ORIGINAL ARTICLE

Marine biogeographical structure in two highly dispersive gastropods: implications for trans-Tasman dispersal

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ABSTRACT

Aim Recent genetic and ecological studies of marine invertebrate species with planktotrophic larvae have inferred high rates of gene flow across wide oceanic barriers. We therefore aim to test for the genetic signature of long-distance dispersal in two widespread and abundant marine gastropod taxa.

Location The intertidal and shallow subtidal zones of southern Australia and New Zealand (NZ), which house similar marine invertebrate assemblages despite being separated by the 2000-km-wide Tasman Sea.

Methods We used mtDNA cytochrome oxidase I gene sequence analysis of two gastropod genera exhibiting trans-Tasman distributions, namely *Austrolittorina* (Littorinidae) (139 specimens; 28 localities) and *Scutus* (Fissurellidae) (154 specimens; 32 localities). The cool-temperate Australian (*A. unifasciata*; *S. antipodes*) and NZ (*A. antipodum*; *S. breviculus*) taxa within each genus are morphologically similar but of uncertain taxonomic status.

Results The mtDNA analyses indicate major trans-Tasman genetic discontinuities for both gastropod genera, with no evidence of recent or ongoing intercontinental gene flow. Although both *Scutus* and *Austrolittorina* show significant east–west structure within southern Australia – consistent with recent studies of regional marine phylogeography – neither taxon exhibits significant differentiation within NZ.

Main conclusions Morphologically conserved but biogeographically disjunct gastropod populations may exhibit striking phylogeographic discontinuities, even when dispersal abilities appear to be high. On the basis of these data we reject recent calls for the synonymy of NZ and Australian lineages.

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Keywords
***Austrolittorina*, mtDNA, oceanic dispersal, pelagic larvae, phylogeography, population structure, *Scutus*, vicariance.**

INTRODUCTION

Long-distance marine dispersal is recognized as an important biogeographical process in the Southern Hemisphere (Waters & Roy, 2004; Donald *et al.*, 2005; de Queiroz, 2005). Many intertidal and shallow-water taxa exhibit broad cool-temperate distributions, mediated either by long-lived planktonic larvae (Ovenden *et al.*, 1992; Booth & Ovenden, 2000; Burridge & Smolenski, 2003; Chiswell *et al.*, 2003; Waters *et al.*, 2005; Burridge *et al.*, 2006) or by long-distance rafting (Waters & Roy, 2004; Donald *et al.*, 2005). It is also possible that a combination of active (mobile planktonic larvae) and passive (rafting) processes may mediate dispersal. Drifting macroalgae, for instance, may provide ecological habitat for oceanic dispersal of pelagic juveniles. Dempster & Kingsford (2004) noted that 'many species of juvenile fish actively seek drifting objects as pre-settlement habitat, which may reduce predation and enhance settlement opportunities', as well as promoting dispersal.

Recently demonstrated cases of Southern Hemisphere dispersal include several examples of apparently ongoing gene flow (i.e. the absence of significant genetic differentiation) across the

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Tasman Sea, a 2000-km-wide marine barrier separating Australia and New Zealand (NZ) (Burridge & Smolenski, 2003; Chiswell *et al.*, 2003; Waters *et al.*, 2005). Additional unpublished mtDNA data for the barnacle *Chamaesipho* and the gastropod *Dicathais* similarly support recent trans-Tasman dispersal (JMW, unpublished data). Conversely, several marine taxa that have clearly dispersed across the Tasman in the past (e.g. *Coscinasterias*: Waters & Roy, 2003; seahorses: Casey *et al.*, 2004; topshells: Donald *et al.*, 2005) show substantial trans-Tasman genetic divergence (e.g. reciprocal monophyly), providing no evidence of *ongoing* population connectivity between NZ and Australia. Hence Australia and NZ house distinct (yet similar) assemblages of, for instance, topshells (Trochidae) and galaxiid fishes (Galaxiidae). Intriguingly, one mtDNA study detected genetic evidence of recent trans-Tasman dispersal 'superimposed' on the genetic signature of long-term population subdivision (reciprocal monophyly) in *Galaxias maculatus* (Waters *et al.*, 2000).

In the current study we present genetic data for two widespread southern gastropods (*Scutus*, *Austrolittorina*) to test for oceanic dispersal. Both taxa have morphologically similar populations on either side of the Tasman Sea, and are thought to possess dispersive planktonic larvae. In the case of *Austrolittorina*, the feeding larval phase is thought to last for about 1 month (Williams *et al.*, 2003), whereas the larval history of *Scutus* is not well known, but almost certainly planktotrophic (M. Barker, pers. comm.). Cernohorsky (1977) argued that the *Scutus* populations under consideration here – Australian *S. antipodes* and NZ *S. breviculus* – are in fact conspecific. Similarly, NZ's *Austrolittorina antipodum* has often been considered a subspecies of the Australian *A. unifasciata* (e.g. Rosewater, 1970), and the two are morphologically very similar (Reid, 2002; Williams *et al.*, 2003) although apparently not indistinguishable. Specifically, Reid & Williams (2004) note that NZ specimens are 'smaller, more tall-spired and have a more pronounced bluish peripheral band'.

Here we use mtDNA data to shed light on the phylogeography and systematics of these morphologically similar species of *Scutus* and *Austrolittorina*, and to discriminate between vicariant (e.g. Rosen, 1978) and dipersalist (e.g. Fell, 1962) explanations for their trans-Tasman distributions. In designing the current study, we chose to sample extensively across south-eastern Australia, incorporating all three temperate biogeographical provinces (Peronian, Flindersian, Maugean; Bennett & Pope, 1953), regions most likely to be sources for NZ colonization.

