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Mitochondrial DNA panmixia in spiny lobster *Palinurus gilchristi* suggests a population expansion

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ABSTRACT: The spiny lobster *Palinurus gilchristi* is endemic to the deep shelf waters along the southern coast of South Africa, where it supports a commercial fishery. Mark-recapture studies and phenotypic differences suggest there are 2 populations of this species along the coast, but it is unknown if the observed differences have arisen because of low gene flow and subsequent genetic differentiation. To investigate population structure and the physical processes that may have influenced gene flow, a portion of the mitochondrial DNA control region was sequenced for 187 lobsters across the entire range of the species. An analysis of molecular variance showed no significant genetic difference between the 2 putative populations. A mismatch distribution and Fu's F_S test indicated that this species has undergone a fairly recent demographic expansion (population size and geographic range). The genetic structure of this species could be panmictic due to a high amount of gene flow between the 2 regions during the larval stage, when the larvae are carried downstream by the Agulhas Current. Furthermore, the lack of genetic differences between the 2 putative populations could be the result of a recent demographic expansion accompanied by low diversity of haplotypes produced by a leading edge effect from the expansion.

KEY WORDS: *Palinurus gilchristi* · Decapoda · Lobster · Demographic expansion · Agulhas Current

INTRODUCTION

The early life history of spiny lobsters (Palinuridae) includes a drifting larval phase that is adapted to a long life in the open ocean, where many opportunities exist for dispersal via ocean currents (Booth & Phillips 1994). The larval period is followed by metamorphosis into a puerulus (post-larval) stage, which settles on the seafloor, and moults into a juvenile spiny lobster. Juveniles of several spiny lobster species migrate long distances back to adult breeding grounds, and in the process may redress dispersal of larvae by ocean currents (Booth 1984, 1997, Moore & MacFarlane 1984, Groeneveld 2002, Groeneveld & Branch 2002). In some species, egg-bearing females position themselves in areas of strong water movement, which presumably helps larval dispersal during spawning (Booth 1986, MacFarlane & Moore 1986). The dispersal mechanism and benthic migrations suggest that extensive gene flow can occur, which in turn will result in little spatial genetic structure (Pollock 1995a). Despite this, the oceanographic mechanisms that affect larval drift and gene flow are impermanent and at times shifts in ocean currents may cause populations to become isolated. Genetic isolation in such semi-closed oceanographic systems, coupled with larval behaviour patterns that result in a high degree of larval retention in the vicinity of the adult stock, may then lead to the development of genetically divergent populations (Pollock 1995a). As a case in point, speciation in the Palinuridae is presumed to have taken place in response to palaeoceanographic changes within the past ca. 20 million years (Myr), particularly as a result of major changes in sea level and ocean current shifts associated with climatic shifts (George & Main 1967, Pollock 1990, 1992, 1993, George 1997).

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The life history of *Palinurus gilchristi*, a spiny lobster species endemic to the deep shelf waters (50–200 m depth) of the South African south coast between Cape Point (18°E) and the eastern Cape Province (28°E) (Fig. 1a), is typical of the spiny lobster group. Its larvae are pelagic for at least 4 mo (Pollock 1995b) and are presumably widely dispersed by the southwesterly flowing Agulhas Current. Puerulus settlement hotspots have been inferred from the occurrence of small juveniles at the western-most (downstream) extreme of its distribution (Groeneveld & Branch 2002). From these hotspots, a long-term migration pattern of juvenile and immature *P. gilchristi*, against the Agulhas Current, from Cape Agulhas toward Algoa Bay has been shown through mark-recapture (Groeneveld & Branch 2002).

Palinurus gilchristi supports a major trap-fishery (1000 t yr^{-1}) along its entire range, and hence has been the subject of many biological studies related to fisheries, summarized in Groeneveld et al. (2005). A striking aspect of the population structure of *P. gilchristi* is the persistent spatial variation in several phenotypic characteristics, including growth rate (Groeneveld 1997), size at sexual maturity (Groeneveld & Melville-Smith 1994), average size (Groeneveld & Rossouw 1995) and fecundity (Groeneveld 2005). Average values for these parameters are all smaller off Port Alfred, the eastern (upstream) extreme of the distribution. The differing phenotypes suggest that there may be 2 separate populations of *P. gilchristi*: one along the edge of the continental shelf between Cape Agulhas and Algoa Bay, and the other offshore from Port Alfred (Groeneveld & Branch 2002). Little is known about larval exchange between these 2 stocks, but the benthic adult migration between Cape Agulhas and Algoa Bay does not extend to Port Alfred, and this latter population is non-migratory (Groeneveld & Branch 2002).

