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RESEARCH ARTICLE

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Marine biogeographic disjunction in central New Zealand

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Abstract We present a phylogeographic analysis of an abundant New Zealand endemic sea-star, *Patiriella regularis*, to help pinpoint the location of an important biogeographic disjunction in central New Zealand. The analysis incorporates 284 mtDNA control region sequences (approximately 800 bp) of *P. regularis* from 22 coastal locations around New Zealand. We detected 132 haplotypes, with a mean divergence of 0.96%. AMOVA analysis of New Zealand samples is consistent with a north-south biogeographic disjunction across central New Zealand (among-group genetic variance = 6.10%; $P = 0.0005$). Cook Strait, the shallow marine strait separating the main islands, is not correlated with the disjunction: samples from northern South Island are genetically indistinguishable from North Island samples (variance = 1.69%; $P = 0.073$). These results are consistent with the hypothesis that upwelling zones south of Cook Strait constitute a significant barrier to larval dispersal.

Introduction

The integration of genetic and geographic data provides a means of elucidating barriers to gene flow in the marine environment (Lessios et al. 2001). Phylogeographic studies of widespread marine taxa have accordingly identified a number of important physical barriers correlated with genetic divergence, e.g. the Isthmus of Panama (Pacific versus Atlantic Oceans; Roy and Sponer 2002) and the Benguela Upwelling (Atlantic vs Indian Oceans; Bowen et al. 2001; Lessios et al. 2001; Sponer 2002). In the case of upwelling, it has been suggested that upwelled water (Harris 1990) may transport larvae offshore and thus prevent recruitment (Apte and Gardner 2002). Alternatively, cold upwelled water masses may directly impact on larval survival (Menge et al. 2003). Either way, upwelling zones apparently are biogeographically important phenomena.

Recent studies of New Zealand's intertidal biota have detected significant phylogeographic structure (Apte and Gardner 2002; Sponer 2002; Star et al. 2003; Waters and Roy 2004). Indeed, the New Zealand archipelago offers much to those interested in marine biogeography due to its isolation, linear coastline, and well-characterised oceanography (Bowman et al. 1983; Heath 1985). Although New Zealand's marine communities show considerable biogeographic structure (Pawson 1961; 1965; Nelson 1994; Francis 1996) and phylogeographic variation (see above), the associated ecological and historical biogeographic factors remain poorly understood.

The New Zealand endemic cushion star, *Patiriella regularis* (Echinodermata: Asterinidae), is abundant across a variety of coastal habitats. The wide distribution of this species may reflect its dispersive feeding larval phase that occupies the plankton for approximately 9–10 weeks (Byrne and Barker 1991) between late spring and early summer (Hart et al. 1997). In a recent genetic study, Waters and Roy (2004) detected significant mtDNA control region sequence differentiation between *P. regularis* populations from northern versus southern New Zealand. Unfortunately, the study's limited sampling of central New Zealand precluded strong conclusions on the precise point of north-south disjunction. In the current study, we address this shortcoming with increased sampling of *P. regularis* from central New Zealand.

Recent genetic studies of New Zealand's greenshell mussel, *Perna canaliculus*, detected a marked north-south disjunction in both haplotypic (Apte and Gardner 2002) and genotypic (Star et al. 2003) composition. The former study suggested that this structure might be

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explained by coastal upwelling regimes detected at latitude 42°S (central New Zealand). Here, we use mtDNA control region sequences of *P. regularis* to address the hypothesis that upwelling provides a barrier to gene flow in central New Zealand. Specifically, we analyse DNA sequences from 284 samples of *P. regularis*, a major improvement on the published analyses (based on 114 sequences) of Waters and Roy (2004). The current study incorporates three new collections from New Zealand waters, including two from the central region that is at issue here.