MATERIAL AND METHODS

Samples of *Scutus* (*S. antipodes* from Australia; *S. breviculus* from NZ) and *Austrolittorina* (*A. unifasciata* from Australia; *A. antipodum* from NZ) were obtained from intertidal (*Austrolittorina*; 139 specimens, 28 localities) and shallow subtidal (*Scutus*; 154 specimens; 32 localities) habitats throughout south-eastern Australia (Fig. 1) and NZ (Fig. 2). DNA was extracted from ethanol-preserved foot or mantle tissue using a CTAB-proteinase K digestion buffer, followed by chloroform extraction.

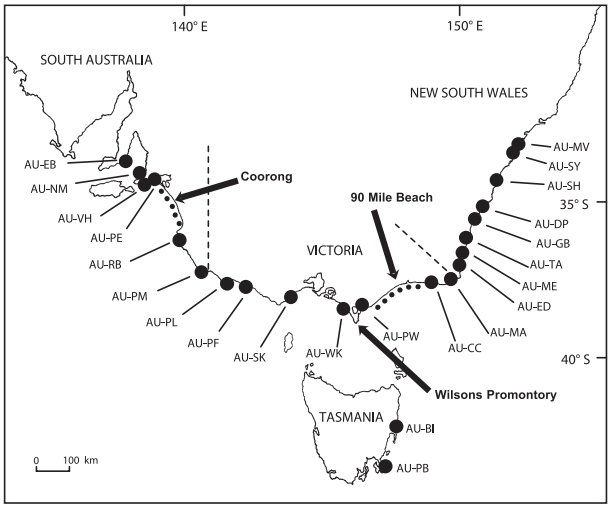

Figure 1 Australian sample sites for *Austrolittorina unifasciata* and *Scutus antipodes*. Code names and sample sizes are listed in Table 1.

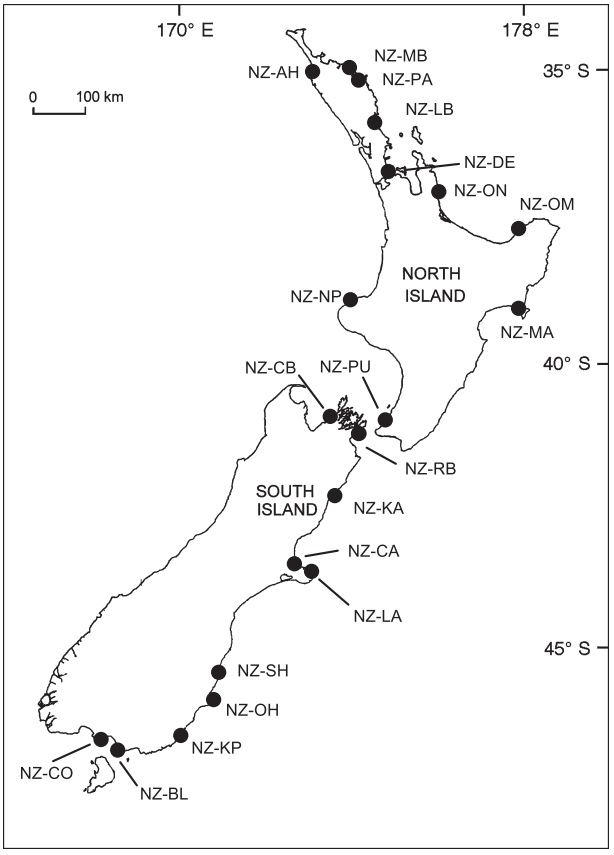

Figure 2 New Zealand sample sites for *Austrolittorina antipodum* and *Scutus breviculus*. Code names and sample sizes are listed in Table 1.

A 1107-bp portion of the mtDNA cytochrome oxidase I gene (COI) was amplified for most specimens using primers LCO1490 (Folmer *et al.*, 1994) and H7005-mod1 (5′-ARTG-NGCNACNACRTARTANGTRTCRTG-3′; Donald *et al.*, 2005).

For specimens that failed to amplify with the above primers, a nested 658-bp fragment was amplified using LCO1490 and HCO2198 (Folmer *et al.*, 1994). Polymerase chain reaction (PCR) (25 μL) conditions comprised 40 cycles (94°C – 30 s; 45°C – 60 s; 72°C – 60 s) and contained 1 unit of RedHot Taq (ABGene) and 1.5 mM $MgCl_2$. Sequencing reactions were performed as recommended using a capillary ABI3730 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA), with primer LCO1490.

As no length variation was detected within the COI of either genus, sequences were aligned manually, yielding a 658-bp alignment for *Scutus*, and 617-bp for *Austrolittorina*. Distinct COI haplotypes were identified using phylogenetic software (PAUP*4.0b10; Swofford, 1998). Pairwise sequence divergences among haplotypes were calculated using the Kimura (1980) 2-parameter model of sequence evolution. Phylogenetic analyses of *Scutus* were rooted with a sequence from the fissurellid genus *Diodora* (GenBank accession number AY377730; Okusu *et al.*, 2003), and *Austrolittorina* analyses included sequences from three additional congeneric taxa: *A. auracana* (AJ488624), *A. fernandezensis* (AJ488620), and *A. cincta* (AJ488623) (Williams *et al.*, 2003). Best-fit models of COI evolution (*Austrolittorina*: HKY + Γ; *Scutus*: TrN + Γ) were selected using MODELTEST 3.06 (Posada & Crandall, 1998), and implemented in phylogenetic analyses, performed using MRBAYES 3.0B4 (Huelsenbeck & Ronquist, 2001; Altekar *et al.*, 2004) (*Austrolittorina*: 'nst = 2'; rates = 'gamma'; *Scutus*: 'nst = 6'; rates = 'gamma') with default priors. The Markov-chain Monte Carlo search was run with four chains for 10^6 generations, with trees sampled every 100 generations (the first 1000 trees were discarded as 'burn in', as based on attainment of asymptotes for LnL and other parameters).

