Journal of Biogeography (J. Biogeogr.) (2017) 44, 217–229

Journal of Biogeography

ORIGINAL ARTICLE

An overview of Australia's temperate marine phylogeography, with new evidence from high-dispersal gastropods

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ABSTRACT

Aim We provide an overview of the location and ages of coastal phylogeographical breaks in southern Australian planktonic dispersers, and test the hypothesis that the absence of such breaks in some species is an artefact of insufficient resolution of genetic markers when such breaks evolved comparatively recently.

Location Temperate coastal Australia.

Methods We generated a large (> 1500 individuals) data set from rapidly evolving microsatellite markers for two codistributed Australian coastal gastropods, and compared it with mitochondrial DNA data. Both study species, the snail *Nerita atramentosa* and the limpet *Siphonaria diemenensis*, have long planktonic dispersal phases, and neither taxon exhibits substantial regional genetic structure on the basis of mitochondrial DNA. We tested for the presence of genetic structure by means of AMOVA, Bayesian clustering (STRUCTURE) and iterated realloction (FLOCK).

Results There was no compelling evidence for the existence of more than one evolutionary lineage in either species.

Main conclusions Discrepancies in the phylogeographical structuring of co-distributed intertidal taxa cannot be attributed to insufficient marker resolution for the two species considered here, and likely reflect a combination of abiotic and biotic factors that include porous dispersal barriers, life history and species age/history. It appears that contemporary oceanography does not explain the presence of phylogeographical breaks, but may serve to maintain breaks that evolved earlier. Deep genetic divergence in some of the previously studied coastal invertebrates suggests that these could be cryptic species, in which case competitive exclusion may play a role in constraining species biogeography.

Keywords
biogeography, dispersal, microsatellites, mitochondrial DNA, molluscs, planktonic larvae, population connectivity

INTRODUCTION

Genetic studies on marine organisms conducted in recent decades have rejected the idea (e.g. Caley *et al.*, 1996; Eckman, 1996) that there are few barriers to connectivity in the sea. Genetic discontinuities between regional clusters within species (phylogeographical breaks, which may be evident on the basis of either phylogenetic monophyly or differences in allele frequencies) are very common, even in species with theoretically high dispersal capabilities (e.g. Waters *et al.*, 2005; Doubleday *et al.*, 2009; Teske *et al.*, 2011).

Molecular dating indicates that phylogeographical breaks shared by co-distributed species did not all evolve contemporaneously, but instead have multiple independent origins, with most of the spatially congruent breaks identified originating throughout the Pliocene and Pleistocene (Ayre *et al.*, 2009; Teske *et al.*, 2013; Mmonwa *et al.*, 2015; Table 1). These epochs were characterized by climate oscillations (alternating glacial and interglacial phases) during which changes in global

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doi:10.1111/jbi.12783

sea levels (Fisher *et al.*, 2010), and the associated alterations in hydrography (Bostock *et al.*, 2006; Luër *et al.*, 2009) and habitat availability (Toms *et al.*, 2014), may have repeatedly resulted in the formation of similar dispersal barriers.

Given the ubiquity of phylogeographical breaks in coastal habitats, and the considerable amount of time available for these to evolve, it is puzzling that some species that disperse by means of planktonic larvae have phylogeographical breaks, whereas co-distributed species with similar and often potentially lower dispersal potential exhibit apparent panmixia (e.g. Ayre *et al.*, 2009; Teske *et al.*, 2014a). Moreover, many high-dispersal species have phylogeographical breaks across environmental features that are assumed to present only modest barriers to gene flow, such as areas of occasional cold-water upwelling (Teske *et al.*, 2011), weak river discharge (Ridgway *et al.*, 1998) and coastal dunefields (Teske *et al.*, 2006; Hidas *et al.*, 2007). These phenomena are usually attributed to unexpected discrepancies between expected and realized dispersal (e.g. Taylor & Hellberg, 2003; Ayre *et al.*, 2009). Physical factors, such as oceanography or habitat continuity, may thus be insufficient to explain coastal phylogeographical breaks, and a greater focus would need to be placed on the role of biological factors, such as larval behaviour, competition, predation or species-specific tolerance ranges to environmental variables. Studying these factors is considerably more challenging, and their roles would have to be assessed individually for each species.

However, before a definite conclusion concerning the role of abiotic factors in driving and maintaining genetic structure can be reached, it is necessary to thoroughly assess the possibility that numerous phylogeographical breaks are in fact present, but could not be detected because previously generated molecular data sets that were mostly based on single-locus data from the mitochondrial genome (mtDNA) (Colgan, 2015), were not sufficiently informative.

Despite the global escalation of phylogeographical surveys using multilocus DNA data (Beheregaray, 2008; Garrick

Table 1 Phylogeographical breaks identified in temperate Australian marine organisms with a planktonic dispersal phase, and their approximate ages. Barrier codes correspond to those in Fig. 1.