Materials and methods

All sampled sea-stars were collected from intertidal rocky areas, placed directly into 70% ethanol, and stored at −20°C. *P. regularis* collections from 19 New Zealand localities were previously sampled by Waters and Roy (2004; Fig. 1) with approximately five specimens sequenced per locality. In the current study, we sequenced an increased number of specimens from many of these sites (Table 1). Additionally, collections from

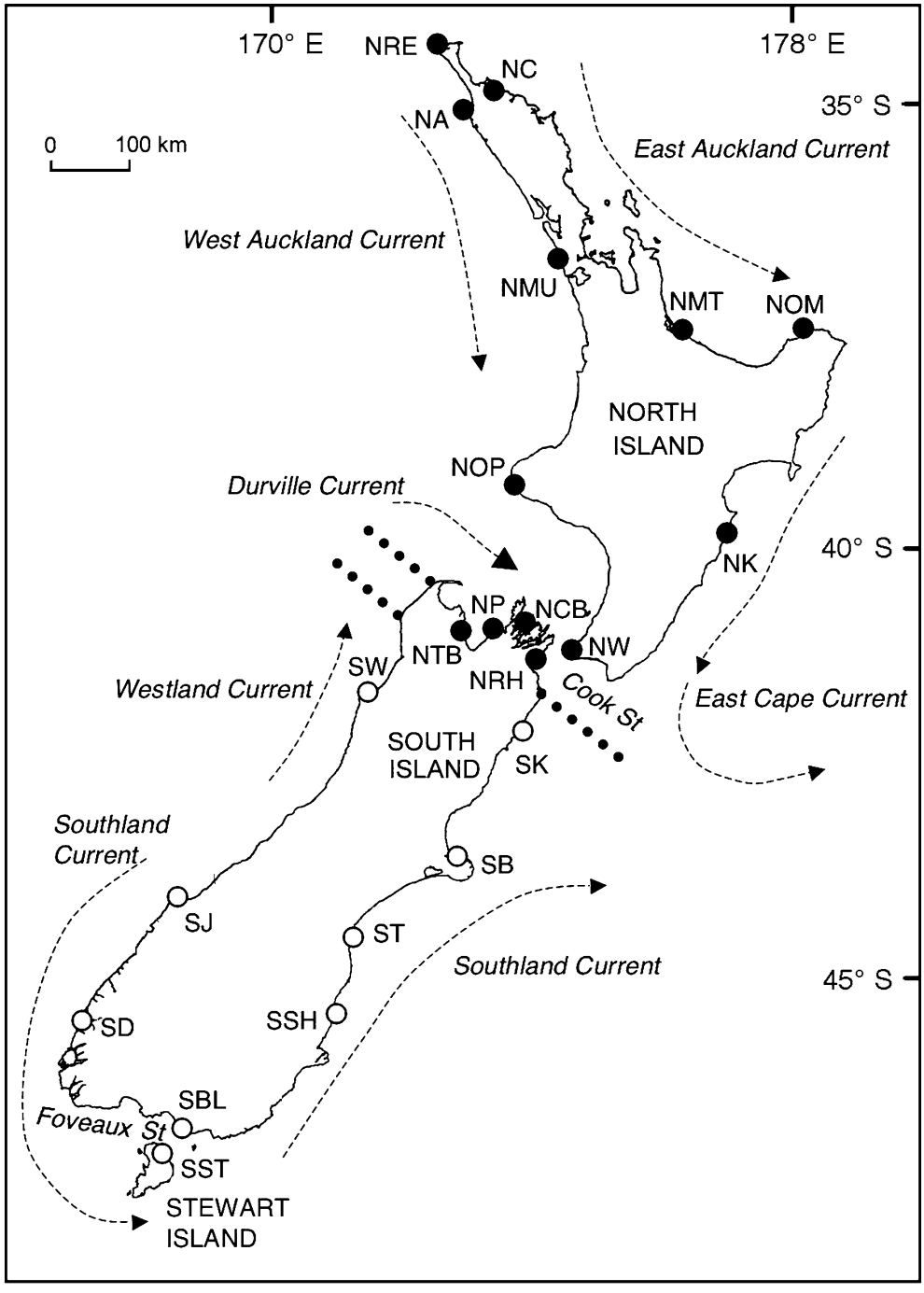

Fig. 1 Twenty-two collection localities for New Zealand *Patiriella regularis* (modified from Waters and Roy 2004). *Dotted lines* indicate upwelling zones in northern South Island (after Apte and Gardner 2002). Sampling localities north of the upwelling zone are by *black circles*, whereas localities to the south are indicated by *open circles*. (codes from Table 1)

