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Gene flow across a major biogeographic barrier is not increasing under climate change for the barnacle *Catomerus polymerus*

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ABSTRACT: On the south-east coast of Australia, the impermeability of the Southeast Australian Biogeographic Barrier (SEABB) limits the dispersal of many intertidal taxa, but current flow across the SEABB is expected to be increasing under climate change. The surf barnacle *Catomerus polymerus* has extensive populations on either side of the barrier that both mitochondrial cytochrome *c* oxidase subunit I (mtCOI) sequence data and surveys using 4–6 microsatellite loci imply have been separated for millennia (>167 000 yr). Nevertheless, these data sets (based on collections from 2005–2012) also imply that there has been some recent dispersal across the SEABB. If trans-barrier migration is now possible, then in the absence of selection the differentiation of lineages should be eroded. Next-generation sequencing provides the opportunity to both better quantify levels of population differentiation attributable to the SEABB and to determine if there is regional selection. Our data (3801 single nucleotide polymorphisms) for individuals collected in 2019 within 3 eastern and 4 western sites support earlier reports of low population differentiation within eastern and western regions (F_{ST} < 0.021) and the strong regional separation of eastern and western lineages (F_{RT} = 0.23). Moreover, in contrast to earlier studies, we did not detect any putative migrants, with all individuals assigning most strongly to their sampling region. Most strikingly, analysis using BAYESCAN implied that 47 loci (1.24%) of our surveyed loci show evidence of significant regional diversifying selection, which implies that even if *C. polymerus* larvae are able to cross the barrier, they will be strongly disfavoured by selection.

KEY WORDS: Larval dispersal · Diversifying selection · Migration · Single nucleotide polymorphisms · SNPs · Gene flow · Southeast Australian Biogeographic Barrier

1. INTRODUCTION

Range limits of marine taxa, including those restricted by biogeographic barriers, are changing worldwide in response to climate change (Tracy et al. 2017, Fredston-Hermann et al. 2020, Pinsky et al. 2020). Climate change can directly affect processes of larval or adult dispersal through alteration of patterns of current flow and can alter the suitability of environmental conditions through changes, including but not restricted to, the thermal environment (Kumagai et al. 2018, Martins et al. 2019, Sanford et al. 2019). On the south-east coast of Australia, the Southeast Australian Biogeographic Barrier (SEABB) marks both the published range limit of many species (Bennett & Pope 1953, Knox 1963, O'Hara & Poore 2000, Hidas et al. 2007, Waters 2008) and the site of persistent genetic differentiation of regional populations of others (see Ayre et al. 2009 and references therein). The SEABB is a complex barrier. During periods of glacial maxima, it includes the physical barrier provided by the Bass Straight Isthmus, while during inter-glacials, it features the convergence zone of the south-flowing Eastern Australian Current

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(EAC) and east-flowing Zeehan Current. The SEABB is characterised by marked variation in sea surface temperatures (Cresswell 2000), and a long stretch of coastline, including Ninety Mile Beach and Corner Inlet, that lacks natural rocky shore (which greatly impacts habitat availability for intertidal taxa) (Fig. 1). To the north of the SEABB, water temperatures are higher and typically decline along a latitudinal gradient, although the magnitude of difference in SSTs across the SEABB varies with the extent of southward flow of the EAC and its pattern of eddy formation (Ridgway & Hill 2009). For benthic marine taxa, there is evidence of species recently extending their range southwards across the SEABB (Ling et al. 2009, Suthers et al. 2011, Ramos et al. 2014). This range expansion is attributed to greater southward flow of the EAC under climate change (Ridgway 2007, Ridgway & Hill 2009). The effects of the barrier on the genetic differentiation of taxa with benthic phases thought to be restricted to intertidal rocky shores are known to be variable (e.g. see Sherman et al. 2008, Ayre et al. 2009). However, there have been few if any tests for changes to contemporary patterns of dispersal and gene flow, and it is unclear if migration is opposed by regional variation in selective regimes.

The south-eastern Australian intertidal barnacle fauna may prove to be an important bellwether for change in the permeability of the SEABB. There are several intertidal barnacle species each with moderate pelagic larval duration (PLD) (Egan & Anderson 1988, 1989) that are considered to occur on either side of the SEABB (Edgar 2008), including *Tetraclitella purpurascens*, which appears able to disperse freely across the barrier (Ayre et al. 2009) and *Tesseropera rosea*, which has its published range limit to the north east of the SEABB but has been reported to form ephemeral populations in both Victoria and Western Australia (Jones 1990, Minchinton pers. comm.). Most interestingly, the surf barnacle *Catomerus polymerus* is considered to have an extensive range on either side of the SEABB (Edgar 2008), but genetic data suggest that gene flow across the barrier has not been possible until very recently. Mitochondrial cytochrome *c* oxidase subunit I (mtCOI) sequence data and limited nuclear, microsatellite DNA surveys (York et al. 2008, Ayre et al. 2009, Aguilar et al. 2015) demonstrated that *C. polymerus* actually represents distinct monophyletic eastern and western lineages that have been separate for >167 000 yr (Ayre et al. 2009). Interestingly, however, studies by York et al. (2008) and Aguilar et al. (2015) each found 1 individual with a western mtDNA haplotype within an eastern population, although Aguilar et al. (2015) reported that the microsatellite genotype of the potential migrant assigned to the eastern cluster. Aguilar et al. (2015) also found that the microsatellite genotypes of ~1% of 1113 adults and recruits assigned more strongly to the alternative region than to their region of collection, despite having local mtDNA haplotypes. Taken together, these findings from collections made by

