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► To cite this version:

Iva Popovic, Nicolas Bierne, Federico Gaiti, Miloš Tanurdžić, Cynthia Riginos. Pre-introduction introgression contributes to parallel differentiation and contrasting hybridisation outcomes between invasive and native marine mussels. *Journal of Evolutionary Biology*, 2021, 34, pp.175-192. 10.1111/jeb.13746 . hal-03033473

HAL Id: hal-03033473

<https://hal.science/hal-03033473v1>

Submitted on 1 Dec 2020

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Pre-introduction introgression contributes to parallel differentiation and contrasting hybridisation outcomes between invasive and native marine mussels

Running title: (Un)parallel evolution in a marine invader

Iva Popovic^{1*}, Nicolas Bierne², Federico Gaiti^{3,4}, Miloš Tanurdžić¹ and Cynthia Riginos¹

¹School of Biological Sciences, University of Queensland, St Lucia, Queensland 4072, Australia

²Institut des Sciences de l'Evolution UMR 5554, Université de Montpellier, CNRS-IRD-EPHE-UM, France

³Weill Cornell Medicine, New York, NY, USA

⁴New York Genome Center, New York, NY, USA

*Corresponding Author:

Email: iva.popovic@uq.net.au

Tel: +61450658950

ORCID ID: 0000-0001-6582-4236

Email contact for other authors:

Nicolas Bierne: nicolas.bierne@umontpellier.fr

Federico Gaiti: feg2007@med.cornell.edu

Miloš Tanurdžić: m.tanurdzic@uq.edu.au

Cynthia Riginos: c.riginos@uq.edu.au

Acknowledgements

We would like to thank F. Viard, J. Thia, D. Matias, M. James, and D. Ortiz-Barrientos for valuable discussions and insight on the manuscript. The QRIScloud computing cluster at the University of Queensland provided computational infrastructure for this project. This work is supported by the Australian Biological Resources Study (ABRS) National Taxonomy Research Grant (grant number RF216-11), and awards from the National Sciences and Engineering Research Council of Canada (to I.P), the Society for the Study of Evolution (to I.P) and the University of Queensland (to I.P).

1 **Pre-introduction introgression contributes to parallel differentiation and contrasting**
2 **hybridisation outcomes between invasive and native marine mussels**

3
4 **Abstract**

5
6 Non-native species experience novel selection pressures in introduced environments and may
7 interbreed with native lineages. Species introductions therefore provide opportunities to investigate
8 repeated patterns of adaptation and introgression across replicated contact zones. Here, we investigate
9 genetic parallelism between multiple introduced populations of the invasive marine mussel, *Mytilus*
10 *galloprovincialis*, in the absence (South Africa and California) and presence of hybridisation with a native
11 congener (*Mytilus planulatus* in Batemans Bay and Sydney Harbour, Australia). Repeatability in post-
12 introduction differentiation from native-range populations varied between genetically distinct Atlantic and
13 Mediterranean lineages, with Atlantic-derived introductions displaying high differentiation ($maxFST > 0.4$)
14 and parallelism at outlier loci. Identification of long non-coding RNA transcripts (lncRNA) additionally
15 allowed us to clarify that parallel responses are largely limited to protein-coding loci, with lncRNAs likely
16 evolving under evolutionary constraints. Comparisons of independent hybrid zones revealed differential
17 introgression most strongly in Batemans Bay, with an excess of *M. galloprovincialis* ancestry and
18 resistance to introgression at loci differentiating parental lineages (*M. planulatus* and Atlantic *M.*
19 *galloprovincialis*). Additionally, contigs putatively introgressed with divergent alleles from a closely
20 related species, *Mytilus edulis*, showed stronger introgression asymmetries compared to genome-wide
21 trends and also diverged in parallel in both Atlantic-derived introductions. These results suggest that
22 divergent demographic histories experienced by introduced lineages, including pre-introduction
23 introgression, influences contemporary admixture dynamics. Our findings build on previous
24 investigations reporting contributions of historical introgression to intrinsic reproductive architectures
25 shared between marine lineages and illustrate that interspecific introgression history can shape
26 differentiation between colonising populations and their hybridisation with native congeners.