Table 1 Sample localities and sample sizes for *Patiriella regularis*. Locality codes apply to Figs. 1, 2 and 3

Region	Location	*n*	Code
North Island, N.Z.	Cape Reinga	6	NRE
North Island, N.Z.	Ahipara	5	NA
North Island, N.Z.	Cable Bay	9	NC
North Island, N.Z.	Mt Maunganui	5	NMT
North Island, N.Z.	Muriwai	5	NMU
North Island, N.Z.	Omaio	5	NOM
North Island, N.Z.	Kairakau	17	NK
North Island, N.Z.	Opunake	19	NOP
North Island, N.Z.	Wellington	17	NW
South Island, N.Z.	Cissy Bay	20	NCB
South Island, N.Z.	Pepin Island	19	NP
South Island, N.Z.	Robin Hood Bay	19	NRH
South Island, N.Z.	Tapu Bay	23	NTB
South Island, N.Z.	Westport	18	SW
South Island, N.Z.	Jackson Bay	4	SJ
South Island, N.Z.	Doubtful Sound	5	SD
South Island, N.Z.	Kaikoura	21	SK
South Island, N.Z.	Banks Peninsula	18	SB
South Island, N.Z.	Timaru	14	ST
South Island, N.Z.	Shag Point	7	SSH
South Island, N.Z.	Bluff	13	SBL
Stewart Island, N.Z.	Paterson Inlet	15	SST

three new sites, Bluff (SBL), Cissy Bay (NCB) and Tapu Bay (NTB) (see Fig. 1) were analysed (approximately 20 sea-stars per site).

Total DNA was extracted from tube foot tissue using chelex (Walsh et al. 1991). Approximately 1.2–1.4 kb of the mitochondrial genome was amplified using the primers E12Sa (5'-ACACATCGCCCGTCACTCTC-3') and E16Sb (5'-GACGAGAAGACCCTATCGAGC-3') (Evans et al. 1998) and approximately 780 bp sequenced with the former primer using a capillary ABI3730 Genetic Analyser (Applied Biosystems). The sequenced region incorporates the 3' end of 12S rRNA, $tRNA^{Thr}$, $tRNA^{Glu}$, the entire putative control region, and the 5' end of 16S rRNA. All of these genes are conserved, with the exception of the rapidly evolving control region. Few insertions/deletions were detected among sequences, and most of these represented short repetitive regions. As a result, the sequences were easily aligned by eye, with a total alignment length of 835 bp.

Bayesian phylogenetic analysis was performed using MRBAYES (Huelsenbeck and Ronquist 2001) under a best-fit model of sequence evolution (HKY + I + Γ) selected using Modeltest 3.06 (Posada and Crandall 1998) and PAUP*4.0b10 (Swofford 1998) (details in Waters and Roy 2004). The phylogenetic tree was rooted with outgroup sequences from asterinid taxa *Patiriella mortenseni* and *Asterina pectinifera* (see Waters and Roy 2004). The Markov chain Monte Carlo search was run with 2,000,000 chains for 100 generations, with trees being sampled every 100 generations, and the first 5,000 trees were discarded as burn-in. Analyses were repeated to ensure that independent runs converged on similar topologies.