Population differentiation was assessed by analysis of molecular variance (AMOVA), incorporating distance information among haplotypes [Tamura-Nei; ARLEQUIN's best available approximation of the sequence evolution models selected (above)], performed using ARLEQUIN Version 2.000 (Schneider *et al.*, 2000). The significance of the resultant Phi statistics was assessed using 100,000 permutations of individuals among populations, and populations among *a priori* geographic groupings. Australian groupings east and west of Wilsons Promontory are based on Waters *et al.* (2005), whereas NZ groupings north vs. south of an upwelling zone, and north and south of Cook Strait are based on Ayers & Waters (2005).

RESULTS

Austrolittorina

One hundred Australian *Austrolittorina* specimens yielded 27 distinct haplotypes (Appendices S1a, S1b in Supplementary Material; GenBank accession numbers DQ836975–DQ837001) (divergence range 0.2–1.1%; mean 0.5%). Individual haplotypes typically differed by just one or a few 'silent' substitutions (transitions at third codon positions; Appendix S1a). Twenty-one of these haplotypes were detected as singletons, whereas

Table 1 Geographic details of the 154 *Scutus* and 139 *Austrolittorina* samples sequenced

Location	Code	No. *Scutus*	No. *Austrolittorina*
New Zealand			
North Island			
Paihia	NZ-PA	1	5
Langs Beach	NZ-LB	6	
Matheson Bay	NZ-MB		5
Devonport	NZ-DE	4	
Ahipara	NZ-AH		5
Onemana	NZ-ON	1	
Omaio	NZ-OM		5
Mahia	NZ-MA	18	
New Plymouth	NZ-NP	16	
Pukerua Bay	NZ-PU	7	
South Island			
Cable Bay	NZ-CB	3	
Robinhood Bay	NZ-RB	3	
Kaikoura	NZ-KA	7	5
Camp Bay	NZ-CA	3	
Little Akaloa	NZ-LA	7	5
Shag Point	NZ-SH	5	
Otago Harbour	NZ-OH	8	
Kaka Point	NZ-KP	3	4
Bluff	NZ-BL	8	
Colac Bay	NZ-CO	3	5
Australia			
New South Wales			
Mona Vale	AU-MV	1	5
Sydney Harbour	AU-SY	1	
Shell Harbour	AU-SH	1	5
Dolphin Point	AU-DP		5
Guerrilla Beach	AU-GB	6	5
Tathra	AU-TA	2	5
Merimbula	AU-ME	4	5
Eden	AU-ED	5	5
Victoria			
Mallacoota	AU-ML	6	5
Cape Conran	AU-CC	4	5
Port Welshpool	AU-PW		5
Walkerville	AU-WK	4	5
Skenes Creek	AU-SK	5	5
Port Fairy	AU-PF	3	5
Portland	AU-PO		5
Tasmania			
Bicheno	AU-BI		5
Pirates Bay	AU-PB		5
South Australia			
Port MacDonnell	AU-PM	3	
Robe	AU-RB		5
Port Elliot	AU-PE		5
Victor Harbour	AU-VH	5	
Normanville	AU-NM		5
Edithburgh	AU-EB	1	5

Table 2 Haplotype frequencies for (a) Australian and (b) New Zealand samples of *Austrolittorina*. Haplotypes are represented by rows, and sample sites by columns

	East of Wilsons Promontory										West of Wilsons Promontory									
Hap/site	MV	SH	DP	GB	TA	ME	ED	ML	CC	PW	BI	PB	WK	SK	PF	PO	RB	PE	NM	EB
(a) Australia																				
TA2					1															
BI2											1									
BI4											1									
common 2	3	4	4	5	3	3	1	2	4	3	1	2			1	4	1			1
BI1											1									
PW5										1										
RB4																	1			
WK4													1							
RB2																	1			
TA1					1															
common 3	1	1					2	1												
PF1															1					
ME4						1														
PW3										1										
PE5																		1		
common 7								1						4	1			1		1
PF2															1					
common 6																			1	2
PO4																1				
common 5							2	1				2	4	1			1	1	4	1
RB1																	1			
DP2			1																	
common 4						1						1						2		
CC1									1											
PF3															1					
MV1	1																			
BI5											1									

	North Island				South Island			
Hap/site	PA	MB	AH	OM	KA	LA	KP	CO
(b) New Zealand								
CO5								1
KA2					1			
common 1	5	5	5	5	4	5	4	3
CO4								1

the other six were detected at multiple sampling locations ('common 2–common 7'; Table 2). The most common haplotype, 'common 2', was detected 42 times (frequency 0.42), incorporating 16 of 20 Australian sites. Moreover, it was recorded 35 times east of Wilsons Promontory (frequency 0.58) vs. seven times to the west (0.18). Haplotype 'common 5', by contrast, was abundant west of Wilsons Promontory (0.30) but rare to the east (0.07). Similarly, 'common 7' showed evidence of east–west disjunction, as it was detected seven times in western samples (frequency 0.18) vs. just once in the east (0.02) (Table 2).