Barrier	Species	Marker	*N*	Time of split (Ma)	References
B	*Aplodactylus* spp.	mtDNA Cyt*b*[P] & COI[P]	1,1	7.8–11.2	Burridge (2000)
B[1]	*Lasaea australis*	mtDNA COIII[P]	4,8	13.1–13.4	Li *et al.* (2013)
		mtDNA 16S[P]	41,66	(not dated)	
		nuDNA ITS2[P]	19,27	(not dated)	
C, E, F	*Catomerus polymerus*	mtDNA COI[P]	23,11	1.1–1.9	York *et al.* (2008)
		mtDNA CR[P]	20,12	(not dated)	
		nuDNA Microsatellites[A]	399[5]	(not dated)	
C	*Meridiastra* spp.[2]	mtDNA COI[P]	17,11	2.1–2.4	Waters *et al.* (2004)
C	*Scutus* spp.	mtDNA COI[P, A]	6,45	(not dated)	Waters *et al.* (2006)
D or E	*Nemadactylus* spp.	mtDNA Cyt*b*[P] & COI[P]	1,1	2.7–3.8	Burridge (2000)
E	*Austrolittorina unifasciata*	mtDNA COI[P, A]	50,50	(not dated)	Waters *et al.* (2006)
E	*Catomerus polymerus*	mtDNA COI[P, A]	23,21	0.2–0.5	Ayre *et al.* (2009)
E	*Catostylus mosaicus*	mtDNA COI	6,6	*c.* 1.4	Dawson (2005)
		nuDNA ITS1	7,5	(not dated)	
E	*Cellana tramoserica*	mtDNA COI[P, A]	23,25	0.2–0.6	Ayre *et al.* (2009)
E	*Coscinasterias muricata*	mtDNA COI[P]	4,2	0.2–0.3	Waters & Roy (2003)
E	*Donax deltoides*	nuDNA Microsatellites[A]	111[5,6]	(not dated)	Miller *et al.* (2013)
E	*Meridiastra calcar*	mtDNA COI[P, A]	25,19	0.2–0.3	Ayre *et al.* (2009)
E	*Meridiastra* spp.[3]	mtDNA COI[P]	19,11	2.1–2.4	Waters *et al.* (2004)
E	*Scutus* spp.	mtDNA COI[P, A]	21,30	(not dated)	Waters *et al.* (2006)
E	*Plaxiphora albida*	mtDNA COI[P, A]	16,12	0.4–11.6	Ayre *et al.* (2009)
F[4], G	*Durvillea potatorum*[4]	mtDNA COI[P]	107[5]	(not dated)	Fraser *et al.* (2009)
		cpDNA *rbc*L[P]	77[5]	(not dated)	
F	*Pyura* spp.	mtDNA COI[P]	245,44	(not dated)	Rius & Teske (2013)
		nuDNA ANT intron[P]	142,76	(not dated)	
G	*Lasaea australis*	mtDNA COIII[P]	2,6	11.7–12.0	Li *et al.* (2013)
		mtDNA 16S[P]	39,27	(not dated)	
		nuDNA ITS2[P]	13,14	(not dated)	
G	*Nerita* spp.	mtDNA COI[P, A]	38,49	5.0–6.0	Waters *et al.* (2005)
G	*Octopus maorum*	nuDNA Microsatellites[A]	93,35	(not dated)	Doubleday *et al.* (2009)

[1]Geographical position differed for different markers; [2]western versus central lineages; [3]central versus eastern lineages; [4]eastern portion of the range only; [5]only total sample size provided (lineages do not have strict geographical divisions); [6]corresponding mtDNA data were not genetically structured; Ma = million years ago; mtDNA = mitochondrial DNA; nuDNA = nuclear DNA; cpDNA = chloroplast DNA. Presence of genetic breaks was identified on the basis of [P] = Phylogenetic monophyly (based trees or haplotype networks) or [A] = Allele frequency differences using *F*-statistics (F_{ST}, Φ_{ST}, AMOVA etc.); *N* = number of samples included per regional lineage.

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et al., 2015), research on marine phylogeographical breaks continues to be dominated by single-locus studies based on mtDNA (e.g. Haye *et al.*, 2014; Teske *et al.*, 2015a; Wright *et al.*, 2015; Table 1). The application of multi-locus genetic data sets has revealed discrepancies in the levels of introgression and lineage sorting between mtDNA and nuclear DNA (nuDNA) that has resulted in conflicting phylogeographical patterns in the same species (Toews & Brelsford, 2012). In many cases, this may be due to factors affecting the demographic history of the mitochondrial genome that may not necessarily reflect that of the population as a whole, including the replacement of the mitochondrial genome of one species with that of its sister species ('mitochondrial capture', Mee & Taylor, 2012), sex-biased dispersal (Petit & Excoffier, 2009) and non-neutrality (Scott *et al.*, 2011). Although there are numerous examples of genetic homogeneity on the basis of mtDNA in species that are genetically structured on the basis of nuDNA (e.g. Bester-van der Merwe *et al.*, 2011; Eble *et al.*, 2011; Miller *et al.*, 2013; Teske *et al.*, 2014a), the inverse has also been found (e.g. Larmuseau *et al.*, 2010; Daly-Engel *et al.*, 2012). Because of this, identifying concordance between different types of markers can be seen as strong evidence for the existence of a particular phylogeographical pattern.

One possible explanation for the lack of genetic structure in some species is that population differentiation has occurred too recently to be identifiable on the basis of mtDNA sequence data, which presents a well-documented challenge to genetics-based species delineations (Meyer & Paulay, 2005). If phylogeographical breaks in co-distributed species have the same underlying causes, but evolved at different times, then it is possible that the most recently evolved breaks are not yet detectable with mtDNA sequence data. This will then create the impression that the species in question are not affected by coastal features that represent significant dispersal barriers to other species. If this is correct, then genetic markers that evolve at a faster rate and have greater power to detect departures from panmixia (Waples & Gaggiotti, 2006), such as microsatellites (where novel mutations can be directly observed in families; Weber & Wong, 1993), should reveal signatures of dispersal barriers where mtDNA data do not. The number of microsatellite-based studies in planktonic dispersers from temperate coastal Australia is small, but in those that have employed both mtDNA and microsatellites, the latter marker always revealed genetic structure even if the former did not (York *et al.*, 2008; Miller *et al.*, 2013; Table 1). A potential additional shortcoming of many previous studies was the effect of small sample sizes (Table 1). This is not a problem when genetic structure is based on distinct regional allele clusters (an approach used by the majority of studies; Table 1). In contrast, lineage sorting can be expected to be incomplete in recently diverged lineages (Meyer & Paulay, 2005), but allele frequencies may already differ, resulting in significant values of F_{ST} (Wright, 1965) and similar statistics. These statistics are sensitive to stochastic variation in the data, and this effect can be reduced by increasing sample sizes (Kalinowski, 2005).