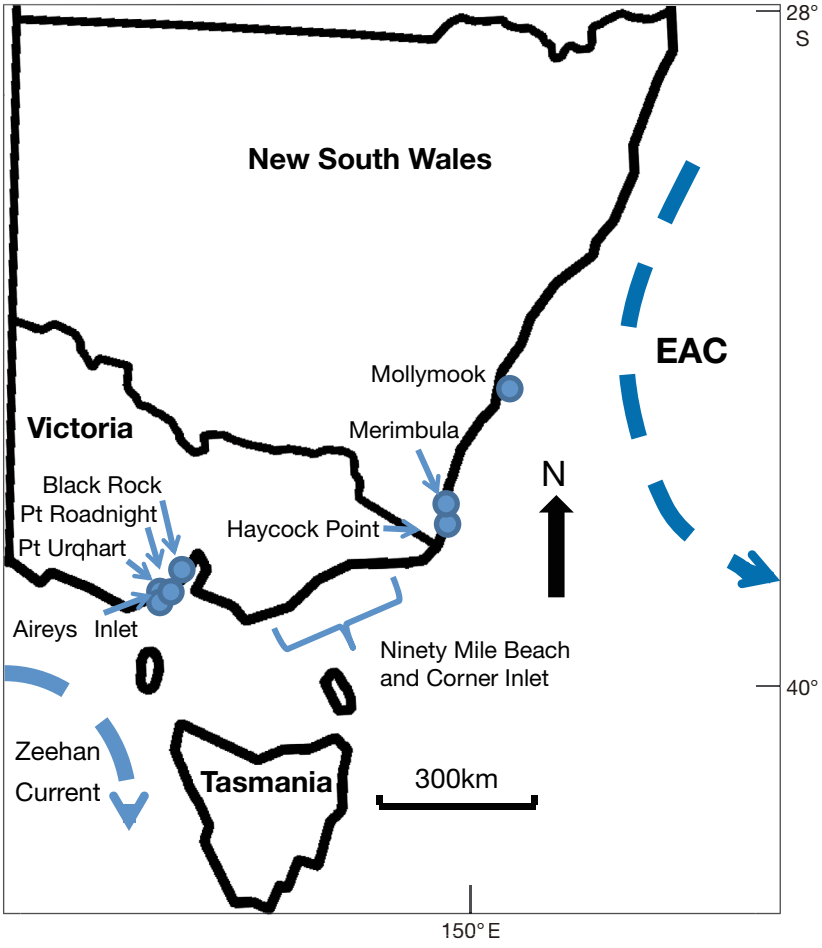

Fig. 1. Sampling locations for *Catomerus polymerus* to the east (Mollymook, Merimbula, Haycock Point) and west (Point Urqhart, Point Roadnight, Aireys Inlet, Black Rock) of the Southeast Australian Biogeographic Barrier. EAC: Eastern Australian Current

York et al. in 2005 and 2006 and Aguilar et al. in 2012 imply that, although they detected no clear first-generation migrants, there had been a small amount of recent, successful migration leading to introgression (Aguilar et al. 2015).

Although the capacity of taxa to disperse across the SEABB may primarily be determined by larval dispersal, successful migration/gene flow may be regulated by the capacity of taxa to respond to different biotic and abiotic selection pressures experienced both before and after settlement (Marshall et al. 2010, Sanford & Kelly 2011, Hargreaves et al. 2014). For marine taxa worldwide, variation in thermal environments appears strongly linked to species and population boundaries (Teske et al. 2019), but species ranges may also be shaped by variation in factors such as prey availability (Sanford et al. 2003, Sanford & Worth 2010). Moreover, several studies have indicated that selection may be restricting species or population spread beyond range limits or causing range contractions (e.g. Sanford & Kelly 2011, Stuart-Smith et al. 2017, Hereward et al. 2020), and in North America, the barnacle *Tetraclita rubescens*, which has undergone recent range expansion, appears limited by 'migration load', with high levels of gene flow preventing adaptation at the range edge (Dawson et al. 2010).

Next-generation sequencing technologies provide a powerful new approach to population genetic studies, allowing us to estimate genetic diversity and differentiation by looking across the whole genome. Single nucleotide polymorphisms (SNPs) can often provide better genome coverage and higher-quality data than microsatellites or mtDNA (Morin et al. 2004), providing better insight into the evolutionary and ecological processes that maintain the spatial distribution of populations and potentially the speciation of persistently separated lineages. In addition to providing increased power to estimate population genetic parameters, genome-wide sequencing provides the opportunity to identify genomic regions under selection. Genomic regions that have significantly increased or decreased differentiation among populations indicate they have likely been under diversifying or stabilising natural selection (Hohenlohe et al. 2010). F_{ST} (standardised genetic variance) outlier tests identify larger values of F_{ST} than expected by drift alone, to identify genes that have evolved under spatially divergent selection (Lotterhos & Whitlock 2014).

Here we used Diversity Array Technology's (DaRT) next-generation sequencing to generate SNP data, for collections made some 14 yr after the earliest collections by York et al. (2008), to better characterise the genetic structure of *C. polymerus* populations on either side of the SEABB. Specifically, we assessed the level of genetic differentiation and gene flow between populations on either side of the SEABB and estimated the number of loci displaying evidence of regionally divergent selection.