In contrast to the mtDNA COI diversity evident in Australia (above), 39 specimens of NZ *A. antipodum* yielded just four haplotypes (GenBank accession numbers DQ837002–05) which were closely related to one another (0.2–0.3%). Thirty-six of the NZ specimens yielded a single common haplotype, 'common 1' (frequency 0.92; Fig. 3a), whereas the other three NZ haplotypes were all singletons. Hence, based on our sampling, no phylogeographic structure was detected within NZ (Table 2).

Phylogenetic analysis resolved Australian and NZ haplotypes as strongly monophyletic assemblages (Fig. 3), with Australian *A. unifasciata* haplotypes sister to the Juan Fernández taxon *A. fernandezensis*, and NZ *A. antipodum* sister to the sympatric NZ congener *A. cincta*. NZ and Australian haplotypes were 16.5–17.8% divergent (mean 17.1%). The net sequence divergence between *A. unifasciata* and *A. antipodum* ($d_{xy} - 0.5(d_x + d_y)$) (Nei, 1987) was 16.7%.

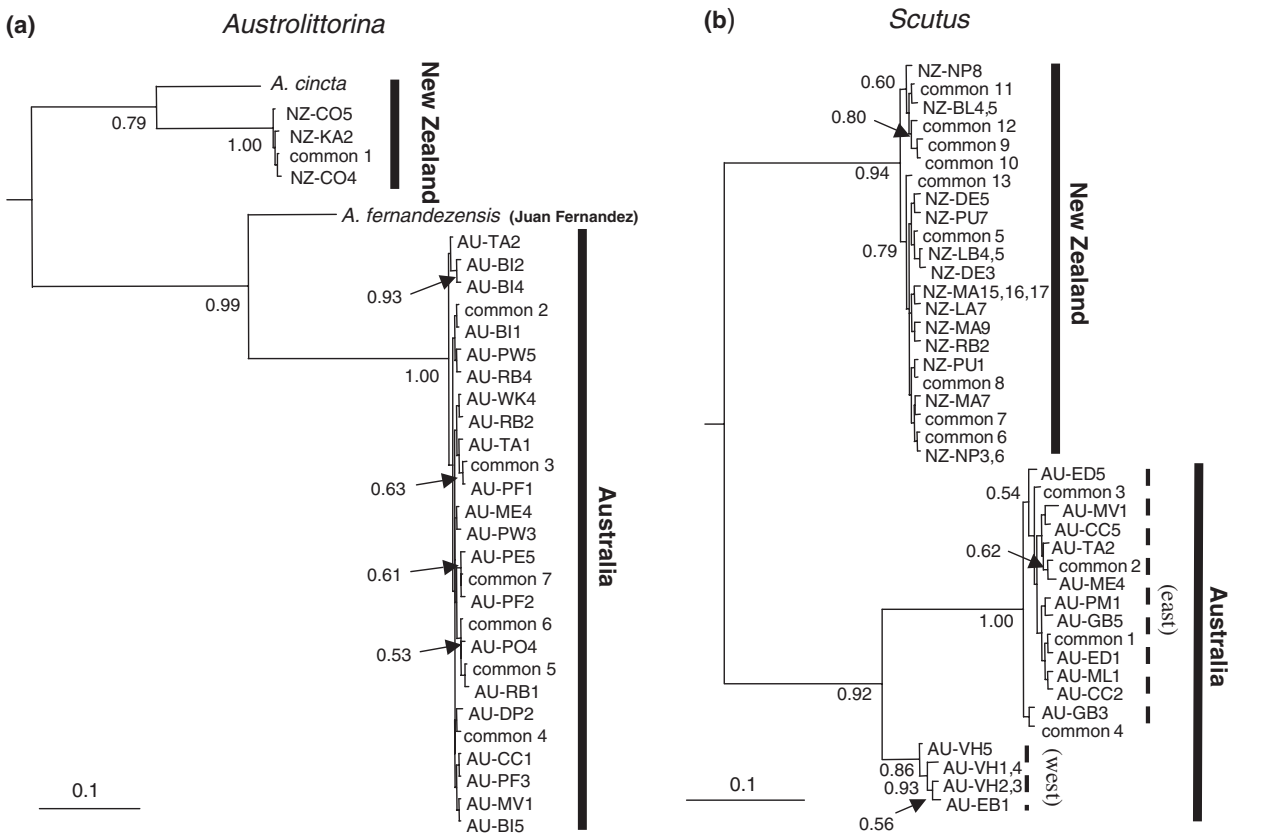

Figure 3 Bayesian phylogenetic relationships of Australian and New Zealand COI haplotypes of (a) *Austrolittorina* and (b) *Scutus*. Numbers below nodes are posterior probability values, and outgroup taxa are excluded for diagrammatic purposes. Sample codes are from Table 1, and haplotypes recorded from multiple localities are designated as 'common'.

AMOVA analysis detected significant geographic partitioning of genetic variation within the Australian region, with significant structure both among populations and among groups of populations. In particular, 8.1% of the variance was explained by grouping samples east and west of Wilson's Promontory (Table 4), an important regional palaeogeographic barrier (Waters *et al.*, 2005).