Here, we present an overview of the ages and locations of phylogeographical breaks on the temperate Australian coast, and explore why such breaks are absent in some coastal species. Specifically, we tested the hypothesis that species that show no broad phylogeographical differentiation on the basis of mtDNA data sets of moderate size should exhibit subtle population genetic differentiation across previously reported marine dispersal barriers on the basis of much larger microsatellite data sets. Specifically, we generated microsatellite data from two widely distributed rocky shore invertebrates from temperate southern Australia, each of which is represented as a single mtDNA lineage throughout the region (Waters *et al.*, 2005; Colgan & da Costa, 2013). The finding of the present study that neither species shows differentiation concordant with the region's previously reported barriers confirms that phylogeographical breaks are indeed present in only some of the region's coastal species, and suggests that contemporary oceanography is insufficient to explain why historical breaks are maintained in only some of the species. This discrepancy can only be explained by gaining a better understanding of the biological factors that uniquely impact each of these species.

MATERIALS AND METHODS

Literature review

The coastline of temperate southern Australia is a particularly useful study system to assess the effect of physical dispersal barriers on genetic structure because phylogeographical breaks have been reported at numerous locations (Fig. 1). It comprises several geological and oceanographic features that define genetic subdivisions in many coastal species (e.g. Ayre *et al.*, 2009; Colgan, 2015). These features are often associated with the boundaries between the region's biogeographical provinces (Fig. 1): Flindersia on the south and south-west coast, Peronia in the east, and Maugea, in the extreme south-east comprising Tasmania and southern Victoria (Bennett & Pope, 1953). In terms of the assumed mechanisms driving the genetic divergence of coastal populations, these features may differ considerably in terms of their strength as dispersal barriers. Perhaps the most significant barrier has been identified on the south-eastern coast, where the connection of the island of Tasmania with the mainland via the Bassian Isthmus (Waters *et al.*, 2005), coupled with a cold-water barrier resulting from a northward shift of the subtropical convergence that reached south-western Tasmania (Sikes *et al.*, 2009), may have significantly prevented gene flow between Flindersia and Maugea. Other, potentially more porous, barriers include extended areas of habitat that is unsuitable for the settlement of most coastal species, including dunefields (Waters *et al.*, 2006; Hidas *et al.*, 2007) and the deep-water barrier represented by the Bass Strait (Ward & Elliott, 2001). Although these are contemporary barriers, it is plausible that phylogeographical

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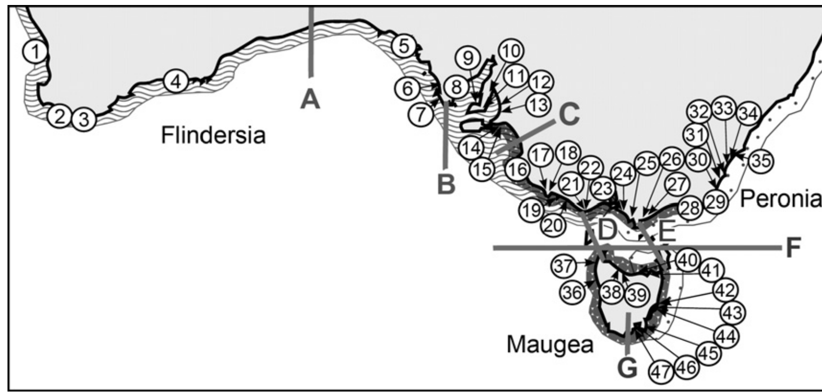

Figure 1 A map of temperate southern Australia depicting the location of sampling sites (white circles) and putative marine dispersal barriers (grey bars). Site numbers correspond to those in Table S1. Putative barriers represent: A: Great Australian Bight; B: Eyre Peninsula; C: Coorong dunefield; D: Cape Otway; E: Wilson's Promontory; F: Bass Strait; G: Zeehan Current – East Australian Current convergence.

breaks detectable on the basis of mtDNA data were driven by similar barriers that were present in the same locations during previous interglacial phases.

A search of the available literature on the ages of phylogeographical breaks and their locations in temperate coastal Australian species with high dispersal potential was conducted using the Web of Science (Thomson Reuters), with various combinations of the following search terms: Australia*, phylogeograph*, biogeograph*, genetic structure, coastal, marine, estuarine, invertebrate, plankton, molecular dating and divergence time. Passively dispersing direct developers were excluded, as these are often structured in the absence of any dispersal barriers (Teske *et al.*, 2011). We then compiled a table (Table 1) in which we listed at which location a particular phylogeographical break was identified and, if available, when the evolutionary lineages separated by a putative dispersal barrier diverged. To determine whether any trends in larval duration were evident (e.g. whether or not some phylogeographical breaks were present only in low-dispersal species), we searched the literature for information on larval development of the species included in the table.