2. MATERIALS AND METHODS

2.1. Sample collection

We collected 75 adult *Catomerus polymerus* from 7 exposed rock platforms arrayed on either side of the SEABB, from Mollymook to Aireys Inlet (Table 1, Fig. 1). On each shore, we collected barnacles within an approximately 60 m^2 area in the mid-intertidal zone and preserved their tissue in absolute ethanol for subsequent DNA extraction.

Table 1. Sampling locations and diversity statistics for *Catomerus polymerus*. N: number of individuals; Poly: % polymorphic loci; H_o: observed heterozygosity; H_e: expected heterozygosity; F: fixation index (equivalent to F_{IS})

Region, site	Site code	N	% Poly	H_o ± SE	H_e ± SE	F ± SE
East						
Mollymook	MM	11	67.4	0.194 ± 0.003	0.217 ± 0.003	0.058 ± 0.006
Merimbula	MR	7	64.9	0.190 ± 0.003	0.226 ± 0.003	0.071 ± 0.006
Haycock Point	HP	10	69.9	0.195 ± 0.003	0.231 ± 0.003	0.097 ± 0.006
Mean			67.4	0.193 ± 0.001	0.225 ± 0.003	0.075 ± 0.006
West						
Point Urqhart	PU	12	86.1	0.220 ± 0.003	0.285 ± 0.003	0.173 ± 0.006
Point Roadnight	PR	12	86.5	0.228 ± 0.003	0.286 ± 0.003	0.148 ± 0.006
Aireys Inlet	AR	12	86.3	0.225 ± 0.003	0.283 ± 0.003	0.148 ± 0.006
Black Rock	BR	11	88.2	0.224 ± 0.003	0.286 ± 0.003	0.162 ± 0.006
Mean			86.8	0.224 ± 0.003	0.285 ± 0.003	0.158 ± 0.006

2.2. SNP genotyping

We generated genome-wide SNP data using a next-generation sequencing platform (DArTseq). DArT-seq technology is a combination of an amplified fragment length polymorphism (AFLP) *Pst*I-based complexity reduction, that enables the reproducible selection of a subset of DNA fragments from a whole genome, and Illumina sequencing, similar to restriction site-associated DNA sequencing (RAD-seq). Our genomic representations were generated following procedures described previously (Jaccoud et al. 2001, Kilian et al. 2012). Sequencing was carried out on a single lane of an Illumina HiSeq2000 to detect SNPs and processed using proprietary DArT analytical pipelines (DArTsoft 14).

We filtered the primary dataset at a stringent level to ensure that only high-quality markers were retained, and therefore genotypes were accurate. We filtered SNP loci by read depth, and excluded loci with an average read depth of <20 because for organisms with a high degree of heterozygosity, it is difficult to identify the genotypes for heterozygous SNP sites with low read coverage (Song et al. 2016). We excluded loci with a minor allele frequency of <0.05, because low-frequency SNPs can bias statistical analyses (Tabangin et al. 2009, Roesti et al. 2012). We also excluded loci with a reproducibility rate (the proportion of replicate assay pairs yielding the same marker score) of <0.99 to ensure marker scores were accurate.

In preliminary analyses, we experimented with filtering the dataset using different call rates. The call rate of each locus refers to the proportion of individuals that were genotyped for that particular locus, i.e. a call rate of >90% means that that locus was genotyped in >90% of individuals. With increasing genetic differences between any 2 samples, the number of loci in common diminishes, so filtering loci by call rate represents a trade-off between including loci with missing data vs. excluding potential variation. For the final dataset, we settled on a call rate of 80% because we did not want to maximise loci that could be scored accurately. Finally, we excluded 2 individuals that had >5% missing data, leaving 75 individuals in our analyses.

2.3. Genetic diversity, structure and gene flow

To measure genetic diversity, we estimated observed heterozygosity (H_o), expected heterozygosity (H_e) and F_{IS} using GenAlEx 6.503 (Peakall & Smouse 2006, 2012). To analyse population genetic structure and estimate patterns of gene flow, we used a combination of approaches. First, we conducted a PCA in the 'adegenet' package in R (Jombart 2008) to visualise spatial structure. Second, we calculated pairwise F_{ST} (Weir & Cockerham 1984) between populations, with p-values based on 999 permutations in GenAlEx, and we estimated gene flow under the island model of Wright (1969) as $N_em = (1/4F_{ST}) - 1$, where N_e is the effective population size and m is the proportion of migrants per generation. Third, we conducted a hierarchical analysis of molecular variance (AMOVA) partitioning variation among regions in GenAlEx, using 999 permutations to assess significance. Finally, we performed a structure analysis using the R program 'ParallelStructure' (Besnier & Glover 2013) (an R package that distributes parallel runs of the population genetics program STRUCTURE on multicore computers; Besnier & Glover 2013), on the CIPRES Science Gateway v3.3 portal (Miller et al. 2010). To determine the number of genetic clusters in the dataset, we set the optimal number of clusters (K) to range from 1 to 7, with 5 independent runs for each value of K, using no prior location information, correlated allele frequencies, admixture and a burn-in length of 50 000 followed by 200 000 Markov chain Monte Carlo iterations. We determined K in the dataset using the online resource StructureSelector (Li & Liu 2018), where we examined ΔK and LnPK (Evanno et al. 2005), and the alternative statistics medmedk, medmeak, maxmedk and maxmeak (Puechmaille 2016).