27
28 **Key words:** *Mytilus*, parallel evolution, introgression, hybrid zone, invasive species, genetic
29 differentiation

31 **Introduction**

32

33 Biological invasions are leading threats to global biodiversity and central components of global change
34 (Chown et al., 2015; Simberloff, 2013). The impacts of introduced species (including invasive species)
35 on native communities can be diverse and complex, and subsequently difficult to predict (Oduor, 2013).
36 Since the earliest studies on biological invasions (Baker, 1965, 1974), the literature now contains
37 numerous examples of shared ecological traits contributing to increased survival and competitive
38 abilities among introduced species (e.g., rapid growth rates and high fecundity through asexual
39 reproduction; Richardson, 2011). There is also growing evidence that local adaptation is often a
40 significant factor in the success of introduced populations (Colautti & Lau, 2015; Dlugosch & Parker,
41 2008; Prentis, Wilson, Dormontt, Richardson, & Lowe, 2008). Indeed, repeated evolution of ecologically
42 important traits related to life history strategies, reproduction, growth and competition have been
43 documented for introduced populations in both plants and animals (Colautti & Lau, 2015; Ferrero et al.,
44 2015; Lee, 2016; Phillips, Brown, Webb, & Shine, 2006; K. G. Turner, Hufbauer, & Rieseberg, 2014;
45 Vandepitte et al., 2014). We know relatively less, however, about how heritable genetic variation is
46 redistributed or altered to yield adaptive responses following introduction (Bock et al., 2015). Because
47 anthropogenic introductions are recent, selection on standing genetic variation from the native range is
48 expected to be the primary genetic mechanism of adaptation in introduced populations (Prentis et al.,
49 2008), thus increasing the likelihood that parallel genetic changes may accompany multiple independent
50 introductions of the same species.

51

52 Genetic and genomic studies examining parallel evolutionary change in natural populations have shown
53 that adaptation can be highly constrained and repeatable (Bolnick, Barrett, Oke, Rennison, & Stuart,
54 2018; Conte, Arnegard, Peichel, & Schluter, 2012; Elmer & Meyer, 2011). Replicated genetic changes
55 across distinct lineages at various genomic scales are now documented, ranging from single amino acid
56 polymorphisms (e.g., Hoekstra, Hirschmann, Bunday, Insel, & Crossland, 2006) to individual genes
57 (e.g., Colosimo et al., 2005; Stern & Orgogozo, 2009) and large genomic regions (e.g., Mérot et al.,
58 2018; Van Belleghem et al., 2018) including at the chromosomal scale (e.g., Riquet et al., 2019).
59 Comparative evidence for parallel evolution has also been demonstrated among closely related
60 populations (Jones et al., 2012; T. L. Turner, Bourne, Von Wettberg, Hu, & Nuzhdin, 2010), suggesting

61 that adaptation can be predictable even on timescales relevant for invasive species research (Marques
62 et al., 2016). Most studies of genetic repeatability, however, are predicated on the assumptions that
63 focal populations have evolved under similar selective pressures (Arendt & Reznick, 2008; Bolnick et
64 al., 2018; Rennison, Delmore, Samuk, Owens, & Miller, 2020; Stern, 2013). Invasive species are likely
65 to experience a variety of new ecological conditions under which they did not evolve (Colautti & Lau,
66 2015) and may occupy vastly diverse abiotic conditions and habitats in their introduced ranges
67 (Guzinski, Ballenghien, Daguin-Thiébaud, Lévêque, & Viard, 2018; Tepolt, 2015). Invasive species are
68 also likely to encounter congeneric species and gene flow may ensue if isolating barriers to reproduction
69 are semi-permeable (Viard, David, & Darling, 2016; Viard, Riginos, & Bierne, 2020).