Study species

The coastal molluscs *Siphonaria diemenensis* Quoy & Gaimard, 1833 and *Nerita atramentosa* Reeve, 1855 were selected as study species because both have wide distribution ranges that span much of the temperate Australian coastline, and both exist as single mtDNA lineages throughout their ranges (Waters *et al.*, 2005; Colgan & da Costa, 2013). *Siphonaria diemenensis* occurs from the region west of the Great Australian Bight (GAB) to the south-east coast, including Tasmania (Fig. 1). The range of *N. atramentosa* extends from Western Australia to the south-east coast, although it occurs only sporadically beyond Wilson's Promontory and on the Tasmanian east coast (Fig. 1), where it is replaced by its sister species, *N. melanotragus* (Waters, 2008; Waters *et al.*, 2014).

Generation of genetic data

To determine whether large data sets from polymorphic microsatellites can identify phylogeographical breaks that are not evident on the basis of smaller data sets from a more slowly evolving mitochondrial gene, we supplemented previously generated sequences from a portion of the cytochrome oxidase *c* subunit I (COI) gene with new sequence data (see Table S1 in Supporting information) following the approach used in Teske *et al.* (2015a). The purpose of generating additional data was to ensure that sites throughout the ranges of both species were represented (see Table S1). As the lengths of sequences from different sources differed, all sequences were trimmed to a length of 510 bp (*S. diemenensis*) or 561 bp (*N. atramentosa*).

Microsatellite data (see Table S1 in Appendix S1) were generated by genotyping 13 microsatellite loci for each species (*S. diemenensis: Side01, Side03, Side04, Side05, Side07, Side09, Side12, Side13, Side15, Side17, Side18, Side19* and *Side20; N. atramentosa*: *Neat01*, *Neat02*, *Neat03*, *Neat04*, *Neat05*, *Neat07*, *Neat09*, *Neat10*, *Neat12*, *Neat14*, *Neat16*, *Neat18* and *Neat19*) as described in Sandoval-Castillo *et al.* (2012a,b). The program MICRO-CHECKER 2.2.3 (Van Oosterhout *et al.*, 2004) was used to test for scoring errors caused by null alleles, stuttering or allele dominance, specifying a 95% confidence interval and 10,000 runs. Tests for linkage disequilibrium and deviation from Hardy–Weinberg equilibrium were performed in GENEPOP 4 (Rousset, 2008), with 1000 dememorizations and 100,000 interactions. Sequential Bonferroni corrections were applied when conducting multiple statistical tests (Rice, 1989). Non-amplification (> 40%) was a problem in *Neat18*, and significant departures from Hardy–Weinberg equilibrium were identified in loci *Neat02* and *Neat16* for at least 10 localities. These three loci were excluded from subsequent analyses.

Tests for genetic structure

We employed tests for genetic structure that fall into three categories: (1) Analysis of Molecular Variance (AMOVA); (2) Bayesian clustering tests and (3) iterated reallocation. The latter two tests require multilocus data and were only used for the microsatellites.

AMOVA

Population genetic differentiation among localities was tested using hierarchical analysis of molecular variance (AMOVA;

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Excoffier *et al.*, 1992) in ARLEQUIN 3.5 (Excoffier & Lischer, 2010). In order to test the possible effects of historical and contemporary biogeographical barriers on genetic structure, we tested up to seven biogeographical grouping hypotheses (Fig. 1), each comprising two groups of sites present on either side of a putative dispersal barrier. Significance was tested using 1000 permutations, and *F*-statistics (F_{CT} for microsatellites and Φ_{CT} for mtDNA data) were estimated by computing distance matrices. For the mtDNA COI sequence data, we specified the following models of nucleotide evolution, as determined using the Bayesian information criterion (BIC; Schwarz, 1978) in MEGA 6 (Tamura *et al.*, 2013): *S. diemenensis*: Tamura 3-parameter model (Tamura, 1992) with a shape parameter α of the gamma distribution of 0.2; *N. atramentosa*: Tamura-Nei model (Tamura & Nei, 1993) with $\alpha = 0.39$, which is the model most similar to the Hasegawa-Kishino-Yano model (Hasegawa *et al.*, 1985) selected by MEGA, which is not implemented in ARLEQUIN. We explored whether or not genetic structure found using AMOVA on mtDNA data of *S. diemenensis* (see Results) could be explained by the existence of regional clusters of haplotypes. To this end, a median-joining haplotype network was constructed in NETWORK 4.613 (Bandelt *et al.*, 1999).

In addition, pairwise F_{ST} values (Wright, 1965) were calculated in GenAlEx 6.5 (Peakall & Smouse, 2012) for the more informative microsatellite data only. *P*-values were based on 999 permutations, and the B-Y false discovery rate method was applied to account for multiple comparisons (Benjamini & Yekutieli, 2001).