2.4. Detection of candidate loci under selection

To identify outlier loci that were potentially under selection, we screened all loci using BAYESCAN 2.1 (Foll & Gaggiotti 2008), which implements a Bayesian model-based approach and provides a more conservative approach to detecting outliers than other programs such as Arlequin and Lositan (Pérez-Figueroa et al. 2010). Analyses were conducted using a sample size of 5000 with a thinning interval of 10, with 60 000 iterations including a burn-in of 10 000 runs. We took a highly conservative approach to identifying loci under selection and increased the prior odds for the neutral model from 10 (the default number in Bayescan) to 100, to reduce the likelihood of detecting false positives (Lotterhos & Whitlock 2014). We also decreased the q-value threshold to define loci under selection as those loci with q < 0.01 (Lotterhos & Whitlock 2014).

3. RESULTS

3.1. Estimation of diversity and differentiation of sites/populations

The DaRT proprietary pipeline produced 82 545 high-quality SNPs, of which 3801 met our more stringent criteria and were retained in our final dataset. After filtering the data, as described above, the average level of missing data per individual was 3.7 %. Our estimates of genetic and genotypic diversity provided by H_o and H_e and the magnitude of departures from Hardy-Weinberg equilibrium expectation F were highly consistent within geographic regions but in all cases differed significantly between regions (t-tests, $p < 0.001$). Both diversity and heterozygous deficiency were greater in the west (Table 1).

Our analyses revealed that, as expected, there was little differentiation among populations within regions but striking and consistent differentiation between populations from the 2 regions. Within regions, our estimates of pairwise F_{ST} revealed some slight (≤0.023, mean = 0.011), though in 3 cases statistically significant ($p \leq 0.05$), differentiation, while in contrast all pairwise F_{ST} values comparing eastern and western sites were large (≥0.2, mean = 0.24) and always significant (p = 0.01) (Table 2). Under Wright's (1969) Island model, these comparisons indicate considerable gene flow within regions ($N_em > 21$) but little gene flow between regions ($N_em \leq 0.8$).

3.2. Clustering of individuals and identification of putative migrants

Conventional F-statistics treat all individuals from a site or region as members of those respective subpopulations or populations even though a site may contain immigrant genotypes. In order to test for the presence of putative immigrants, we therefore asked whether all individuals within each of the sets of eastern and western sites formed discrete regional clusters using PCA and Bayesian clustering analysis in STRUCTURE. Our PCA analysis revealed 2 completely discrete regional clusters (Fig. 2). Individuals within the less genetically variable eastern collections clustered more tightly than those within the western collections, but in each case there was considerable overlap of groups from individual sites. This pattern was also supported by the STRUCTURE plots, which also showed that at the highest level of genetic structure, the regions formed 2 discrete genetic clusters (Fig. 3). Indeed, using StructureSelector, we found that 2 clusters, corresponding to the groups of eastern and western populations, was the most strongly supported outcome, although the Puechmaille method (Puechmaille 2016) suggests that there are 3 clusters (with additional complexity present within the western region). Most critically, STRUCTURE analysis indicated that every individual assigned most strongly to its region of collection, and 53 of the 75 specimens were assigned to their region of collection with p > 0.95 (although 1 individual displayed a largely intermediate genotype, assigning to its region of collection with p = 0.55).

Table 2. *Catomerus polymerus*. Pairwise F_{ST} values (below diagonal) and significance values (above diagonal) showing significant values ($p < 0.05$) in **bold**. Eastern sites are shaded in dark blue and western sites are shaded in light blue. Site codes as in Table 1

	MM	HP	MR	AR	PU	PR	BR
MM	0.000	0.050	0.090	**0.010**	**0.010**	**0.010**	**0.010**
HP	0.023	0.000	0.230	**0.010**	**0.010**	**0.010**	**0.010**
MR	0.016	0.005	0.000	**0.010**	**0.010**	**0.010**	**0.010**
AR	0.267	0.237	0.239	0.000	0.450	0.440	**0.040**
PU	0.257	0.229	0.229	0.000	0.000	0.430	0.120
PR	0.272	0.243	0.245	0.000	0.000	0.000	**0.030**
BR	0.226	0.195	0.196	0.013	0.010	0.021	0.000

3.3. Screening for evidence of regional diversifying selection

Using the filtered dataset of 3801 loci, our genome-wide scans for loci under selection identified 47 loci as being under strong diversifying selection, i.e. they

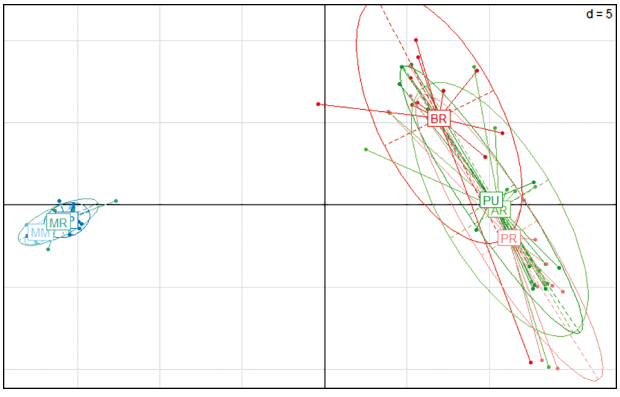

Fig. 2. PCA calculated from individual pairwise genotypic distance for *Catomerus polymerus* from 3801 loci. Individuals are coded according to population (see Table 1 for population codes). Blue cluster includes MM, HP and MR; red/green cluster includes AR, PU, PR and BR. Note that the Haycock Point label is partially obscured