The application of mitochondrial DNA (mtDNA) has been useful for fisheries stock assessments due to its rapid rate of evolution, coupled with a haploid state and maternal inheritance, causing the effective population size of this locus to be one-quarter that of nuclear DNA (Brown 1983, Ovenden 1990, Moritz 1994). Recent examples of mtDNA analysis of decapod crustacean populations include *Jasus edwardsii* and *J.* (Sagmariasus) *verreauxi* (Ovenden & Brasher 2000), *Panulirus longipes* (Ravago & Juinio-Menez 2003) and *Nephrops norvegicus* (Stamatis et al. 2004). In *J. edwardsii* mtDNA studies have produced no evidence of genetic subdivision among widespread populations from southern Australia and New Zealand (Ovenden et al. 1992). In contrast, however, analysis of mtDNA in *J.* (Sagmariasus) *verreauxi* has shown a genetic division of Australian and New Zealand populations, suggesting that they had become genetically isolated across the Tasman Sea (Brasher et al. 1992, Ovenden & Brasher 2000).

In the present study, the key question is whether the phenotypic differences between the 2 putative populations of *Palinurus gilchristi* structure can be linked to genetic structure within the species. For subdivision to have occurred in this species, some isolating factor must have been present in the past. For example, a historical shift to an offshore movement of the Agulhas Cur-

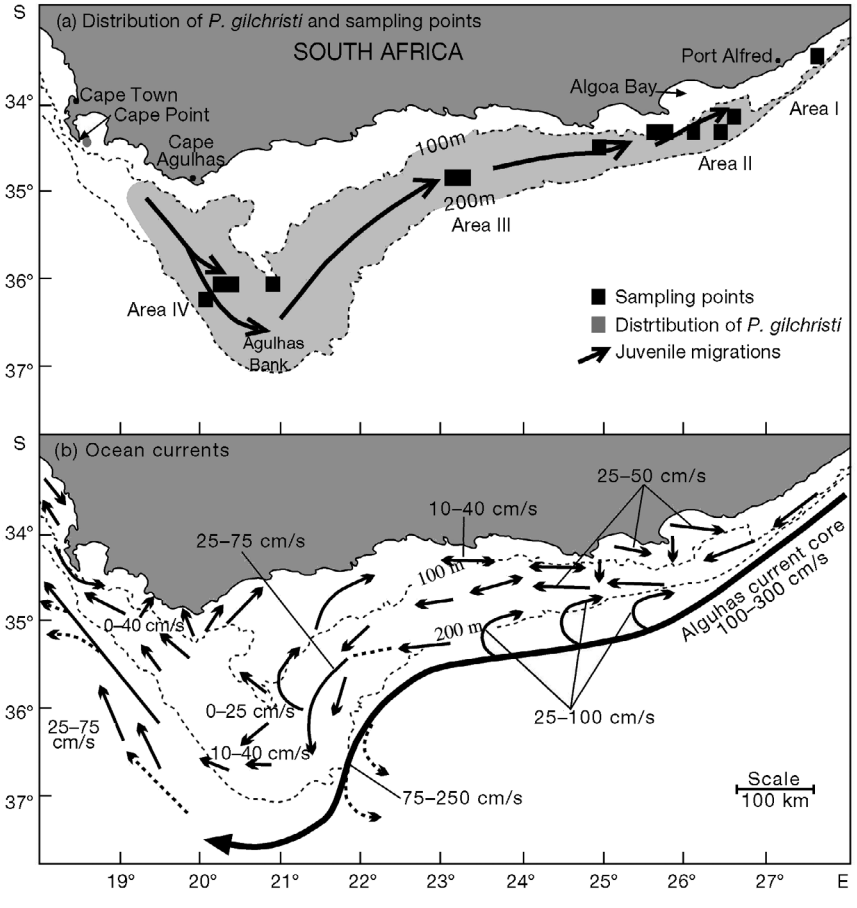

Fig. 1. *Palinurus gilchristi*. (a) Geographic distribution of *P. gilchristi* off South Africa, with sampling points for the genetic study indicated by ■. Also shown is the juvenile migration route between Cape Agulhas and Algoa Bay. (b) Flowfield of near-surface currents off the South African south coast based on ACDP data collected between 1989 and 1992 (redrawn from Boyd et al. 1992)

