b*	0.815	0.046	0.054

Table 3 *Pareledone turqueti*. Tests for departure from Hardy–Weinberg equilibrium where the null hypothesis is H_0: $f = 0$ (f Weir and Cockerham's fixation index; n number of individuals in the sample)

Sample	f	$f\sqrt{n}$	Reject H_0?
Shag Rocks	0.126	0.85	No
North-West South Georgia	0.062	0.56	No
South-East South Georgia	0.020	0.30	No

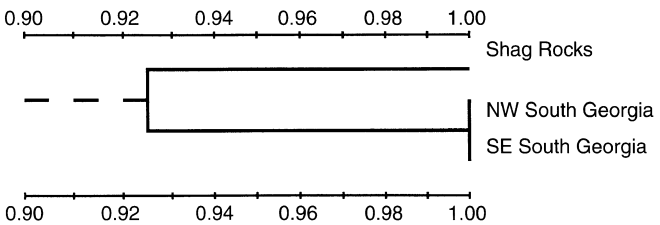

Fig. 3 *Pareledone turqueti*. UPGMA dendrogram of Nei's (1978) genetic identity between three samples

Discussion

Stock structure

Larval ecology strongly influences the structuring of a population and there has been much speculation concerning the evolutionary advantages of pelagic larvae (reviewed by e.g. Strathmann 1985; Todd 1985). If panmixia is maintained in geographically widespread marine species this is often due to the dispersal of planktonic larvae in ocean currents. In a species where the paralarvae are benthic and thus occupy the same physical niche as the adults, however, larval dispersal can be more limited, and the ability to cross large areas uninhabitable by the adult form may be lost. Many species of octopus, including *Octopus vulgaris*, that were once thought to be cosmopolitan now appear to be geographically fragmented (see Boyle and von Boletzky 1996). Wright (1978) produced a classification scale for *F*-statistics. Values can range between 0 and 1, where 0 represents complete genetic homogeneity, 1 represents complete genetic heterogeneity (i.e., no alleles in common), and any value greater than 0.25 is indicative of "very great genetic differentiation" (Wright 1978). The pairwise matrix of θ (Table 4) therefore suggests that populations around South Georgia are panmictic. Although an imbalance of sample sizes may have had a slight influence on the statistical analysis, it is apparent that, in contrast, gene flow between South Georgia and Shag Rocks is severely restricted. The apparent genetic homogeneity between the two South Georgia samples suggests that *Pareledone turqueti* is capable of maintaining panmixia in shallow on-shelf waters over a range of at least 150 km. Tracts of deep ocean (>1000 m) however, as between South Georgia and Shag Rocks, apparently present a major physical barrier to dispersal and impose consequences for gene flow. The *F*-statistic value obtained between South Georgia and Shag Rocks suggests that there is almost no migration between the two populations in these areas. Of 31 examples of *F*-statistic values presented by Wright (1978) only one (that for the Carribean lizard, *Anolis brevirostris*, at 0.78) exceeds the values calculated here (Table 4), and Larson et al. (1984) suggest that F_{ST} values of this order are indicative of populations completely isolated from genetic exchange. This is remarkable when it is considered that the two demes from which we sampled are probably separated by not more than 30 km of deep ocean.

Table 4 *Pareledone turqueti*. Pairwise estimates of Weir and Cockerham's (1984) *F*-statistic, θ, amongst three samples

	Shag Rocks	North-West South Georgia
North-West South Georgia	0.66	
South-East South Georgia	0.72	0.00

Although octopuses can swim fast for short periods of time their normal movement is a slow crawl and migration in this manner across unsuitable habitats is unlikely. In many marine organisms with non-planktonic larvae, rafting has been suggested as an alternative dispersal mechanism (e.g. Johannesson 1988; Jokiel 1989; Parker and Tunnicliffe 1994). This has been shown to occur on, for example, both floating and submerged drift algae (Worcester 1994, cf. Holmquist 1994) and is not confined to species normally inhabiting algae (Ingolfsson 1995). Furthermore, it has been shown that kelp-rafting may serve as a "significant means of genetic exchange between populations" in a sub-antarctic brooding mollusc (Helmuth et al. 1994). Since the *F*-statistic values indicate that there is little genetic exchange between South Georgia and Shag Rocks neither rafting nor any other mechanism seems to be acting to facilitate gene flow between these areas. Evidence from studies on fish also suggests that there is a barrier to planktotrophic dispersal in this region. Temporal differences in maturation as well as genetic differences have been found in Antarctic icefish, *Champsocephalus gunnari*, from Shag Rocks and South Georgia (G. Carvalho personal communication), and differences have also been found in the infestation loads of digenean trematodes in other species of inshore fish from the two sites (Zdzitowiecki and White 1992). Furthermore another fish species, *Patagonotothen guntheri*, which is found in depths of 120 to 250 m and which has a geographical range from Patagonia to Shag Rocks, has never been reported from South Georgia although data from commercial catches indicate that it spawns in the Shag Rocks area (Dewitt et al. 1990).