Scutus

Fifty-one Australian *Scutus* specimens yielded a monophyletic assemblage of 19 haplotypes (Appendices S1c, S1d, S1e in Supplementary Material; GenBank accession numbers DQ836934–52) (divergence range 0.2–8.3%; mean 3.0%). Phylogenetic analysis resolved a distinctive clade of four haplotypes ('west'; Fig. 3b) sister to other Australian haplotypes ('east'; Fig. 3b) (mean 7.1%). This divergent clade was restricted geographically to the two western-most sample sites (AU-EB, AU-VH). Fifteen of the Australian haplotypes were restricted to single sampling locations, whereas four were detected at multiple locations ('common 1'–'common 4'; Table 3). One haplotype, 'common 4', showed some additional evidence of east–west disjunction, as it was detected eight times in samples west of Wilsons Promontory (frequency 0.38), but was rare in the east (0.03). The most abundant haplotype, 'common 1', detected at 12 of 15 Australian sites, had a frequency of 0.47 to the east of Wilsons Promontory vs. 0.29 to the west (Table 3).

One hundred and three NZ *Scutus* samples yielded a clade of 22 closely related haplotypes (GenBank accession numbers DQ836953–74) (0.2–0.8%; mean 0.4%), of which nine were detected at multiple localities ('common 5'–'common 13'; Fig. 3b). The most abundant haplotype ('common 5') was recorded at 15 of 17 sites, with an overall frequency of 0.34. Individual haplotypes differed by just one or a few 'silent' nucleotide substitutions, typically transitions at third codon positions (Appendix S1e in Supplementary Material).

Phylogenetic analysis resolved reciprocally monophyletic clades associated with NZ and Australia, with no shared or closely related haplotypes between continents (10.5–14.2% divergence; mean 12.4%). After accounting for within-clade diversity (see above), the net mtDNA divergence between NZ and Australian *Scutus* was 10.7%.

AMOVA analysis detected no significant hierarchical structuring of genetic diversity within NZ *Scutus*, but highly significant components of genetic variation were explained by east–west groupings of Australian *Scutus* haplotypes (Wilsons Promontory: 18–25% of variance; Coorong: 96%; Table 4).

Table 3 Haplotype frequencies for (a) Australian and (b) New Zealand samples of *Scutus*. Haplotypes are represented by rows, and sample sites by columns.

	East of Wilsons Promontory									West of Wilsons Promontory					
	MV	SY	SH	GB	TA	ME	ED	ML	CC	WK	SK	PF	PM	VH	EB
(a) Australia															
ED5							1								
common 3								1	1						
MV1	1														
CC5									1						
TA2					1										
common 2				2			1								
ME4						1									
PM1													1		
GB5				1											
common 1		1	1	2	1	3	2	3	1	1	3	1	1		
ED1							1								
ML1								1							
CC2									1						
GB3				1											
common 4								1		3	2	2	1		
VH5														2	
VH1														2	
VH2														1	
EB1															1

	North Island							South Island									
	PA	LB	DE	ON	MA	NP	PU	CB	RB	KA	CA	LA	SH	OH	KP	BL	CO
(b) New Zealand																	
NP8						1											
common 11						5					1			1		1	
BL4																2	
common 12												1			1		
common 9							1										1
common 10					1	1											
common 13		1			4		1			1							1
DE5			1														
PU7							1										
common 5	1	1	2	1	8	4	3	3		2	1	2		2	1	3	1
LA4		2															
DE3			1														
MA15					3												
LA7												1					
MA9					1												
RB2									1								
PU1							1										
common 8						1							1	1		1	
MA7					1												
common 7		1								2		1	1	1	1		
common 6		1				2			2	2	1	2	3	3		1	
NP3						2											

Table 4 AMOVA results showing geographic differentiation associated with regional groupings of *Austrolittorina* and *Scutus* samples. For each grouping, the associated percentages of among-group variance, within-group variance, and associated probabilities of non-differentiation are listed (significant values in bold). Values in parentheses are for analyses repeated after the deletion of the 'west' Australian clade of *Scutus* haplotypes. New Zealand sample groupings (north/south of upwelling) are based on Ayers & Waters (2005).

Taxon	*Austrolittorina*		*Scutus*	
Hierarchical grouping	Variance	*P*	Variance	*P*
Australia				
East vs. west of Wilsons Promontory				
Among groups	**8.09%**	**0.002**	**18.14% (24.75%)**	**< 0.001 (0.002)**
Among samples within groups	**12.30%**	**< 0.001**	**68.68%** (−2.12%)	**< 0.001** (0.635)
East vs. west of Coorong				
Among groups	−1.65%	0.400	**96.48%**	**< 0.001**
Among samples within groups	**21.55%**	**< 0.001**	**0.30**	**0.030**
New Zealand				
North Island vs. South Island				
Among groups	0.40%	0.121	3.66%	0.056
Among samples within groups	−3.33%	0.952	0.38%	0.330
North vs. south of upwelling				
Among groups	0.40%	0.121	2.56%	0.151
Among samples within groups	−3.33%	0.952	1.02%	0.212

DISCUSSION

Southern biogeography

Sanmartin & Ronquist's (2004) overview of austral biogeography concluded that southern botanical interrelationships emphasized the importance of trans-Tasman dispersal. Indeed, Tasmania and NZ, themselves geographically isolated for *c.* 80 Myr, share at least 200 plant species (Jordan, 2001). By contrast, Sanmartin & Ronquist's (2004) analysis of zoogeographic pattern produced results more consistent with vicariant explanations. The extent to which the 'southern Gondwanan pattern' applies to NZ animals remains in doubt, however, pending further genetic analyses (see Waters & Craw, 2006).