70
71 Introduced species adaptation frequently occurs in the context of gene flow between previously
72 allopatric taxa (Bay, Taylor, & Schluter, 2019; Fitzpatrick et al., 2010). Such examples of very recent
73 secondary contact can provide new insights into speciation genetics, especially how different genomic
74 elements are shaped by selection and gene flow (Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015;
75 Ravinet et al., 2017). For instance, introgression from differentiated genetic backgrounds, such as native
76 species, can contribute locally adapted alleles or new beneficial allelic combinations to introduced
77 lineages (Bay & Ruegg, 2017; Huerta-Sánchez et al., 2014; Martin & Jiggins, 2017). Conversely, gene
78 flow is expected to break down linkage disequilibria between sets of already well-adapted alleles,
79 potentially impeding opportunities for post-introduction adaptation (Kirkpatrick & Barton, 2006; Nachman
80 & Payseur, 2012; Sousa & Hey, 2013). Disassociation of locally adapted alleles can be slowed down,
81 however, if beneficial alleles are tightly linked in low recombination regions, leading to heterogeneous
82 genomic differentiation between populations in the presence of gene flow (Bierne, Roze, & Welch, 2013;
83 Harrison & Larson, 2016). These low-recombining regions likely experience strong linked selection
84 during periods of allopatry that can accelerate lineage sorting and promote 'islands of differentiation'
85 between closely related lineages (Burri, 2017; Burri et al., 2015; Cruickshank & Hahn, 2014). Low-
86 recombining regions are also the most likely to accumulate differences associated with reproductive
87 barriers or local adaption loci that resist or delay introgression during secondary contacts (Barton &
88 Bengtsson, 1986; Duranton et al., 2018; Ravinet et al., 2017; Riquet et al., 2019).

89

90 Islands of genomic differentiation are common in natural divergence-with-gene-flow situations and
91 emerging results suggest they are also frequent when secondary contact is human-caused. Genomic
92 islands in regions of low recombination have been implicated in maintaining interspecific differences
93 through association with introgression barriers between native-introduced oysters (Gagnaire et al.,
94 2018). Similarly, empirical evidence for parallel differentiation between replicated anthropogenic contact
95 zones suggests that genome-wide admixture can lead to repeatable divergence when secondary
96 contact is recent (Bay et al., 2019; Simon, Arbiol, et al., 2020). More broadly, theory suggests that
97 interactions between concurrent divergent selection and gene flow may further constrain where
98 differentiation can occur, thus favouring genomic 'reuse' or repeated differentiation in genomic regions
99 (i.e. co-adapted alleles) that are less likely to be broken up by recombination (Samuk et al., 2017). Such
100 genomic constraints may therefore increase the probability that the same loci are involved in maintaining
101 differentiation between populations (Samuk et al., 2017), despite the likelihood of diverse selective
102 pressure experienced by introduced populations in novel environments (Riquet et al., 2019; Tepolt,
103 2015).

104

105 Successful marine invasions provide exceptional opportunities to gain a better understanding of how
106 gene flow and selection shape differentiation in introduced environments. Processes limiting adaptation
107 rates in marine environments appear to be less severe than theory would predict (Dlugosch & Parker,
108 2008; Nei, Maruyama, & Chakraborty, 1975). In general, high fecundity and highly dispersive larvae
109 promote successive introductions of large numbers of individuals through human-mediated vectors
110 (e.g., ballast water discharge; Carlton, 1996). High propagule pressure is therefore a key mechanism
111 suspected to help founding populations avoid the impacts of genetic drift and associated reductions in
112 genetic diversity (Blackburn, Lockwood, & Cassey, 2015; Lockwood, Cassey, & Blackburn, 2005; Narum
113 et al., 2017; Roman & Darling, 2007). Empirical studies in marine invasive species have supported these
114 predictions, rarely demonstrating strong genetic bottlenecks in introduced populations (Bernardi,
115 Azzurro, Golani, & Miller, 2016; Gagnaire et al., 2018; Riquet et al., 2019; Rius, Turon, Bernardi,
116 Volckaert, & Viard, 2015), such that establishment could be aided by ample standing genetic variation
117 available to selection (Viard et al., 2016). Furthermore, the combination of frequent and dense
118 introductions that likely underpin successful marine invasions ensure multiple worldwide introductions