Bayesian clustering

Bayesian clustering was performed using the program STRUCTURE 2.4 (Pritchard *et al.*, 2000; Falush *et al.*, 2003). We assumed admixture, allele frequencies correlated between populations, and sampling locations specified as priors. In addition to treating each site as a distinct population, and letting the program determine the best-supported combination without any *a priori* assumptions, we also treated groups of sites as distinct populations, with different populations separated by previously reported dispersal barriers. This approach can considerably improve the likelihood that genetic structure is identified when levels of genetic divergence between sites are low (Hubisz *et al.*, 2009). As different assignments of sites into groups were possible depending on whether or not Tasmanian sites were grouped separately (Barrier F) or assigned to western and eastern mainland groups (Barrier G), we performed two STRUCTURE runs per species: *Nerita atramentosa*, seven groups (including Barrier F): group 1 (sites 2–4), group 2 (sites 5–7), group 3 (sites 8–10, 12, 14), group 4 (site 19), group 5 (sites 21, 25), group 6 (site 27) and group 7 (sites 36–38, 41, 43 and 45); *N. atramentosa*, six groups (including Barrier G): Groups 1–3 identical; group 4 (sites 19, 36 and 37), group 5 (sites 21, 25, 38 and 41) and group 6 (sites 43 and 45). *Siphonaria diemenensis*, six groups (including Barrier F): group 1 (sites 5 and 6), group 2 (sites 8, 9, 12 and 14), group 3 (site 18), group 4 (sites 21 and 25), group 5 (site 27) and group 6 (sites 36-38, 41, 43 and 45); *S. diemenensis*, five groups (including Barrier G): Groups 1 and 2 identical; group 3 (sites 18, 36 and 37), group 4 (sites 21, 25, 38 and 41) and group 5 (sites 43 and 45); note that for both species, site 27 was not grouped with sites 43 and 45 in the arrangement including Barrier G because it is not strongly influenced by the East Australian Current (EAC), which defines the area east of Barrier G. Ten independent runs were performed for each value of *K*, each with an initial burn-in of 10^5 steps followed by 10^6 Markov chain Monte Carlo iterations. The results of the replicate runs were merged in STRUCTURE HARVESTER (Earl & von Holdt, 2012), and both the highest mean Pr(X/k) (Pritchard *et al.*, 2000) and the highest second order rate of change of Ln[Pr(X/k)] (ΔK; Evanno *et al.*, 2005) were assessed to determine the best-supported number of distinct populations. CLUMPAK (Kopelman *et al.*, 2015) was then used to confirm that the same individuals were assigned to the specified clusters in all 10 replicate runs, and to produce a Q-matrix reporting the most likely ancestry (Q) of each individual.

Iterative reallocation

The iterative reallocation approach implemented in FLOCK 3.1 (Duchesne & Turgeon, 2012) represents an alternative approach to identifying clusters of sites for multilocus data sets. This program randomly partitions individuals into clusters and then repeatedly re-allocates individuals to clusters until homogeneity within clusters and differentiation between clusters are maximized. FLOCK is considered to provide more accurate allocation of individuals to clusters, and more reliable estimates of *K*, than STRUCTURE (Duchesne & Turgeon, 2012). The program was run using default settings, with 50 runs of 20 iterations for each value of *K* (ranging from 2 to the total number of sampling sites in a particular data set). The best value of *K* was determined using ‘plateau analysis’ as described in Duchesne & Turgeon (2012).

RESULTS

Temperate Australian phylogeographical breaks

A survey of the literature on phylogeographical breaks in temperate coastal Australia ($n = 14$ studies) revealed that these breaks are in most cases shared by multiple taxa (Table 1). The best-studied of the regions in which phylogeographical breaks have been reported is the area that includes the south-east Australian mainland and the island of Tasmania, where numerous studies have identified east–west breaks in the vicinity of Wilson’s Promontory (Barrier E in Fig. 1). In species whose ranges extend to Tasmania, the western lineages tend to be associated with the Zeehan Current (ZC) and the eastern lineages with the EAC, with phylogeographical breaks located at the ZC–EAC

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convergence in southern Tasmania (Barrier G in Fig. 1; Waters, 2008).

Comparatively few studies have focused on the remainder of the temperate southern coastline, a finding consistent with a recent review of population genetic surveys of Australian marine organisms (Pope et al., 2015). Our understanding of phylogeographical patterns in this region is thus limited. One common finding that has emerged is the existence of phylogeographical breaks in South Australia that separate 'Maugean' (south-eastern) and 'Flindersian' (western) lineages. In several studies, this break was identified across the Coorong (Barrier C in Fig. 1), an extensive sandy area in South Australia that lacks rocky shore habitat, while in others, it was found near the Eyre Peninsula (Barrier B). Additional breaks proposed in this study are the GAB (Barrier A) and the Bass Strait (Barrier F).

A trend that clearly emerges is that congruent breaks have evolved repeatedly over a period of millions of years, with divergence times ranging from the Middle Pleistocene to the Miocene. There was no compelling evidence that phylogeographical breaks are more likely to be present in species with comparatively short larval durations. For example, the planktonic larval durations of *Austrolittorina unifasciata* (Williams et al., 2003), *Coscinasterias muricata* (Barker, 1978), *Donax deltoides* (King, 1975) and *Lasaea australis* (Ó Foighil, 1989) are comparable to the 1-month larval duration of *S. diemenensis* (Creese, 1980), while the life span of the medusa stage of the jellyfish *Catostylus mosaicus* (Pitt, 2000) exceeds the 6-month larval duration of *N. atramentosa* (Underwood, 1975). In contrast, *Cellana tramoserica* completes larval development within only 48 h (Anderson, 1962).

Tests for genetic structure

AMOVAs identified genetic structure in two cases in *S. diemenensis*, but for different regional population groupings (Table 2). For the mtDNA data, genetic structure was found across the Coorong (Barrier C in Fig. 1), whereas the microsatellite data identified samples from either side of Bass Strait (Barrier F) as distinct populations. No phylogeographical breaks were found in *N. atramentosa* for either marker. A haplotype network (see Fig. S1 in Appendix S2) constructed from the mtDNA sequences of *S. diemenensis* collected on either site of the Coorong indicates that the significant genetic structure identified is not the result of the presence of distinct phylogroups on either side of the barrier. Instead,

Table 2 Analyses of molecular variance (AMOVA) testing for genetic structure among groups of sites located on either side of previously reported temperate Australian marine barriers. Only results for the highest hierarchical level are shown (groups of populations). Barrier codes and site numbers correspond to those in Fig. 1.