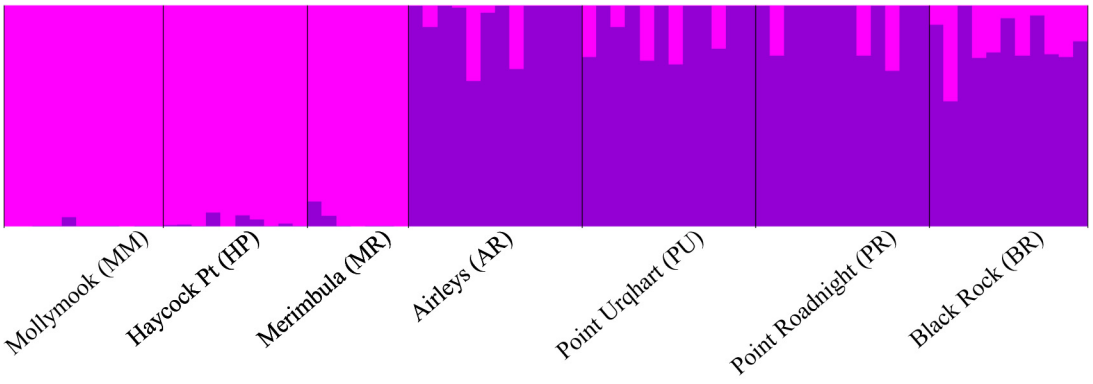

Fig. 3. Results of hierarchical clustering analysis for *Catomerus polymerus* when K = 2 as implemented in STRUCTURE with no *a priori* information on location and using 3801 loci. Each individual is shown as a column, showing the membership coefficients for each K, and the populations are indicated below the plots

had a positive (indicative of diversifying selection) q-value of <0.01.

4. DISCUSSION

Our DaRT sequencing survey of almost 4000 SNPs in the surf barnacle *Catomerus polymerus* provides the best estimate of the genetic differentiation of its eastern and western populations and provides the first indication that migration of this species across the SEABB may be limited by diversifying selection. Similar effects of regional selection have been shown to limit successful migration across marine biogeographic barriers and to limit range expansion for several species (Sanford et al. 2003, Sanford & Worth 2010, Teske et al. 2019, Galindo et al. 2021), including the barnacle *Tetraclita rubescens* (Dawson et al. 2010).

Analysis of our data largely supports the population genetic patterns previously reported for *C. polymerus* in studies using variation at 4 to 6 microsatellite loci and mtCOI sequence data (York et al. 2008, Ayre et al. 2009, Aguilar et al. 2015). All studies have found little differentiation among populations arrayed on either side of the SEABB, implying that *C. polymerus* can disperse widely, and eastern and western populations are strongly intermixed by gene flow. Conversely, the 2 regions separated by the SEABB are highly differentiated, as predicted by the lack of gene flow. However, in partial contrast to the earlier studies, our estimate of regional differentiation F_{RT} = 0.32 was almost twice the value reported by York et al. (2008) and Aguilar et al. (2015). Moreover, analysis of our data using both PCA and STRUCTURE revealed completely discrete eastern and western clusters, and within STRUCTURE, every individual genotyped assigned most strongly to its regional cluster (53 with p > 0.95 and most with p > 0.99). This contrasts slightly with the studies by York et al. (2008) and Aguilar et al. (2015), who reported small numbers of individuals with apparently migrant or hybrid nuclear DNA (15 of 1093; Aguilar et al. 2015) and 2 of 154 individuals with migrant mtDNA. However, this contrast could reflect our smaller sample size, which decreases the probability of detecting rare migrants. In the absence of detectable migrants, estimates of gene flow should be treated with caution, but a crude estimation derived from F_{ST} using Wright's (1969) island model implies that there is <1 trans-barrier migrant per generation. This regional differentiation is consistent with previous phylogeographic studies using mtCOI sequence data, which show that the deeply differentiated eastern and western lineages of *C. polymerus* exhibit reciprocal monophyly and are estimated to have evolved separately over hundreds of thousands of years (York et al. 2008, Ayre et al. 2009).

The persistent separation of eastern and western lineages of *C. polymerus* may appear surprising given that other intertidal taxa with apparently similar PLD (13–20 d), including the barnacles *Tesseropera rosea* and *Tetraclitella purpurascens,* are clearly able to cross the barrier in sufficient numbers to either establish ephemeral populations (*T. rosea*; T. Minchinton pers. comm.) or prevent genetic differentiation of eastern and western populations (*T. purpurascens*) (Jones 1990, Ayre et al. 2009). However, this contrast could reflect either variation in dispersal ability, a difference in the capacity of migrants to cope with differing selective environments on either side of the

barrier or a combination of the 2 factors. *C. polymerus* differs from *T. rosea* and *T. purpurascens* with respect to at least 1 key life history character that should affect its dispersal. *C. polymerus* spawns predominantly in winter, whereas both *T. rosea* and *T. purpurascens* are summer spawners (Anderson & Anderson 1985, Egan & Anderson 1988, 1989; but see Wisely & Blick 1964), and oceanographic modelling implies that dispersal across the SEABB should only be possible for planktonically dispersing species that spawn during summer (Aguilar et al. 2019). The same modelling also suggests that even summer dispersal will be limited unless PLDs exceed 30 d. It is important to note that the published estimates of PLD are based on single laboratory studies, for barnacles from 1 location, while PLDs are known to vary within species (Cowen 1991, Bay et al. 2006) and may be only roughly estimated by laboratory studies (Annis et al. 2007). Moreover, we must emphasise that it remains entirely possible that, as concluded by York et al. (2008) and Aguilar et al. (2015), *C. polymerus* does cross the SEABB, with rare colonists persisting long enough to achieve limited introgression of eastern and western lineages. Our data imply that successful colonisation may remain rare or is limited by regional variation in selective regimes. The failure of *T. rosea* to establish permanent populations to the west of the SEABB implies that these are also limited by selection.