119 as (un)naturally replicated experiments of independent introduced populations occupying diverse
120 coastal habitats alongside recent secondary contacts.

121
122 Despite these advantages, few studies have investigated genome-wide variation and differentiation in
123 marine non-native species across both native and introduced ranges (e.g., Bernardi et al., 2016;
124 Gagnaire et al., 2018; Guzinski et al., 2018; Riquet, Daguin-Thiébaud, Ballenghien, Bierne, & Viard,
125 2013; Rohfritsch et al., 2013; Saarman & Pogson, 2015; Tepolt & Palumbi, 2015). Inadequate resolution
126 of population differentiation (e.g., Riquet et al., 2019) or complex demographic introduction histories
127 (e.g., Rohfritsch et al., 2013), however, have precluded a detailed examination of whether introduced
128 populations show parallel genetic responses to colonisation. Additionally, genomic studies of marine
129 non-native species have either largely focused on genome scans of random genetic loci (Bernardi et
130 al., 2016; Guzinski et al., 2018; Riquet et al., 2013; Saarman & Pogson, 2015; but see Tepolt & Palumbi,
131 2015), or have not discriminated among putative sources of functional variation (i.e. protein-coding and
132 non-coding variation) driving differentiation between native and introduced populations (Tepolt &
133 Palumbi, 2015). Thus, we still have little insight regarding the genomic components of potentially
134 selectively favoured variation that may underlie differentiation in introduced environments.

135
136 Here, we capitalise on a uniquely replicated series of introductions of the invasive marine mussel *Mytilus*
137 *galloprovincialis* to investigate the role of recent evolutionary changes in the absence and presence of
138 gene flow with a native congener. Within the native range of *M. galloprovincialis*, introgression with its
139 sister species, *Mytilus edulis*, in Atlantic Europe, has led to pronounced genetic differentiation (Fraïsse,
140 Belkhir, Welch, & Bierne, 2016; Quesada, Wenne, & Skibinski, 1995) and partial reproductive isolation
141 (El Ayari, El Menif, Hamer, Cahill, & Bierne, 2019) between Atlantic and Mediterranean *M.*
142 *galloprovincialis* lineages. In the present study, we validate that each of these native lineages has been
143 the source of multiple introductions in the northern and southern hemispheres (Fig. 1a). Moreover, there
144 has been additional replication in the nature of receiving communities with respect to hybridisation:
145 Atlantic *M. galloprovincialis* introduced into South Africa is not sympatric with any native congeners
146 (Branch & Steffani, 2004; Daguin & Borsa, 2000; Grant & Cherry, 1985), whereas Atlantic *M.*
147 *galloprovincialis* introduced into Australia hybridises with an endemic Australian taxon, *Mytilus*
148 *planulatus* (Batemans Bay: Popovic, Matias, Bierne, & Riginos, 2020). Similarly, Mediterranean *M.*

149 *galloprovincialis* has displaced native *Mytilus trossulus* in southern California (Geller, 1999; Hilbish et
150 al., 2010; Rawson, Agrawal, & Hilbish, 1999) and only few hybrids are detected (Saarman & Pogson,
151 2015), whereas Mediterranean *M. galloprovincialis* introduced to Australia is admixed with *M. planulatus*
152 (Sydney Harbour: Popovic et al., 2020). The unintentional introduction history of *M. galloprovincialis*
153 provides an exceptional framework for investigating the reuse of standing genetic variation in the context
154 of adaptation to new environments with contrasting opportunities for gene flow with native species.