Species	Barrier	Genetic marker	Group 1	Group 2	% var.	Φ_{CT} or F_{CT}	P
Siphonaria diemenensis	B	MtDNA	6	8, 9, 12, 14	0.00	0.000	0.80
		µsats	5, 6	8, 9, 12, 14	0.39	0.004	0.14
	C	mtDNA	8, 9, 12, 14	17, 18, 20	6.02	0.060	0.03*
		µsats	8, 9, 12, 14	18	0.78	0.008	0.18
	D	mtDNA	17, 18, 20	21–25	2.89	0.029	0.38
		µsats	18	21, 25	0.00	0.000	1.00
	E	mtDNA	21–25	27–35	0.10	0.001	0.51
		µsats	21, 15	27	0.00	0.000	0.68
	F	mtDNA	21–25, 27	36, 37, 39–47	0.16	0.002	0.34
		µsats	21, 25, 27	36–38, 41, 43, 45	0.25	0.002	0.02*
	G	mtDNA	17, 18, 20, 36, 37	28–35, 42–47	0.00	0.000	0.71
		µsats	18, 36, 37	43, 45	0.17	0.002	0.18
Nerita atramentosa	A	mtDNA	1–4	5–7	0.00	0.000	0.43
		µsats	2–4	5–7	0.03	0.000	0.38
	B	mtDNA	5–7	8–15	0.00	0.000	0.75
		µsats	5–7	8–10, 13, 14	0.00	0.000	0.71
	C	mtDNA	8–15	16, 18, 19	0.00	0.000	0.37
		µsats	8–10, 13, 14	19	0.09	0.001	0.32
	D	mtDNA	16, 18, 19	21, 22, 25	0.74	0.007	0.40
		µsats	19	21, 25	0.00	0.000	1.00
	E	mtDNA	21, 22, 25	26, 27	0.40	0.004	0.49
		µsats	21, 25	27	1.29	0.013	0.34
	F	mtDNA	21, 22, 25–27	36–38, 41, 43, 45	1.35	0.013	0.23
		µsats	21, 25, 27	36–38, 41, 43, 45	0.06	0.001	0.26
	G	mtDNA	18, 19, 36, 37	43, 45	0.00	0.000	0.59
		µsats	19, 36, 37	43, 45	0.14	0.001	0.21

Barriers codes: A: Great Australian Bight; B: Eyre Peninsula; C: Coorong; D: Cape Otway; E: Wilson's Promontory; F: Bass Strait; G: Zeehan Current – East Australian Current convergence; mtDNA: mitochondrial DNA sequence data; µsats: microsatellite data; % var.: per cent variation; Φ_{CT}: F-statistic used for mtDNA and F_{CT}: F-statistic used for microsatellites.

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this result seems to be an artefact of a large number of rare haplotypes resulting in different haplotypes being represented on either side of the barrier. Only five of the 33 haplotypes identified were found in more than one individual, and three of these were present in both regions. Pairwise F_{ST} values revealed that the microsatellite data sets of both species were highly informative, with 85 out of 120 pairwise comparisons being significant after B-Y correction (71%) for *S. diemenensis*, and 72 out of 231 (31%) being significant for *N. atramentosa* (see Table S2 in Appendix S1).

STRUCTURE analysis identified the highest mean Pr(X/k) for $K = 1$ for both species and all combinations of sites (see Figs S2a and S2b in Appendix S2; groups of sites reflect the arrangements used for the AMOVA). The highest values of ΔK determined for the *S. diemenensis* data were identified for $K = 2$ (each site unique, i.e. 16 groups), $K = 3$ (6 groups) and $K = 4$ (5 groups) (see Fig. S3a in Appendix S2). For the *N. atramentosa* data, ΔK was highest for $K = 3$ (for 21 groups and 7 groups) and $K = 2$ (6 groups) (see Fig. S3b in Appendix S2). None of the individuals of either species could be assigned to a single cluster unequivocally using this approach. Instead, individuals differed in terms of the relative proportion of how much of their ancestry coefficient (Q) was assigned to a particular cluster. A barplot is shown in Fig. S4 (see Appendix S2); note that in this example, non-contiguous sites were grouped in the same cluster: Cluster 1 comprised sites 5 and 6 (located west of Barrier A), sites 18, 21 and 25 (located west of Barrier E, and east of the four sites assigned to Cluster 2, rather than sites 5 and 6) and site 27 (east of Barrier E).

Lastly, FLOCK analyses found no support for more than one cluster in either species. Plateau analysis revealed that not a single value of K (ranging from 2 to the maximum number of sites in a particular data set) had any plateaus (a plateau length ≥ 6 supports a particular value of K; Duchesne & Turgeon, 2012).