Heterogeneous landscapes provide avenues in which populations experiencing divergent selective pressures can differentiate into locally adapted subpopulations, and in this case divergent selection may be driven by trans-barrier variation in the physical (e.g. sea surface temperature and salinity; chlorophyll *a* levels, and mean and extreme rocky shore temperatures) (e.g. Cresswell 2000, Ridgway 2007, Lathlean et al. 2011, 2014, 2015) and biological environments (variation in community composition) (e.g. Knox 1963, Hidas et al. 2007, Waters 2008, Ayre et al. 2009, McWilliam et al. 2013). Our present data do not allow us to determine the function of the C. *polymerus* loci under diversifying selection, but several studies indicate that trans-SEABB colonists would face substantially different communities of competitors and predators (Knox 1963, Hidas et al. 2007, Coulson et al. 2011, McWilliam et al. 2013, Lathlean et al. 2015) and there is substantial regional variation in both sea surface temperatures (Cresswell 2000, Ridgway 2007) and variation in both mean and extreme rocky shore temperatures (Lathlean et al. 2011, 2014, 2015). In particular, the whelks *Morula marginalba* and *Haustrum vinosum* are potentially the dominant barnacle predators on the eastern and western sides of the SEABB, respectively (Coulson et al. 2011, McWilliam et al. 2013). The thermal sensitivity of *C. polymerus* has not been formally investigated, but thermal imaging studies with the partially sympatric *T. rosea* have shown that even natural temperature variation among 20 × 20 cm quadrats, or indeed the shade provided by a nearby adult, can alter the early survival and growth of its recruits (Lathlean et al. 2012, 2013). The abundance of this species is correlated with nearshore sea surface temperatures (Lathlean et al. 2015), and studies in the northern hemisphere have reported range expansions and contractions of barnacles in response to rapid climate change (e.g. Wethey 1983, 2002, Crickenberger & Moran 2013). More detailed demographic and genomic surveys and analyses in combination with experimental cross-barrier transplantations may be needed to establish the relative fitness of eastern and western genotypes on each side of the barrier and to understand if either dispersal or colonisation is actually limited by disruptive selection.

Our findings emphasise the potential complexity of the SEABB as a biogeographic barrier and help to explain why, for many taxa, the effects of the barrier region have persisted for the millennia despite varying sea levels and patterns of current activity (Waters 2008, Ayre et al. 2009). These findings suggest that even for taxa such as *C. polymerus* with ranges that are considered to span the SEABB, the present effects of global warming are not sufficient to break down existing patterns of genetic differentiation. Moreover, it seems likely that the east–west population differentiation experienced by *C. polymerus* may be producing allopatric speciation, and introgression may therefore be limited by reproductive incompatibility. Nevertheless, the southward penetration of the EAC or its associated eddies is expected to increase with continued warming (Ridgway & Hill 2009, Cetina-Heredia et al. 2014). Further investigation of the role of selection in limiting the migration of *C. polymerus* and other taxa should ideally involve a combination of more detailed genomic investigation, including the development of an annotated genome that would facilitate the identification of loci under selection, and experimental transplantation of early settlers and later life stages. Barnacles are readily transplanted either individually or on settlement plates (Hoch 2011), and assessment of the performance of transplants and local individuals would allow tests of both the intensity of selection and traits under selection.

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LITERATURE CITED

Aguilar LA, Roberts DG, Minchinton TE, Ayre DJ (2015) Genetic differentiation in the barnacle *Catomerus polymerus* despite migration across a biogeographic barrier. Mar Ecol Prog Ser 524:213–224

Aguilar LA, Matthews SA, Ayre DJ, Minchinton TE (2019) Modelling the differences between El Niño and La Niña years and planktonic larval duration on dispersal across the southeast Australian biogeographic barrier. Geo: Geogr Environ 6:e00074

Anderson DT, Anderson JT (1985) Functional morphology of the balanomorph barnacles *Tesseropora rosea* (Krauss) and *Tetraclitella purpurascens* (Wood) (Tetraclitidae). Aust J Mar Freshw Res 36:87–113

Annis ER, Incze L, Wolff NH, Steneck RS (2007) Estimates of *in situ* larval development time for the lobster, *Homarus americ*anus. J Crustac Biol 27:454–462

Ayre DJ, Minchinton TE, Perrin C (2009) Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? Mol Ecol 18:1887–1903

Bay LK, Buechler K, Galiano M, Caley MJ (2006) Intraspecific variation in the pelagic larval duration of tropical reef fishes. J Fish Biol 68:1206–1214

Bennett I, Pope EC (1953) Intertidal zonation of the exposed rocky shores of Victoria, together with a rearrangement of the biogeographical provinces of temperate Australian shores. Aust J Mar Freshw Res 4:105–159