A priori sample groupings (Table 2) were assessed using the molecular analysis of variance (AMOVA) function of ARLEQUIN version 2.000 (Schneider et al. 2000). This method evaluated hierarchical groupings for their contribution to the partitioning of genetic variance (Excoffier et al. 1992) between North Island and South Island (test 1), between north and south of the upwelling zone (test 2), between central New Zealand and North Island (test 3), and between central New Zealand and south of the upwelling zone (test 4). The Tamura and Nei (1993) model of molecular distance (Arlequin's best approximation of HKY + I + Γ) was used to calculate haplotype divergences, incorporating a gamma shape parameter of 0.6559 estimated by ModelTest (Posada and Crandall 1998) and PAUP*4.0b10 (Swofford 1998). F_{ST} *P* values were calculated with 110 permutations, and were considered significant if smaller than 0.05. Sequential Bonferroni adjustment (Rice 1989) was used to account for type I error. Population pairwise F_{ST}

Table 2 AMOVA analysis of hierarchical groupings of New Zealand *P. regularis*. For each a priori grouping of samples, the associated percentage of among-group genetic variance and probability of non-differentiation is given (significant values in bold)

Test / grouping	Pooled localities	*n*	Variance	*P*
Test 1			1.69%	0.0727 ± 0.0025
North Island	NRE, NA, NC, NMU, NOP, NOM, NMT, NK, NW	89		
South Island	NP, NTB, NRH, NCB, SW, SJ, SD, SK, SB, ST, SSH, SBL, SST	195		
Test 2			**6.10%**	**0.0005 ± 0.0002**
North of upwelling	NRE, NA, NC, NMU, NOP, NOM, NMT, NK, NW, NP, NCB, NTB, NRH	169		
South of upwelling	SK, SB, ST, SSH, SW, SJ, SD, SBL, SST	115		
Test 3			−0.36%	0.5478 ± 0.0049
North Island	NRE, NA, NC, NMU, NOP, NOM, NMT, NK, NW	89		
Central NZ	NP, NCB, NTB, NRH	80		
Test 4			**6.99%**	**0.0051 ± 0.0007**
Central NZ	NP, NCB, NTB, NRH	80		
South of upwelling	SK, SB, ST, SSH, SW, SJ, SD, SBL, SST	115		