rent near Algoa Bay (Fig. 1b) could have formed a barrier to larval exchange between the 2 putative populations. This barrier would have to be in place long enough to allow for genetic divergence. Alternatively, if a barrier to larval exchange does not exist, genetic structure would be lacking, with migration sufficiently high to form a single panmictic population. In this case, the observed phenotypic differences could potentially be attributed to environmental influences on growth rates of *P. gilchristi* (Groeneveld 1997). The aims of this study were to determine whether genetic structure could be detected for this species by sequencing the hypervariable region I of the mtDNA control region. Inferences regarding the contemporary genetic population structure, combined with information on life-history of the species and the oceanographic history of the Agulhas Current region were used to infer the recent evolutionary history of the species.

MATERIALS AND METHODS

Tissue samples (n = 187) were obtained opportunistically by observers during fisheries operations off the south coast of South Africa during 2003 and 2004 (Fig. 1a). Muscle tissue was preserved in 100% ethanol and total genomic DNA was extracted using Chelex-100 Resin (Bio-Rad Laboratories). The mtDNA control region was amplified using the polymerase chain reaction (PCR). Primers were specifically designed for *Palinurus gilchristi* (alignment of primer sequences against the Japanese spiny lobster *Panulirus japonicus*, GenBank accession no. NC004251); L13473 (5′ TCA CAC CAA TAC TCG CAT AC) situated in the 12S ribosomal RNA gene, and H14306 (5′ CAA ACC TTT TAT CAG GCA TC) situated in the $tRNA^{Ile}$ gene. Amplification was carried out with 50 ng of genomic DNA in a reaction containing 50 mM KCl, 10 mM Tris-HCl pH 9.0, 1.5 to 5 mM $MgCl_2$, 0.3 µM of each primer, 0.2 mM dNTPs and 1.0 unit of thermostable DNA polymerase. The PCR thermal profile used was 94°C for 30 s for initial denaturation, followed by 35 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 30 s, and a final extension at 72°C for 5 min. Amplified PCR products were purified on 1% agarose gel, and the excised bands were cleaned with the Wizard SV Gel and PCR Clean-Up System (Promega). The cleaned products were cycle sequenced using fluorescent labelled dye-terminators (ABI), purified with sephadex spin columns, and analysed on a ABI 3100 Genetic Analyzer. A 400 bp region was aligned using ClustalX (Thompson et al. 1997) with the default alignment parameters, and checked manually for misalignments.

Total haplotype diversity (h) and nucleotide diversity (π) were estimated in Arlequin 2.0 (Schneider et al. 2000). An analysis of molecular variance (AMOVA) was conducted to estimate the degree of differentiation between the 2 putative populations (Port Alfred vs. Algoa Bay/Central and Western Agulhas Bank) using 2 measures of genetic differentiation (F_{ST} and Φ_{ST}) in Arlequin 2.0. Φ_{ST} was estimated using a Tamura-Nei model of evolution with a gamma correction ($\alpha = 0.29$) as determined by Modeltest 3.6 (Posada & Crandall 1998). In addition, the AMOVA was run with the sampling areas partitioned into 4 smaller geographic areas (Area I: Port Alfred; Area II: Port Elizabeth; Area III: Central Agulhas Bank; Area IV: Western Agulhas Bank), based solely on fishery management areas. Because sampling was opportunistic, samples from these fisheries areas may not be representative of the entire fisheries area (Fig. 1).

Fu's F_S test (Fu 1997) was used to test for mutation-drift equilibrium for all areas combined. In the case of a recent demographic change, such as a population expansion, a population would be expected to be out of mutation-drift equilibrium and a significant negative value would be obtained (Fu 1997, Schneider et al. 2000). To further investigate the possibility of demographic change, Arlequin 2.0 (Schneider et al. 2000) was used to construct a mismatch distribution (Harpending 1994, Schneider & Excoffier 1999). A median-joining network of haplotypes was constructed in Network 4.0 (Bandelt et al. 1999) including all individuals (n = 187).