In this study we have shown that two morphologically conserved southern gastropod taxa exhibit substantial divergence between Australia and NZ. It is important, therefore, to consider vicariant (e.g. Gondwanan separation 80 Ma) vs. dispersalist (e.g. post-Oligocene colonization of NZ) explanations for these findings. Discrimination of such hypotheses requires molecular calibrations based on geological data (e.g. dated fossils, island formation, habitat fragmentation) correlated with cladogenesis. Here we implement fossil-based calibrations for molluscs (Williams *et al.*, 2003) along with calibrations based on the Panama Isthmus closure (Hellberg & Vacquier, 1999; Marko, 2002).

Austrolittorina divergence

Williams *et al.* (2003) concluded that the distinctive 'blue' *Austrolittorina* species [*A. unifasciata* (Australia), *A. antipodum* (NZ), and *A. fernandezensis* (Juan Fernández)] represent a paraphyletic assemblage. Their finding was based on just one sample per taxon. Our current data, based on a more intensive sampling effort, strongly support their findings. We concur that the large divergence detected between 'blue' species (listed above) contrasts strikingly with the fact that they 'are so similar in morphology that they have in the past been classified as subspecies' [Williams *et al.* (2003); see Reid & Williams (2004) for a more recent assessment of morphological variation].

The phylogenetic affinity detected between eastern Pacific (Juan Fernández) and western Pacific (Australasia) taxa, to the exclusion of mainland South American taxa (see Reid & Williams, 2004), is intriguing. A similar biogeographical pattern has recently been documented for kelpfish taxa (Burridge *et al.*, 2006), and also for fishes and seaweeds in general (Santelices, 1992; Pequeño & Lamilla, 2000). Overall, the affinities of Juan Fernández and Desventuradas island biotas suggest that (counter-current) westward marine dispersal (e.g. 550 km from Chile) is extremely rare, whereas eastward dispersal (e.g. > 8000 km from Australasia) is relatively important.

Using a fossil-based calibration for *Littoraria* COI, Williams *et al.* (2003) estimated that Australian (*A. unifasciata*) and NZ taxa (*A. antipodum* and *A. cincta*) diverged 23–44 Ma (based on one sequence per taxon). It must be underlined that this finding depends on the accuracy of the molecular calibration applied. If the calibration substantially overestimates divergence rates, the NZ vs. Australia split could be consistent with vicariance. Alternatively, if the calibration is an underestimate (as Williams *et al.*, 2003 argued), the divergence of *A. antipodum* and *A. cincta* could conceivably reflect colonization of

NZ subsequent to Oligocene marine inundation (LeMasurier & Landis, 1996; Campbell & Landis, 2003).

Under strict vicariance, we would predict deeply divergent, reciprocally monophyletic mtDNA clades associated with now-distinct continents derived from Gondwana (see Waters & Roy, 2004). Although *Austrolittorina* exhibits a phylogeographic pattern consistent with this prediction, the implementation of published molluscan calibrations favours post-Gondwanan gene flow. This divergence date should be reassessed if and when more refined molluscan calibrations become available.

Scutus divergence

The deep divergence between Australian vs. NZ *Scutus* COI haplotypes suggests a considerable period of isolation, and this result is supported by divergent sequences at a nuclear locus (histone H3; Eason, unpublished data). *Scutus* first appears during the Eocene of NZ's fossil record (Fleming, 1979), around 40 Ma. This predates the Oligocene drowning (LeMasurier & Landis, 1996) thought to have eliminated much – possibly all – of NZ's terrestrial 'Gondwanan' biota (Pole, 1994; McGlone, 2005; Waters & Craw, 2006) (although we note that the impact of this event on coastal species remains undetermined). *Scutus* shells lack the synapomorphic character states required for species discrimination – hence the taxonomic uncertainty regarding the status of Australian vs. NZ populations. Moreover, it is very difficult to assign fossil *Scutus* to extant taxa. We therefore lack reference points for *Scutus* mtDNA calibration. However, if we implement the molluscan COI calibrations derived from the Panama Isthmus vicariance (0.7–2.4% per Myr; Hellberg & Vacquier, 1999; Marko, 2002) [or the littorinid calibration of Williams *et al.* (2003)], it seems clear that the Australia–NZ divergence (10.7%) reflects post-Oligocene trans-Tasman dispersal.

Trans-Tasman dispersal

In summary, neither *Austrolittorina* nor *Scutus* samples provide evidence of recent or ongoing trans-Tasman dispersal, a finding that contrasts with a similar mtDNA study recently conducted on *Nerita* (Waters *et al.*, 2005). It should be noted, however, that *Nerita* has a larval phase extending for 5–6 months. Similarly, several other taxa that possess long-lived planktonic larvae, for example *Dicathais*, *Chamaesipho* (Waters, unpublished data), *Jasus* (Ovenden *et al.*, 1992), *Nemadactylus* (Burridge & Smolenski, 2003), and *Galaxias* (Waters *et al.*, 2000), also show some evidence of recent or ongoing dispersal. The substantial trans-Tasman differentiation observed for *Austrolittorina* and *Scutus* therefore suggests that their planktotrophic larval phases (perhaps about 1 month for the former species; Williams *et al.*, 2003) are insufficiently long to facilitate dispersal across the Tasman Sea. Indeed, Chiswell *et al.*'s (2003) simulation-based study suggests that, in the absence of rafting, a period of several months is required for even a low probability of successful transit in this region. Future studies of larval life history may help to shed additional light on the dispersive capabilities of these gastropod taxa.