Besnier F, Glover KA (2013) ParallelStructure: a [sic] R package to distribute parallel runs of the population genetics program STRUCTURE on multi-core computers. PLOS ONE 8:e70651

Cetina-Heredia P, Roughan M, van Sebille E, Coleman MA (2014) Long-term trends in the East Australian Current separation latitude and eddy driven transport. J Geophys Res Oceans 119:4351–4366

Coulson LA, Perrin C, Roberts DG, Minchinton TE, Ayre DJ (2011) Can limited dispersal or biotic interaction explain the declining abundance of the whelk, *Morula marginalba*, at the edge of its range? Biol J Linn Soc 103: 849–862

Cowen RK (1991) Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher.* Mar Ecol Prog Ser 69:9–15

Cresswell G (2000) Currents of the continental shelf and upper slope of Tasmania. Pap Proc R Soc Tasman 133: 21–30

Crickenberger S, Moran A (2013) Rapid range shift in an introduced tropical marine invertebrate. PLOS ONE 8: e78008

Dawson MN, Grosberg RK, Stuart YE, Sanford E (2010) Population genetic analysis of a recent range expansion: mechanisms regulating the poleward range limit in the volcano barnacle *Tetraclita rubescens.* Mol Ecol 19: 1585–1605

Edgar GJ (2008) Australian marine life: the plants and animals of temperate waters, 2nd edn. Reed New Holland, Sydney

Egan EA, Anderson DT (1988) Larval development of the coronuloid barnacles *Austrobalanus imperator* (Darwin), *Tetraclitella purpurascens* (Wood) and *Tesseropora rosea* (Krauss) (Cirripedia, Tetraclitidae). J Nat Hist 22: 1379–1405

Egan EA, Anderson DT (1989) Larval development of the chthamaloid barnacles *Catomerus polymerus* Darwin, *Chamaesipho tasmanica* Foster and Anderson and *Chthamalus antennatus* Darwin (Crustacea, Cirripedia). Zool J Linn Soc 95:1–28

Evanno G, Regnault S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14: 2611–2620

Foll M, Gaggiotti OE (2008) A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 180:977–993

Fredston-Hermann A, Selden R, Pinsky M, Gaines SD, Halpern BS (2020) Cold range edges of marine fishes track climate change better than warm edges. Glob Change Biol 26:2908–2922

Galindo J, Carvalho J, Sotelo G, Duvetorp M and others (2021) Genetic and morphological divergence between *Littorina fabalis* ecotypes in Northern Europe. J Evol Biol 34:97–113

Hargreaves AL, Samis KE, Eckert CG (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. Am Nat 183: 157–173

Hereward HFR, King NG, Smale DA (2020) Intra-annual variability in responses of a canopy forming kelp to cumulative low tide heat stress: implications for populations at the trailing range edge. J Phycol 56: 146–158

Hidas EZ, Costa TL, Ayre DJ, Minchinton TE (2007) Is the species composition of rocky intertidal invertebrates across a biogeographic barrier in south-eastern Australia related to their potential for dispersal? Mar Freshw Res 58:835–842

Hoch MJ (2011) Effects of crowding and wave exposure on cirrus morphology of the acorn barnacle *Semibalanus balanoides.* J Crustac Biol 31:401–405

Hohenlohe PA, Bassham S, Etter PD, Stiffler N, Johnson EA, Cresko WA (2010) Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. PLOS Genet 6:e1000862

Jaccoud D, Peng K, Feinstein D, Kilian A (2001) Diversity arrays: a solid state technology for sequence information independent genotyping. Nucleic Acids Res 29:e25

Jombart T (2008) adegenet: a [sic] R package for the multivariate analysis of genetic markers. Bioinformatics 24: 1403–1405

Jones DS (1990) Occurrence of the barnacle *Tesseropora rosea* (Krauss) (Thoracica, Balanomorpha, Tetraclitidae) in Western Australian waters. Rec West Aust Mus 14: 665–668

Knox GA (1963) The biogeography and intertidal ecology of the Australasian coasts. Oceanogr Mar Biol Annu Rev 1: 341–404

Kumagai NH, Molinos JG, Yamano H, Takao S, Fujii M, Yamanaka Y (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. Proc Natl Acad Sci USA 115:8990–8995

Lathlean JA, Ayre DJ, Minchinton TE (2011) Rocky intertidal temperature variability along the southeast coast of Australia: comparing data from *in situ* loggers, satellite-