RESULTS

There was a total of 57 haplotypes detected for the 187 individuals sequenced (Table 1). There was a single common haplotype (pg4) found in 35% of the individuals sequenced. A second haplotype (pg2) was relatively common occurring in 12% of all lobsters sequenced. The majority of haplotypes were unique (72%), occurring in 22% of the individuals sequenced.

The AMOVA showed no significant differences between the 2 putative populations (Port Alfred vs. Algoa Bay/Central/Western Agulhas Bank ($F_{ST} = 0.000$, $\Phi_{ST} = 0.000$) or among the 4 fishing areas ($F_{ST} = 0.000$, $\Phi_{ST} = 0.003$). Fu's F_S test was significant for all the areas combined (10000 permutations), suggesting the species is not at equilibrium (Fu's $F_S = -27.9$, $p < 0.001$). A mismatch distribution for all areas shows a strong expansion wave ($\tau = 1.7$; 95% CI = 0.956 to 1.991; $\tau_0 = 0.000$; $\tau_1 = 4087.5$), indicating that there has been a population increase in the recent past (Fig. 2). Accurate dating of this expansion was not possible since mutation rates for the mtDNA control region in this species have not been estimated. However, a mitochondrial mutation rate for shrimp has been estimated at 19% per

Table 1. *Palinurus gilchristi.* Frequencies of haplotypes from 4 fishing areas along the coast of South Africa, Port Alfred (I), and the Agulhas Bank (II–IV). GenBank accession numbers for each haplotype are given

Haplo-type	Area I	Area II	Area III	Area IV	Total	GenBank
pg1	1	0	0	0	1	AY746499
pg2	6	3	5	9	23	AY746500
pg3	1	1	2	2	6	AY746501
pg4	17	11	17	20	65	AY746502
pg5	2	1	0	1	4	AY746503
pg6	4	0	3	1	8	AY746504
pg7	1	0	0	0	1	AY746505
pg8	1	0	0	0	1	AY746506
pg9	1	0	1	0	2	AY746507
pg10	1	0	0	1	2	AY746508
pg11	1	0	0	0	1	AY746509
pg12	1	0	0	0	1	AY746510
pg13	1	0	0	0	1	AY746511
pg14	2	1	0	4	7	AY746512
pg15	2	0	1	2	5	AY746513
pg16	0	1	0	0	1	AY746514
pg17	0	3	1	0	4	AY746515
pg18	0	0	2	0	2	AY746516
pg19	0	0	1	0	1	AY746517
pg20	0	0	1	0	1	AY746518
pg21	0	0	0	1	1	AY746519
pg22	1	2	3	4	10	AY746520
pg23	0	0	0	2	2	AY746521
pg24	0	1	0	0	1	AY746522
pg25	1	0	0	0	1	AY746523
pg26	1	0	0	1	2	AY746524
pg27	0	0	0	1	1	AY746525
pg28	0	0	0	1	1	AY746526
pg29	0	0	0	1	1	AY746527
pg30	0	0	0	1	1	AY746528
pg31	0	1	0	0	1	AY746529
pg32	0	1	0	0	1	AY746530
pg33	0	1	1	0	2	AY746531
pg34	0	1	0	0	1	AY746532
pg35	0	1	0	0	1	AY746533
pg36	0	1	0	0	1	AY746534
pg37	0	1	0	0	1	AY746535
pg38	0	1	0	0	1	AY746536
pg39	0	1	0	0	1	AY746537
pg40	0	1	0	0	1	AY746538
pg41	0	1	0	0	1	AY746539
pg42	0	0	1	0	1	AY746540
pg43	0	0	1	0	1	AY746541
pg44	0	0	2	0	2	AY746542
pg45	0	0	1	0	1	AY746543
pg46	0	0	0	1	1	AY746544
pg47	0	0	0	1	1	AY746545
pg48	0	0	0	1	1	AY746546
pg49	0	0	0	1	1	AY746547
pg50	0	0	0	1	1	AY746548
pg51	0	0	1	0	1	AY746549
pg52	0	0	1	0	1	AY746550
pg53	1	0	0	0	1	AY746551
pg54	1	0	0	0	1	AY746552
pg55	1	0	0	0	1	AY746553
pg56	1	0	0	0	1	AY746554
pg57	1	0	0	0	1	AY746555
Total	50	35	45	57	187	

MYR (McMillen & Bert 2003, 2004). Considering this, universal mitochondrial mutation rates (μ) ranging between 10 and 20% across lineages per MYR (e.g. Wilson et al. 1985) were applied to the model $T = \tau/2u$ (Rogers & Harpending 1992), where T = time since expansion, $2u = \mu \times$ number bases sequenced $\times$ generation time (400 bp sequenced, 4 yr generation time respectively) to produce rough dates of expansion. Given these upper and lower limits on the mutation rate, the population expansion would be dated between ca. 5300 to 10 600 yr.