Intracontinental genetic structure

The finding that both gastropod taxa sampled here exhibit significant partitioning of genetic variation either side of Wilsons Promontory (southern Australia; AMOVA: Table 2), but not within NZ, is consistent with the findings of Waters *et al.* (2005) for another widespread coastal gastropod (*Nerita*). Although the east–west Australian partitioning observed in the current study is far less marked than that previously detected for *Nerita*, it may be consistent with the role of Wilsons Promontory as a palaeogeographic barrier (i.e. a landbridge connection between Tasmania and mainland Australia during historical low-sea-level stands). Indeed, recent studies of dispersive marine taxa have suggested that the genetic signatures of historical barriers to gene flow may persist long after the barriers themselves have disappeared (Benzie & Williams, 1997; Dawson, 2001; Waters *et al.*, 2005).

The marked phylogenetic structure detected within Australian *Scutus* (Fig. 3b) represents an east–west split either side of South Australia's Coorong region (Fig. 1), an extensive sandy area devoid of the rocky habitat required for *Scutus*. It should be noted that this region is several hundred kilometres west of Wilsons Promontory, the site of east–west disjunction in other gastropod taxa (*Nerita*; Waters *et al.*, 2005). Based on the present sampling, it is not clear whether this *Scutus* phylogeographic break is associated with the existing Coorong ecological 'gap' (Edgar, 1986), contemporary temperature gradients (e.g. see O'Hara & Poore, 2000), or historical isolation in the Great Australian Bight region (see Waters & Roy, 2003; Waters *et al.*, 2004). Additional research is required in order better to characterize this phylogeographic break and to assess its broader biological and taxonomic significance.

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REFERENCES

Altekar, G., Dwarkadas, S., Huelsenbeck, J.P. & Ronquist, F. (2004) Parallel metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics*, **20,** 407–415.

Ayers, K.L. & Waters, J.M. (2005) Marine biogeographic disjunction in central New Zealand. *Marine Biology*, **147,** 1045–1052.

Bennett, I. & Pope, E.C. (1953) Intertidal zonation of the exposed rocky shores of Victoria, together with a rearrangement of the biogeographical provinces of temperate Australian shores. *Australian Journal of Marine and Freshwater Research*, **4,** 105–159.

Benzie, J.A.H. & Williams, S.T. (1997) Genetic structure of giant clam (*Tridacna maxima*) populations in the west Pacific is not consistent with dispersal by present-day ocean currents. *Evolution*, **51,** 768–783.

Booth, J.D. & Ovenden, J.R. (2000) Distribution of *Jasus* spp. (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment. *Marine Ecology Progress Series*, **200,** 241–255.

Burridge, C.P. & Smolenski, A.J. (2003) Lack of genetic divergence found with microsatellite DNA markers in the tarakihi *Nemadactylus macropterus*. *New Zealand Journal of Marine and Freshwater Research*, **37,** 223–230.

Burridge, C.P., Meléndez, R. & Dyer, B.S. (2006) Multiple origins of the Juan Fernández kelpfish fauna, and evidence for frequent and unidirectional dispersal of cirrhitoid fishes across the South Pacific. *Systematic Biology*, **55,** 566–578.

Campbell, H.J. & Landis, C.A. (2003) New Zealand awash. *New Zealand Geographic*, **2003,** 6–7.

Casey, S.P., Hall, H.J., Stanley, H.F. & Vincent, A.C.J. (2004) The origin and evolution of seahorses (genus *Hippocampus*): a phylogenetic study using the cytochrome *b* gene of mitochondrial DNA. *Molecular Phylogenetics and Evolution*, **30,** 261–272.

Cernohorsky, W.O. (1977) A study of *Scutus antipodes* Montfort (Gastropoda: Fissurellidae). *Auckland Museum Conchology Bulletin*, **2,** 18–24.

Chiswell, S.M., Wilkin, J., Booth, J.D. & Stanton, B. (2003) Trans-Tasman sea-larval transport: is Australia a source for New Zealand rock lobsters? *Marine Ecology Progress Series*, **247,** 173–182.

Dawson, M.N. (2001) Phylogeography in coastal marine animals: a solution from California? *Journal of Biogeography*, **28,** 723–736.

Dempster, T. & Kingsford, M.J. (2004) Drifting objects as habitat for pelagic juvenile fish off New South Wales, Australia. *Marine and Freshwater Research*, **55,** 675–687.

Donald, K.M., Kennedy, M. & Spencer, H.G. (2005) Cladogenesis as the result of long-distance rafting events in Pacific topshells (Gastropoda: Trochidae). *Evolution*, **59,** 1701–1711.

Edgar, G.J. (1986) Biogeographical processes in the southern hemisphere marine environment. *Actas del segundo congreso sobre algas marinas Chilenas* (ed. by R. Westermeier), pp. 29–46. Universidad Austral de Chile, Valdivia.

Fell, H.B. (1962) West-wind drift dispersal of echinoderms in the southern hemisphere. *Nature*, **193,** 759–761.

Fleming, C.A. (1979) *The geological history of New Zealand and its life*. Auckland University Press, Auckland, New Zealand.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3,** 294–299.