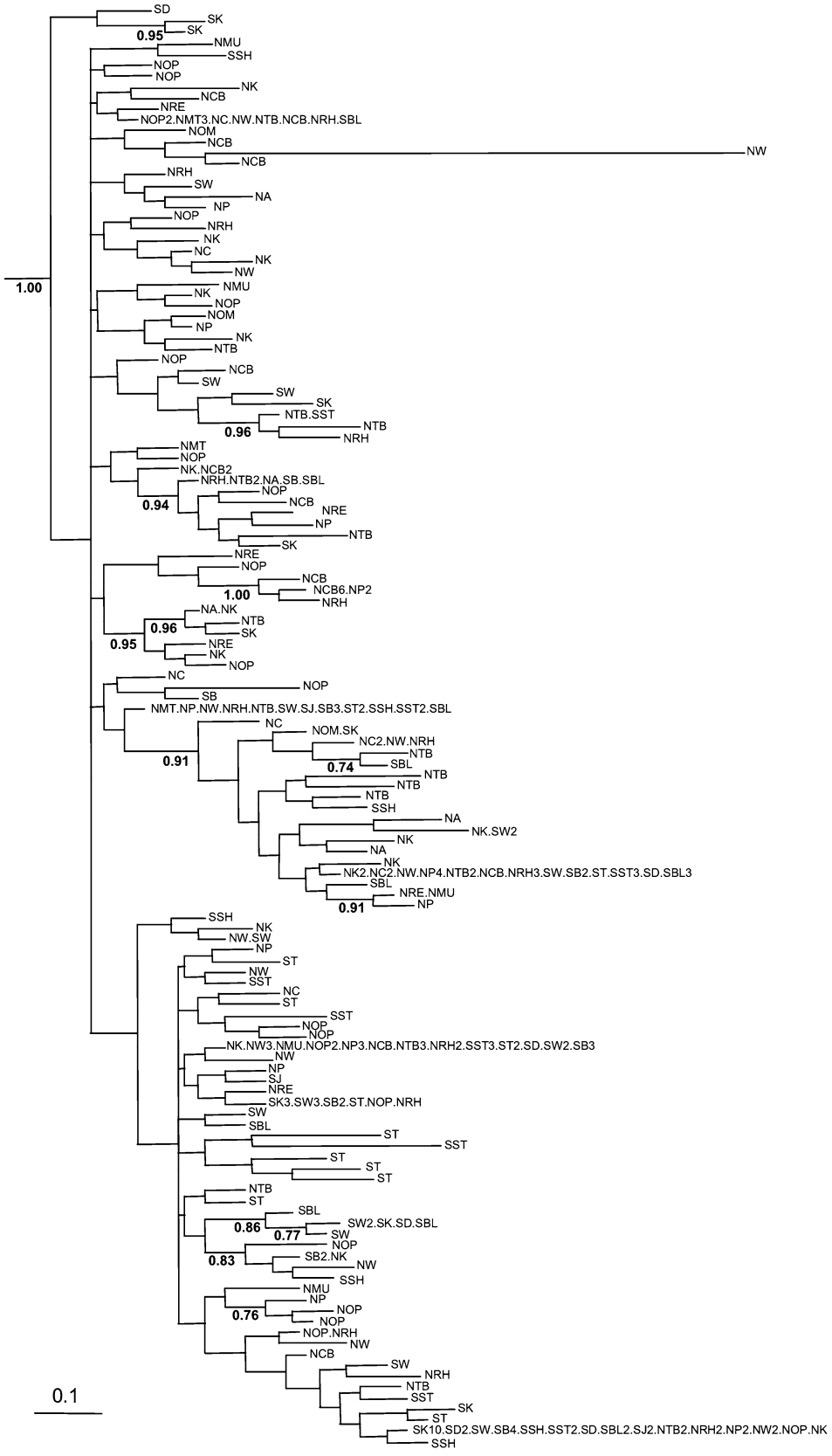

Fig. 2 Bayesian phylogenetic analysis of *P. regularis* mtDNA haplotypes, with outgroups excluded for diagrammatic purposes. Posterior probability values ≥0.70 are indicated below associated nodes. Repeated haplotypes per locality are indicated as numbers following site codes (see Table 1)

values based on Tamura and Nei's genetic distances were calculated with ARLEQUIN and visualised by non-metric multidimensional scaling (MDS), using the option MDS with 1,000 restarts in the program PRIMER version 5 (Clarke and Gorley 2001). The fit of the data in two dimensions was measured by stress factor.

Table 3 Pairwise F_{ST} values, incorporating Tamura and Nei (1993) genetic distances, among New Zealand populations of *Patiriella regularis*. Significant values ($P < 0.05$) are underlined, and those significant after sequential Bonferroni adjustment (Rice 1989) are in bold