DISCUSSION

In this study, we (1) reviewed the available literature on phylogeographical breaks in temperate Australian marine organisms, and (2) assembled large, high-resolution population genetic data sets for two coastal invertebrate taxa, both of which are represented by monophyletic mtDNA lineages in temperate Australia. The fact that dated divergence events in most previous studies were ancient (Middle Pleistocene or older) gives credence to idea that mtDNA fails to identify congruent phylogeographical breaks that evolved, for example, during the Holocene. However, although the microsatellite data from the two high-dispersal gastropods contained sufficient signal not only to detect genetic differentiation between sites, but also to identify positive correlations between genetic and geographical distances (Teske *et al.*, 2015b), there was no compelling evidence that genetic structure was linked to *a priori* marine phylogeographical barriers identified in previous studies. Instead, our results suggest that such apparent 'barriers' have no effect on some taxa. The absence of phylogeographical breaks in some species cannot be attributed to insufficient genetic signal of mtDNA data to detect recently evolved regional genetic differentiation, and our study suggests that contemporary oceanography and other physical features that formed relatively recently (e.g. at the beginning of the present interglacial period) are not reliable proxies for phylogeography.

Ages of phylogeographical breaks

A survey of the literature of phylogeographical breaks revealed that these often considerably pre-date the age of the dispersal barriers that presently separate geographically isolated sister lineages (Table 1). Phylogeographic breaks in rocky shore or estuarine species are particularly striking when they are associated with coastal dunefields (e.g. Teske *et al.*, 2006; Hidas *et al.*, 2007). The long stretches of unsuitable habitat are unlikely to be the primary drivers of genetic divergence, as all the dunefields adjacent to rocky shores/estuaries were formed during the present interglacial period, and most probably in the last 10,000 years or less (Hesp & Short, 1999), whereas the phylogeographical breaks are much older (Benzie, 1999; Teske *et al.*, 2006; Li *et al.*, 2013). Also, it is difficult to explain why genetic discontinuities driven by the formation of land bridges during glacial phases, when sea levels were lower, are maintained after the demise of the former vicariant barriers (Waters, 2008). Again, molecular dating suggests that although glacial phases may explain the geographical structuring of divergent lineages, genetic divergence likely occurred long before the Last Glacial Maximum (Table 1).

Phylogeography of the study species

The results of tests for population genetic structure in the genetic data of *S. diemenensis* and *N. atramentosa* fall into two categories. STRUCTURE [using mean Pr(X/k)] and FLOCK supported the existence of a single population at a range-wide scale. In contrast, STRUCTURE (using ΔK) and AMOVA for *S. diemenensis* provided some support for the existence of regional groups of sites, although the latter approach identified genetic structure in different locations for the two markers. In the case of ΔK, sites were not grouped into geographically contiguous clusters, which suggests that these results may be an artefact of genetic structure arising from non-random gene flow, perhaps as a result of larval retention near natal sites and isolation by geographical distance (Banks *et al.*, 2007; Piggott *et al.*, 2008; White *et al.*, 2010; Coleman *et al.*, 2011; Teske *et al.*, 2015b). Simulation tests conducted by Duchesne & Turgeon (2012) indicated that ΔK often produces incorrect results, and it is possible that all the methods that supported the existence of more than one population suffered from type I error. In contrast, FLOCK is considered to be highly conservative; in cases where no structure exists or where the data are not sufficiently informative to identify

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clusters, this program will produce an 'undecided conclusion' rather than provide an incorrect result (Duchesne & Turgeon, 2012).

Discrepancies in phylogeographical patterns

While contemporary oceanography and coastal topography may limit gene flow between populations residing on either side of a porous dispersal barrier (Aguilar *et al.*, 2015), they may be insufficient to explain how the often deep phylogeographical breaks associated with these barriers evolved in the first place. For example, contemporary coastal dunefields are no more than *c.* 10,000 years old (Hesp & Short, 1999), yet they may separate sister taxa that have diverged at least a million years ago (Table 1). It therefore seems clear that explanations for biogeographical structuring of high-dispersal lineages should focus on the role of both historical factors in driving initial population divergence, and contemporary factors maintaining population structure.

Lack of genetic population structure is often interpreted as species dispersing readily across a marine barrier, whereas the presence of structure indicates that dispersal is constrained by unexpectedly high levels of larval retention (Taylor & Hellberg, 2003; Ayre *et al.*, 2009). The two species studied here both have high larval dispersal potential, with the larvae of *S. diemenensis* remaining in the water column for up to a month (Creese, 1980), and those of *N. atramentosa* even longer (Underwood, 1975). These planktonic phases should be sufficient to facilitate dispersal across known habitat discontinuities, such as the Coorong (Barrier C in Fig. 1). The presence of an mtDNA-based phylogeographical break detected with increased sampling in this study in the high-dispersal taxon *S. diemenensis* mirrors findings for two other temperate Australian invertebrate species with pelagic larval durations of several weeks: *Austrolittorina unifasciata* shows strong genetic structure across Wilson's Promontory (Waters *et al.*, 2006), and *Catomerus polymerus* has phylogeographical breaks across both Wilson's Promontory and the Coorong (York *et al.,* 2008). However, the fact that Barrier C in *S. diemenensis* was neither based on reciprocal monophyly of mtDNA haplotypes (see Fig. S1 in Appendix S2), nor was it confirmed by the microsatellite data (Table 2), suggests that at least some of the breaks identified in previous studies on the basis of allele frequency differences could be the artefacts of stochastic differences between the data sets of regional populations. Marine invertebrate populations tend to have high genetic diversity because of their large effective population sizes (DeWoody & Avise, 2000). Because of the large number of rare alleles present, methods that identify genetic structure on the basis of allele frequency differences (e.g. AMOVA) perform poorly when moderate sample sizes capture only a small fraction of the genetic diversity present (Kalinowski, 2005). As larval duration does not reliably predict the presence/absence of such differentiation patterns (Weersing & Toonen, 2009), we suggest that alternative factors, such as taxon age and competitive interactions among sister lineages (possibly cryptic taxa), might help to explain the maintenance of historical phylogeographical features in some taxa but not others.