derived SST and terrestrial weather stations. Mar Ecol Prog Ser 439:83–95
Lathlean JA, Ayre DJ, Minchinton TE (2012) Using infrared imagery to test for quadrat-level temperature variation and effects on the early life history of a rocky-shore barnacle. Limnol Oceanogr 57:1279–1291
Lathlean JA, Ayre DJ, Minchinton TE (2013) Temperature variability at the larval scale affects early survival and growth of an intertidal barnacle. Mar Ecol Prog Ser 475: 155–166
Lathlean JA, Ayre DJ, Minchinton TE (2014) Estimating latitudinal variability in extreme heat stress on rocky intertidal shores. J Biogeogr 41:1478–1491
Lathlean JA, McWilliam RA, Ayre DJ, Minchinton TE (2015) Biogeographical patterns of rocky shore community structure in south-east Australia: effects of oceanographic conditions and heat stress. J Biogeogr 42: 1538–1552
Li YL, Liu JX (2018) StructureSelector: a web-based software to select and visualize the optimal number of clusters using multiple methods. Mol Ecol Resour 18: 176–177
Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon M (2009) Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. Glob Change Biol 15:719–731
Lotterhos KE, Whitlock MC (2014) Evaluation of demographic history and neutral parameterization on the performance of F_{ST} outlier tests. Mol Ecol 23:2178–2192
Marshall DJ, Monro K, Bode M, Keough MJ, Swearer S (2010) Phenotype–environment mismatches reduce connectivity in the sea. Ecol Lett 13:128–140
Martins GM, Harley CDG, Faria J, Vale M, Hawkins SJ, Neto AI, Arenas F (2019) Direct and indirect effects of climate change squeeze the local distribution of a habitat-forming seaweed. Mar Ecol Prog Ser 626:43–52
McWilliam RA, Minchinton TE, Ayre DJ (2013) Despite prolonged association in closed populations, an intertidal predator does not prefer abundant local prey to novel prey. Biol J Linn Soc 108:812–820
Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, p 1–8
Morin PA, Luikart G, Wayne RK (2004) SNPs in ecology, evolution and conservation. Trends Ecol Evol 19:208–216
O'Hara TD, Poore GCB (2000) Patterns of distribution of southern Australian marine echinoderms and decapods. J Biogeogr 27:1321–1335
Peakall R, Smouse PE (2006) GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295
Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research – an update. Bioinformatics 28:2537–2539
Pérez-Figueroa A, García-Perez MJ, Saura M, Rolán-Alverez E, Caballera A (2010) Comparing three different methods to detect selective loci using dominant markers. J Evol Biol 23:2267–2276
Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species ranges: scaling from organisms to communities. Annu Rev Mar Sci 12:153–179
Puechmaille SJ (2016) The program STRUCTURE does not reliably recover the correct population structure when sampling is uneven: subsampling and new estimators alleviate the problem. Mol Ecol Resour 16:608–627
Ramos JE, Pecl GT, Moltschaniwskyj NA, Strugnell JM, Leon RI, Semmens JM (2014) Body size, growth and life span: implications for the polewards range shift of *Octopus tetricus* in south-eastern Australia. PLOS ONE 9: e103480
Ridgway KR (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. Geophys Res Lett 34:L13613
Ridgway K, Hill K (2009) The East Australian Current. In: Poloczanska ES, Hobday AJ, Richardson AJ (eds) A marine climate change impacts and adaptation report card for Australia 2009. NCCARF Publication, Hobart, p 1–16
Roesti M, Salzburger W, Berner D (2012) Uninformative polymorphisms bias genome scans for signatures of selection. BMC Evol Biol 12:94–100
Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. Annu Rev Mar Sci 3:509–535
Sanford E, Worth DJ (2010) Local adaptation along a continuous coastline: Prey recruitment drives differentiation in a predatory snail. Ecology 91:891–901
Sanford E, Roth MS, Johns GC, Wares JP, Somero GN (2003) Local selection and latitudinal variation in a marine predator–prey interaction. Science 300:1135–1137
Sanford E, Sones JL, García-Reyes M, Goddard JHR, Largier JL (2019) Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. Sci Rep 9:4216
Sherman CDH, Hunt A, Ayre DJ (2008) Is life history a barrier to dispersal? Contrasting patterns of genetic differentiation along an oceanographically complex coast. Biol J Linn Soc 95:106–116
Song K, Li L, Zhang G (2016) Coverage recommendation for genotyping analysis of highly heterologous species using next-generation sequencing technology. Sci Rep 6:35736
Stuart-Smith RD, Edgar GJ, Bates AE (2017) Thermal limits to the geographic distributions of shallow-water marine species. Nat Ecol Evol 1:1846–1852
Suthers IM, Young JW, Baird ME, Roughan M and others (2011) The strengthening East Australian Current, its eddies and biological effects—an introduction and overview. Deep Sea Res II 58:538–546
Tabangin ME, Woo JG, Martin LJ (2009) The effect of minor allele frequency on the likelihood of obtaining false positives. BMC Proc 3:S41
Teske PR, Sandoval-Castillo J, Golla TR, Emami-Khoyi A, Tine M, von der Heyden S, Beheregaray LB (2019) Thermal selection as a driver of marine ecological speciation. Proc R Soc B 286:20182023
Tracy BM, Larson KJ, Ashton GV, Lambert G, Chang AL, Ruiz GM (2017) Northward range expansion of three non-native ascidians on the west coast of North America. BioInvasions Rec 6:203–209
Waters JM (2008) Marine biogeographical disjunction in temperate Australia: historical landbridge, contemporary currents, or both? Divers Distrib 14:692–700
Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. Evolution 38: 1358–1370
Wethey DS (1983) Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. Biol Bull (Woods Hole) 165:330–341

Wethey DS (2002) Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. Integr Comp Biol 42:872–880

Wisely B, Blick RAP (1964) Seasonal abundance of first stage nauplii in 10 species of barnacles at Sydney. Aust J Mar Freshw Res 15:162–171

Wright SE (1969) The evolution and genetics of populations, Vol 2. The theory of gene frequencies. University of Chicago Press, Chicago, IL

York KL, Blacket J, Appleton BR (2008) The Bassian Isthmus and the major ocean currents of southeast Australia influence the phylogeographical and population structure of a southern Australian intertidal barnacle *Catomerus polymerus* (Darwin). Mol Ecol 17:1948–1961

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