	NRE	NA	NOM	NMT	NK	NC	NMU	NOP	NW	NP	NCB	NTB	NRH	SW	SJ	SK	SB	SSH	ST	SST	SD
NRE																					
NA	−0.023																				
NOM	−0.048	−0.043																			
NMT	−0.041	0.079	−0.073																		
NK	0.009	−0.058	−0.041	0.040																	
NC	0.072	−0.057	0.040	0.185	−0.025																
NMU	−0.111	−0.057	−0.146	−0.066	−0.076	−0.009															
NOP	−0.008	0.144	0.085	0.092	0.094	0.197	−0.035														
NW	0.065	0.083	0.104	0.154	0.084	0.118	−0.014	0.027													
NP	0.018	0.032	0.065	0.131	0.022	0.045	−0.033	0.035	0.004												
NCB	0.052	0.162	0.069	0.049	0.165	0.214	0.077	0.153	**0.209**	0.164											
NTB	−0.034	−0.020	−0.019	0.030	−0.009	0.014	−0.062	0.035	0.040	−0.014	**0.143**										
NRH	0.009	0.048	0.072	0.127	0.032	0.053	−0.035	0.026	−0.001	−0.038	0.151	−0.017									
SW	0.140	0.152	0.223	0.294	0.109	0.171	0.071	0.070	−0.012	0.005	**0.295**	0.047	0.010								
SJ	0.062	0.193	0.329	0.489	0.150	0.253	0.003	−0.017	−0.108	−0.018	0.236	0.037	−0.033	−0.032							
SK	0.148	0.291	0.310	0.348	**0.226**	**0.296**	0.127	0.071	0.020	0.085	**0.282**	0.124	0.054	0.070	−0.120						
SB	0.110	0.189	0.228	0.299	0.116	0.206	0.042	0.027	−0.020	0.003	**0.276**	0.043	0.001	−0.028	−0.075	0.033					
SSH	0.069	0.100	0.202	0.325	0.060	0.139	0.000	0.019	−0.056	−0.041	0.250	−0.003	−0.036	−0.078	−0.114	0.033	−0.077				
ST	0.112	0.212	0.247	0.301	0.177	0.245	0.049	0.071	0.018	0.061	**0.304**	0.103	0.064	0.024	−0.101	0.042	−0.008	−0.038			
SST	0.061	0.125	0.173	0.242	0.086	0.131	0.011	0.046	−0.010	−0.011	**0.253**	0.025	−0.015	−0.016	−0.079	0.039	−0.030	−0.070	0.002		
SD	−0.002	0.039	0.147	0.249	0.035	0.095	−0.050	−0.006	−0.068	−0.054	0.196	−0.028	−0.055	−0.074	−0.083	0.013	−0.047	−0.092	−0.015	−0.070	
SBL	0.062	−0.004	0.068	0.176	−0.008	−0.008	−0.006	0.096	0.027	−0.021	**0.224**	−0.015	−0.009	0.019	0.084	0.162	0.053	−0.009	0.109	0.014	−0.052

Results

Genetic diversity

The 284 ingroup sequences yielded 132 distinct haplotypes (GenBank accession AY692489-AY692548, DQ001541-DQ001613) that were aligned easily due to the small number of insertions and deletions. Forty-one parsimony informative characters were detected within *P. regularis*, and the majority (36) of these were located within the putative control region (positions 196–663 of the 835 bp alignment) as based on *Asterina pectinifera* mtDNA (GenBank accession NC001626; Asakawa et al. 1995). Bayesian phylogenetic analysis (Fig. 2) revealed a strongly monophyletic assemblage of closely-related *P. regularis* haplotypes, but relatively little intraspecific phylogenetic signal, with only 13 interior nodes receiving posterior probability values >0.70. The mean haplotype divergence was 0.0096 ± 0.0061 (maximum 0.0692). Nineteen of the haplotypes were shared across multiple collection sites, and 12 were detected in both northern New Zealand and southern New Zealand. Six haplotypes were relatively common (frequency >0.03), accounting for approximately 44% of all sampled individuals. The most common haplotype was detected in 35 individuals (frequency 0.12), including 10 specimens from Kaikoura (SK; Fig. 2). Haplotypic diversity was substantially higher in northern New Zealand (169 specimens: 95 haplotypes) relative to southern New Zealand (115 specimens: 49 haplotypes)