Alternative explanations for phylogeographical breaks

An improved understanding concerning the biology and demography of the geminate lineages delineated by marine barriers is required to understand their persistence as geographical isolates in terms of the minimal exchange of migrants across the barrier. Species' life history is frequently invoked to explain the presence/absence of phylogeographical breaks, and most studies have found that low-dispersal species with direct development are more likely to exhibit genetic structure when planktonic dispersers do not (Sherman *et al.*, 2008; Pelc *et al.*, 2009; Teske *et al.*, 2014a; but see Ayre *et al.*, 2009). In the latter, realized dispersal distances may be strongly dependent on larval behaviour, and species whose larvae employ mechanisms that result in their retention near natal sites often settle close to their parent habitat (Shanks, 2009). Information on larval behaviour is available for few species, and although it is undoubtedly important, additional biological factors that explain both the historical evolution of phylogeographical breaks, and their subsequent maintenance, need to be considered.

In some cases, geminate lineages have subsequently been identified as distinct species (Teske *et al.*, 2009; Rius & Teske, 2013), including the two species of *Nerita* that are separated by Wilson's Promontory (Spencer *et al.*, 2007). The stochastic nature of phylogeographical breaks in both space and time suggests that the evolution of geminate sister species does not occur uniformly in all co-distributed species. During a period of isolation that affected the region's entire biota (e.g. the formation of the Bassian Isthmus barrier), novel mutations that eventually resulted in reproductive isolation would have randomly evolved in some species but not in others. Following the demise of the barrier, some populations would then have merged, while in those that have speciated, competitive or density-dependent interactions between sister taxa may help to explain their apparent inability to establish themselves in each other's ranges (Waters *et al.*, 2005, 2013; Fraser *et al.*, 2009). This effect is independent of both planktonic larval duration and larval behaviour.

In other cases, the apparent lack of gene flow across barriers may be explained by diversifying selection and fitness-related competition. In southern Africa, where biogeographical provinces are defined by sea-surface temperatures (Teske *et al.*, 2011), the maintenance of phylogeographical breaks is primarily explained by the different thermal tolerance ranges of the regional lineages of a particular species (Teske *et al.*, 2008; Papadopoulos & Teske, 2014). While corresponding physiological data are not available from temperate Australian species, thermal adaptation likely explains the distinctness of the Maugean lineages, as water temperatures around Tasmania and in the Bass Strait are typically cooler

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than those elsewhere (Banks *et al.*, 2007). This is illustrated by two sister taxa of the ascidian genus *Pyura* that were historically separated by Barrier F. While the Tasmanian *P. doppelgangera* has recently established itself in the range of its mainland sister species, *P. praeputialis*, it is only present in areas from which the latter was absent due to a lack of natural substrate, and occurs exclusively on artificial structures (Rius & Teske, 2013; Teske *et al.*, 2014b).

A factor that has received virtually no attention in the literature on temperate Australian phylogeographical breaks is the role of extinction. While climate oscillations are believed to be important drivers in the evolution of new biodiversity, the shifts in the location of biogeographical regions, and associated changes in habitat availability, can also result in the extinction of populations associated with specific marine bioregions (Teske *et al.*, 2013). The surviving taxon could then readily establish itself in the habitat of its former sister lineage. Climate-driven range expansions in coastal species are well documented in the fossil record (Kensley, 1985; Clark *et al.*, 2009), and it is feasible that post-glacial range expansions following the demise of a dispersal barrier may explain numerous cases of apparent panmixia across formidable barriers such as the Bassian Isthmus, including that identified in *S. diemenensis*. Unlike the region's two species of *Nerita*, this limpet does not comprise a western and an eastern lineage, despite a greater likelihood of divergence because of less connectivity among populations, as is evident from the higher levels of genetic structure.

CONCLUSION

Coastal phylogeographical breaks have received much attention in the recent literature (e.g. Pelc *et al.*, 2009; Teske *et al.*, 2011; Colgan, 2015), and it has become clear that the most common explanation for their existence (low-dispersal potential coupled with porous physical barriers) is insufficient to explain why such breaks are present in some species but not in others. Having established that the lack of genetic structure in some species is not an artefact of insufficient marker resolution or small sample sizes, we suggest that many contemporary dispersal barriers that on their own are unlikely to completely isolate regional sister taxa merely re-inforce genetic structure that evolved earlier. To gain a deeper understanding of phylogeographical breaks, future studies need to focus increasingly on the roles of competition, predation, diversifying selection and larval behaviour in maintaining genetic structure in coastal habitats.

ACKNOWLEDGEMENTS

We are grateful to Don Colgan (Australian Museum, Sydney) for sharing sequence data, to Tess Cole for helping with the sampling, and to three anonymous referees for their comments on earlier versions of this manuscript. This study was supported by the Australian Research Council (DP110101275 to Beheregaray, Möller and Waters) and the University of Johannesburg. Beheregaray also acknowledges support from an Australian Research Council Future Fellowship (FT130101068). The present paper is publication no. 57 of the Molecular Ecology Group for Marine Research (MEGMAR).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary tables.
Appendix S2 Supplementary figures.

BIOSKETCHES

The authors are interested in uncovering the drivers of marine biogeographical patterns in temperate Australia and South Africa.

Author contributions: L.B.B. and J.W. conceived the study and contributed to the writing of the paper; J.S-C. and P.R.T. collected the samples, and generated and analysed the data; P.R.T. led the writing of the paper; all authors read and approved the final version.

Editor: Luiz Rocha

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