Given the degree of genetic separation between South Georgia and Shag Rocks, it is likely that the *Pareledone turqueti* of the Scotia Ridge (Fig. 1) will comprise several isolated populations. Although in the Scotia Ridge island chain distances between populations may be as little as a few kilometers (e.g. for islands of the South Sandwich group) they range to over 500 km (e.g. between the South Sandwich Islands and the South Orkney Islands), and other islands in the Southern Ocean from which *P. turqueti* has been recorded are separated from their neighbours and from continental Antarctica by similarly large distances. The island populations of *P. turqueti* are apparently surrounded by insurmountable barriers to gene flow, and each is likely to exhibit the genetic manifestations of isolation, which over time may lead to speciation.

Along the coast of continental Antarctica there are no obvious barriers to gene flow, and there geographical distance between sites is likely to constitute the major restriction on gene flow. Wright (1943) described a situation where the migration distance of an individual was very small in comparison to the area over which the species was continuously distributed. This prevented the species from forming a single panmictic unit and pro-

duces "isolation by distance". Our data indicate that *Pareledone turqueti* can maintain panmixia over 150 km (between NWSG and SESG). It is not known, however, whether *P. turqueti* is distributed as densely around continental Antarctica and, even if this is so, it is unlikely that any species without a planktonic larval stage could maintain panmixia over a linear distribution covering approximately 16 000 km of coastline.

It is apparent that within the nominate octopus species *Pareledone turqueti* which has a wide circum-Antarctic distribution there are numerous opportunities for genetic drift by isolation, and there are likely to be many pockets of stock that act as reservoirs of genetic variability. In some species conservation priorities are indicated by currents; for example Ovenden et al. (1992) suggest that since homogeneity is maintained in the Australian red rock lobster *Jasus edwardsii* by larval dispersal in ocean currents flowing to the east, westerly populations deserve special conservation status to protect the stock since they cannot be easily replenished. Clearly a simple approach such as this would not be applicable to *P. turqueti* as the conservation of each local race would be paramount to the well-being of the stock as a whole.

Stock fitness

Genetic variability, as detected by isozyme electrophoresis, is particularly low in cephalopods in comparison to other marine invertebrates (Nevo et al. 1984); mean heterozygosity per locus has been found to be close to zero in many species (Ally and Keck 1978; Thorpe et al. 1986) and *Pareledone turqueti* appears to be no exception. It is possible that in cases such as these the numbers of "idealised individuals" required to maintain such a small amount of variability is correspondingly low. For instance, N_e has been found to be exceptionally low in hatchery stocks of oysters (Hedgecock and Sly 1990), where genetic variability may have been lost. The effective population size of 3600 calculated here is inclusive of both the Shag Rocks and South Georgia populations. Since it appears that these populations are strongly differentiated and probably represent distinct reproductive units, it is highly likely that N_e within each island population is substantially less. Although there may be an evolutionary explanation for the observed lack of variability based on the concept of environmental grain (Levins and MacArthur 1966), the underlying theory for this remains controversial (see Nevo et al. 1984).

Acknowledgements We wish to express our thanks to the Captain and crew of the Falkland Islands fishery patrol vessel "Cordella". Thanks also to colleagues aboard "Cordella" for their assistance, especially I. Everson and G. Parkes for their organisation of the cruise and H. Daly for assistance with collecting the samples. This work was supported by a CASE studentship between NERC and BAS, awarded to ALA. We are also grateful for the support of a Trans-Antarctic Association travel grant to ALA.

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