The haplotype network showed a star-like phylogeny with most of the unique haplotypes closely related to the common central haplotype (Fig. 3). The high frequency (35%) of a single common haplotype (pg4) and many closely related haplotypes is reflected by the low nucleotide diversity ($\pi = 0.0042$) and the high haplotype diversity ($h = 0.858$). Values for haplotype and nucleotide diversity were similar for each of the 4 areas examined (Table 2).

DISCUSSION

The mtDNA results suggest that there is no significant genetic structure for *Palinurus gilchristi* along the South African coast. *P. gilchristi* is therefore panmictic at the level detected by the hypervariable control region of mtDNA. The lack of genetic population structure then invites the question as to what factors may be responsible for panmixia in this species. A recent tag-recapture study showed a contranatant long-distance migration pattern between Cape Agulhas and Algoa Bay, but the Port Alfred population was non-migratory and did not receive immigrants from elsewhere (Groeneveld & Branch 2002), suggesting that migration does not contribute to the observed panmixia. Larval exchange within the environment of the Agulhas Current is highly likely, despite the offshore flow of the current west of Port Alfred. The current has a highly variable flow with regularly occurring meanders and frontal eddies on the inshore boundary (Schumann et al. 1991). These oceanographic features originating near the Port Alfred area could move the larvae downstream and inshore. The result would be mixing of larvae with those originating from the region between Algoa Bay and Cape Agulhas, thus establishing a well-mixed gene pool at the time of larval settlement. Panmixia in other marine crustaceans has been suggested through a number of genetic population studies, and has been partially attributed to mixing during planktonic stages (e.g. McMillan-Jackson & Bert 2004).

The absence of genetic structure in *Palinurus gilchristi* suggests that the observed phenotypic differences in lobsters off Port Alfred are probably the result of inhab-

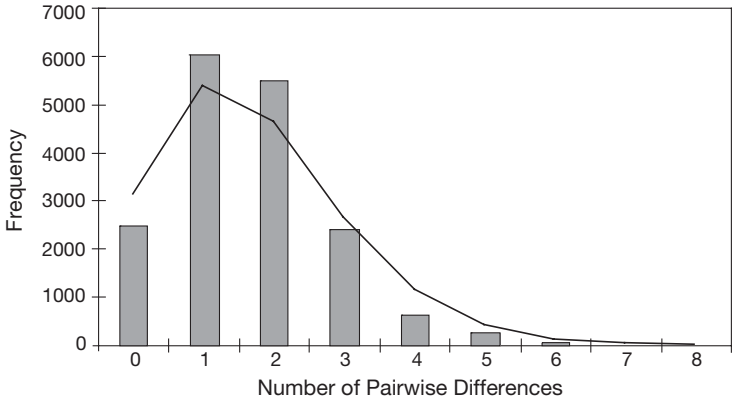

Fig. 2. *Palinurus gilchristi*. Observed frequency distribution (grey bars) for the number of pairwise differences among all individuals sampled from the coast of South Africa. Solid line shows the expected distribution given a population expansion