Population structure

Prior to Bonferroni adjustment, pairwise F_{ST} values were significantly larger than zero for 71 of 231 population comparisons (Table 3). Fifty-two (73%) of these significant values reflected differences between northern and southern New Zealand (117 comparisons). Within southern New Zealand, by contrast, just 3 of 36 pairwise F_{ST} values were significant, and 16 of 78 northern New Zealand comparisons yielded significant values. Interestingly, the Cissy Bay sample (NCB; Marlborough Sounds, central New Zealand) was significantly different from 17 of the remaining 21 New Zealand samples, and 8 of these comparisons remained significant after sequential Bonferroni adjustment (Rice 1989). Additionally, the Kaikoura sample (SK) was significantly different to 13 of 21 other New Zealand samples, with three of these comparisons remaining significant after Bonferroni adjustment (Table 3). Multidimensional scaling (MDS) of these F_{ST} values revealed largely distinct sample groupings (Fig. 3) of northern and southern New Zealand *P. regularis*, consistent with upwelling as a barrier to gene flow. MDS also illustrates the unusual genetic composition of Cissy Bay (NCB; Fig. 3). Regardless of hierarchical sample grouping (Table 2), approximately 90% of the observed genetic variation

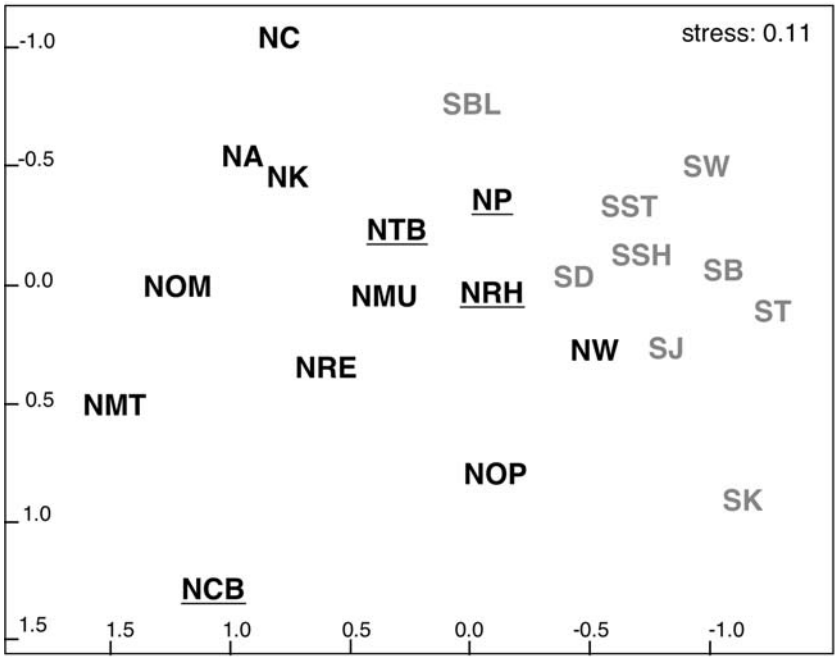

Fig. 3 Multidimensional scaling of the pairwise population F_{ST} matrix and associated stress value for *P. regularis* samples. Localities from north of the upwelling zone are in *black*, whereas localities from southern New Zealand are shown in *grey*. Samples from northern South Island (central New Zealand) are *underlined*

was distributed within populations. Additionally, AMOVA analysis (Table 2) indicated that:

1. North Island versus South Island population groupings exhibited no significant differentiation ($P = 0.073$), with only 1.69% of genetic variance attributable to among-group differences (test 1).
2. Northern New Zealand versus southern New Zealand population groupings (delineated by upwelling zones; Fig. 1) showed strongly significant differentiation ($P = 0.0005$), with 6.10% of genetic variance attributable to among-group differences (test 2).
3. Northern South Island (central New Zealand) versus North Island population groupings showed non-significant genetic differentiation (−0.36% of variance; $P = 0.548$) (test 3).
4. Northern South Island (central New Zealand) versus southern South Island population groupings showed significant genetic differentiation (6.99% of variance; $P = 0.005$) (test 4).