Hellberg, M.E. & Vacquier, V.D. (1999) Rapid evolution of fertilization selectivity and lysine cDNA sequences in teguline gastropods. *Molecular Biology and Evolution*, **16,** 839–848.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, **17,** 754–755.

Jordan, G.J. (2001) An investigation of long-distance dispersal based on species native to both Tasmania and New Zealand. *Australian Journal of Botany*, **49,** 333–340.

Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16,** 111–120.

LeMasurier, W.E. & Landis, C.A. (1996) Mantle-plume activity recorded by low-relief erosion surfaces in West Antarctica and New Zealand. *Geological Society of America Bulletin*, **108,** 1450–1466.

Marko, P.B. (2002) Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the Isthmus of Panama. *Molecular Biology and Evolution*, **19,** 2005–2021.

McGlone, M.S. (2005) Goodbye Gondwana. *Journal of Biogeography*, **32,** 739–740.

Nei, M. (1987) *Molecular evolutionary genetics*. Columbia University Press, New York, NY.

O'Hara, T.D. & Poore, G.C.B. (2000) Patterns of distribution for southern Australian marine echinoderms and decapods. *Journal of Biogeography*, **27,** 1321–1335.

Okusu, A., Schwabe, E., Eernisse, D.J. & Giribet, G. (2003) Towards a phylogeny of chitons (Mollusca, Polyplacophora) based on combined analysis of five molecular loci. *Organisms Diversity and Evolution*, **3,** 281–302.

Ovenden, J.R., Brasher, D.J. & White, R.W.G. (1992) Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia. *Marine Biology*, **112,** 319–326.

Pequeño, G. & Lamilla, J. (2000) The littoral fish assemblage of the Desventuradas Islands (Chile) has zoogeographical affinities with the Western Pacific. *Global Ecology and Biogeography*, **9,** 431–437.

Pole, M. (1994) The New Zealand flora – entirely long-distance dispersal? *Journal of Biogeography*, **21,** 625–635.

Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14,** 817–818.

de Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution*, **20,** 68–73.

Reid, D.G. (2002) The genus *Nodilittorina* von Martens, 1897 (Gastropoda: Littorinidae) in the eastern Pacific Ocean, with

a discussion of biogeographic provinces of the rocky-shore fauna. *Veliger*, **45,** 85–169.

Reid, D.G. & Williams, S.T. (2004) The subfamily Littorininae (Gastropoda: Littorinidae) in the Southern Hemisphere: the genera *Nodilittorina*, *Austrolittorina* and *Afrolittorina*. *Records of the Australian Museum*, **56,** 75–122.

Rosen, D.E. (1978) Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, **27,** 159–188.

Rosewater, J. (1970) The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. *Indo-Pacific Mollusca*, **2,** 417–506.

Sanmartin, I. & Ronquist, F. (2004) Southern hemisphere biogeography inferred by event-based models: plant vs. animal patterns. *Systematic Biology*, **53,** 216–243.

Santelices, B. (1992) Marine phytogeography of the Juan Fernandez Archipelago: a new assessment. *Pacific Science*, **46,** 438–452.

Schneider, S., Kueffer, J.M., Roessli, D. & Excoffier, L. (2000) *Arlequin, Version 2.000: A software for population genetic data analysis*. Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland.

Swofford, D.L. (1998) *Phylogenetic analysis using parsimony (and other methods) PAUP*4.0b10*. Sinauer Associates, Sunderland, MA.

Waters, J.M. & Craw, D. (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology*, **55,** 351–356.

Waters, J.M. & Roy, M.S. (2003) Marine biogeography of southern Australia: phylogeographical structure in a temperate sea-star. *Journal of Biogeography*, **30,** 1787–1796.

Waters, J.M. & Roy, M.S. (2004) Out of Africa: the slow train to Australasia. *Systematic Biology*, **53,** 18–24.

Waters, J.M., Dijkstra, L.H. & Wallis, G.P. (2000) Biogeography of a southern hemisphere freshwater fish: how important is marine dispersal? *Molecular Ecology*, **9,** 1815–1821.

Waters, J.M., O'Loughlin, P.M. & Roy, M.S. (2004) Cladogenesis in a starfish species complex from southern Australia: evidence for vicariant speciation? *Molecular Phylogenetics and Evolution*, **32,** 236–245.

Waters, J.M., King, T.M., O'Loughlin, P.M. & Spencer, H.G. (2005) Phylogeographic disjunction in abundant high-dispersal littoral gastropods. *Molecular Ecology*, **14,** 2789–2802.

Williams, S.T., Reid, D.G. & Littlewood, D.T.J. (2003) A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution*, **28,** 60–86.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Variable nucleotide positions distinguishing closely related COI haplotypes of (a and b) *Austrolittorina* and (c to e) *Scutus*. Dots indicate matches with the first (reference) sequence. Numbers indicate nucleotide position in the associated sequence alignment.

This material is available as part of the online article from: http://www.blackwell-synergy.com/10.1111/j.1365-2699.2006/01615.x (This link will take you to the article abstract).

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BIOSKETCHES

Jonathan Waters is a lecturer in zoology and genetics. His research program focuses on the biogeography and evolution of the Southern Hemisphere marine and freshwater biota. Current projects are centred on the use of freshwater vicariant events to calibrate molecular clocks, and the importance of macroalgae as facilitators for oceanic rafting.

Janelle Eason's MSc research investigated systematics and phylogeography of *Scutus*; **Graham McCulloch's** BSc (Hons) project tested for phylogeographic signal in *Austrolittorina*.

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