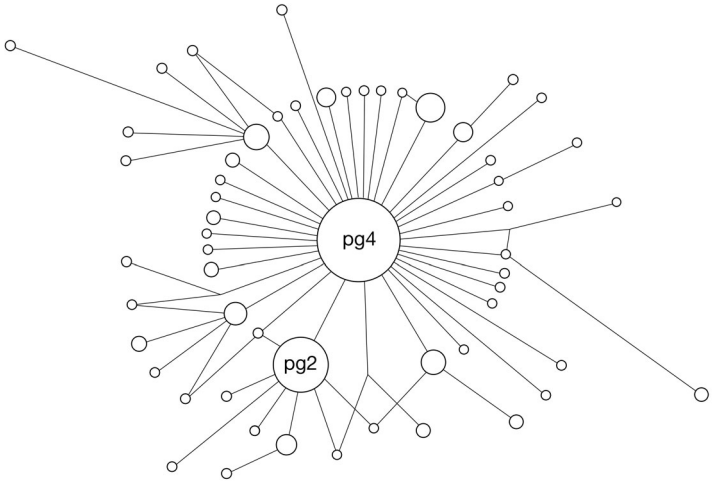

Fig. 3. *Palinurus gilchristi.* Haplotype network for individuals sampled from the coast of South Africa. Sizes of the circles are proportional to the frequency of each haplotype; lengths of the lines are relative to the number of mutations between haplotypes (shortest lines = 1 mutation)

iting a less optimal habitat towards the eastern extreme of the distribution of this species. The environmental factors influencing *P. gilchristi* are not clear, but in general, lobster growth rates are labile and very sensitive to food availability and diet (Newman & Pollock 1974, Chittleborough 1975, McKoy & Esterman 1981). In *P. gilchristi*, lower growth rates at Port Alfred (Groeneveld 1997), possibly as a result of reduced per capita food availability, would in turn reduce size at sexual maturity (Groeneveld & Melville-Smith 1994), population size composition (Groeneveld & Rossouw 1995) and fecundity (Groeneveld 2005). All these factors are age, rather than size specific (Pollock 1995a), and none of them contradict the finding that *P. gilchristi* is panmictic.

Analysis of the mtDNA control region sequences suggested that there has been a relatively recent demographic change in this species. The mismatch distribution showed a strong expansion curve (Fig. 2), and Fu's F_S test was significant, indicating the population is not at equilibrium. The lack of population structure coupled with recent population expansion has been found for several other marine crustaceans (e.g. Benzie et al. 2002, McMillen-Jackson & Bert 2003, 2004) and suggests that the marine environment is highly dynamic through time, affecting the distribution and population sizes of some species. A study on tiger prawns *Penaeus monodon* from the Indo-Pacific and the coast of South Africa also showed a recent population expansion (Benzie et al. 2002). For *Palinurus gilchristi*, the pattern of demographic change is probably due to a historical increase in population size coupled with an increase in range size, possibly between ca. 5300 and 10 600 yr ago (given rough estimates of mutation rates). Although recent bottlenecks can also produce similar results, the star-shaped haplotype network (Fig. 3) and high haplotype diversity (Table 2) are also suggestive of a population expansion. The network is characterised by a high number of unique haplotypes, all closely related to a single central haplotype (pg4), suggesting the central haplotype is the ancestral haplotype for this species with the closely related haplotypes recently derived from this ancestral haplotype.

The most likely explanation for the range expansion is an increase in available habitat as the Agulhas Bank became submerged following the last glacial period. George & Main (1967), and more recently Pollock (1990, 1992, 1993), have drawn attention to the possible role of glacial/interglacial alternations and related oceanographic changes in inducing speciation in several *Jasus* and *Panulirus* species. The same mechanism may also have been responsible for population level changes within *Palinurus*. The rough dating of the population expansion post-dates the Last Glacial Maximum (LGM) and corresponds to the time frame of the present interglacial. Taking into account that the sea level has increased by more than 150 m since the LGM (Anderson et al. 1988) and that the average depth of

Table 2. *Palinurus gilchristi*. Sample sizes (n), haplotype (*h*) and nucleotide (π) diversity for collected from 4 fishing areas (Area I: Port Alfred; Area II: Port Elizabeth; Area III: Central Agulhas Bank; Area IV: Western Agulhas Bank) along the coast of South Africa.

	n	*h*	π
Area I	50	0.869	0.0038
Area II	35	0.896	0.0042
Area III	45	0.843	0.0045
Area IV	57	0.850	0.0040

the Agulhas Bank is less than 200 m, a small population restricted to a refuge of suitable habitat in deeper waters may have expanded to occupy the larger habitat as it became available. Thus, the lack of genetic structure between Port Alfred and the remaining areas could also be the result of a leading edge effect (Hewitt 1996) where expansion is so recent (i.e. within the Holocene as the habitat on the Agulhas Bank became available) that the leading edge of the expansion has not yet diversified genetically. A leading edge effect coupled with some level of contemporary larval mixing seems to be the main source of panmixia in this species.

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