Discussion

Biogeographical disjunction

On the basis of Apte and Gardner's (2002) data, we hypothesised that upwelling regimes, present in New Zealand at around latitude 42°S, represent a barrier to gene flow in *P. regularis*. Our results are consistent with this prediction, as northern and southern samples delineated by this zone were significantly different genetically ($P = 0.0005$). In contrast, phylogeographic analyses indicated that inter-group variance between North Island and South Island haplotypes was not significant ($P = 0.073$). Furthermore, AMOVA analysis indicated that northern South Island samples of *P. regularis* were genetically indistinguishable from North Island samples ($P = 0.548$), but significantly differentiated from southern South Island samples ($P = 0.005$). These findings indicate that the Cook Strait itself is not a barrier to gene flow, and provide compelling evidence that an oceanographic barrier exists just to the south.

To reliably infer biogeographic processes, it is desirable to have concordant phylogeographic data for multiple taxa (Avise 2000). As previously mentioned, the mussel *Perna canaliculus* exhibits strong north-south genetic structure concordant with the data presented here. The location and timing of upwelling regimes appear to best explain the phylogeographic disjunctions observed for mussels (Apte and Gardner 2002) and seastars (current study). Gardner (1954) attributed cold water in northwest South Island (Cape Farewell) to the Kahurangi upwelling, a process which forces cold water into western Cook Strait (Harris 1990; Heath 1985; Fig. 1). In northeast South Island, (Cloudy Bay/Clifford Bay) upwelling is associated with southward winds (Bowman et al. 1983; Barnes 1985) that often predominate from November (Stanton and Moore 1992) throughout January and February (Bowman et al. 1983) and as late as April (Barnes 1985; Stanton 1976). *Patiriella regularis* larvae are known to occupy the plankton during these months (Byrne and Barker 1991; Evans et al. 1998).

Divergent populations

The finding that the Cissy Bay *P. regularis* population (NCB; Marlborough Sounds, central New Zealand) is genetically distinct from most other populations (17 of 21) may warrant further investigation. We suggest the

unusual genetic composition of this sample most likely reflects larval retention and local recruitment within the Marlborough Sounds, a sheltered region of "drowned" river valleys. If larval retention is indeed a general characteristic of such fiordic systems (Perrin et al. 2004), we would predict similar genetic drift for populations inhabiting Fiordland in southwest New Zealand. However, our sample from Doubtful Sound (SD; five individuals) may be too small to detect such differentiation. It should be noted, for instance, that the only samples not significantly differentiated from the Cissy Bay population were small samples from North Island (NMU, NMT, NOM, NRE; $n \leq 6$). As an alternative explanation for the divergent Cissy Bay population, it might be argued that importation of mussel spat for aquaculture in Marlborough Sounds (Rhodes et al. 1994) has artificially translocated *P. regularis* from the far north of New Zealand. But we suggest that the effect of such translocations would be minimal given the high abundance of the species throughout coastal New Zealand. Regardless, the Cissy Bay sample does not significantly impact the findings of the current study: when it was excluded from the AMOVA, central versus southern New Zealand populations remained significantly differentiated (3.95% of genetic variance; $P = 0.043$).

The high genetic diversity detected in *P. regularis* suggests that large populations of this species are an ongoing evolutionary phenomenon. Furthermore, it is clear that our sampling detected only a fraction of the haplotypic diversity present in the species (113 of 132 haplotypes detected were singletons). It therefore seems noteworthy that the Kaikoura sample (SK; 20 individuals) exhibited unusually low haplotypic diversity, with 10 of 20 individuals sharing a single common haplotype. Interestingly, Kaikoura sits at the boundary between two major current systems; the D'Urville Current and the Southland Current (Fig. 1), and this may facilitate local recruitment. Alternatively, the lack of diversity could be explained by asexual reproduction (by fission; Perrin et al. 2004). However, this phenomenon occurs only rarely in *P. regularis* (Bennett 1927), and the morphological asymmetry that results from fission was not observed in any of our samples.

Management implications

This phylogeographic study adds to growing evidence that oceanographic barriers, cryptic or otherwise, shape the genetic structure of marine populations. The resultant understanding of marine biota and their interaction with the environment will enable policy-makers to better manage marine resources, predict the spread of invasive species, and preserve biodiversity (Apte and Gardner 2002).

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