155
156 We use transcriptome-wide markers and focus on repeated patterns of genomic differentiation to
157 investigate whether introduced *M. galloprovincialis* in Australia and (non-hybridising) introductions in
158 California and South Africa have undergone parallel genetic change relative to their native genetic
159 backgrounds. We also quantify the extent of repeatability between independent admixture events in
160 Australia involving divergent *M. galloprovincialis* lineages that differ in colonisation histories.
161 Comparisons of allele frequency deviations from the average genomic admixture rate allowed us to
162 estimate genome-wide introgression patterns in each hybrid population and to determine whether loci
163 differentiating parental taxa deviate towards introduced *M. galloprovincialis* ancestry or resist
164 introgression (due to isolating barriers or selective processes). Because resolving the sources of
165 selectively favoured variation can improve our understanding of the genetic mechanisms underlying
166 adaptation (Prentis et al., 2008), we also examine whether differentiation and parallel responses involve
167 both protein-coding transcripts and major non-coding elements of the transcriptome, long non-coding
168 RNAs (lncRNAs). Non-coding elements of the transcriptome have been implicated as important sources
169 of genetic variation during invasion (Stapley, Santure, & Dennis, 2015) and there is evidence that higher
170 RNA structures are involved with thermal adaptation in bacteria and may have similar roles in eukaryotes
171 (de la Fuente, Valera, & Martínez-Guitarte, 2012; Gaiti, Calcino, Tanurdžić, & Degnan, 2017; Somero,
172 2018). Thus, lncRNAs may experience selection on ecological timescales relevant for studying
173 populations or congeners (Pang, Frith, & Mattick, 2006; Somero, 2018), but remain unexamined in the
174 context of biological invasions.

175
176 Our comparative investigation shows that repeatability of post-introduction differentiation and admixture
177 varies between genetically distinct introduced lineages, where historical introgression influences
178 contemporary evolution in independent introductions. The genetic data presented here represent the

179 first genomic investigation of multiple *M. galloprovincialis* introductions at a global scale and the first
180 comparative investigation of lncRNA evolution in an invasive species to date.

181

182 **Methods**

183

184 *Sample collection, RNA extraction and sequencing*

185

186 We obtained published RNAseq data for three *Mytilus* species: *M. galloprovincialis* from its native (n=15)
187 and introduced range (n=18) in Australia, *M. planulatus* (n=5) and *M. edulis* (n=3) from our previous
188 investigation of *M. galloprovincialis* introductions in the southern hemisphere (Table 1; Popovic et al.,
189 2020; BioProject ID: PRJNA560413). We combined these data with new samples from introduced *M.*
190 *galloprovincialis* in California (n=5) and South Africa (n=5) (Fig. 1a). Mussels were collected from rocky
191 intertidal or subtidal environments (Table 1). Individuals in California were sampled outside of the
192 southern hybrid zone boundary with *Mytilus trossulus*, to avoid sampling introgressed individuals
193 (Saarman & Pogson, 2015). All individuals were genotyped for the species diagnostic marker *Glu-5'*
194 (Rawson et al., 1996) to confirm species identity. RNA was extracted from 10-20 mg of mantle tissue
195 (preserved in RNAlater), using the RNeasy Plant Mini Kit (Qiagen, MD, USA) and following the Animal
196 Tissues protocol. Strand specific cDNA libraries were constructed using the TruSeq stranded mRNA kit
197 (Illumina) with average insert sizes of 250-300 bp. Paired-end libraries were sequenced across three
198 lanes of an Illumina HiSeq2000 or across one lane of an Illumina HiSeq4000.

199

200 *RNAseq data processing*

201

202 We removed adapters from paired reads using Trimmomatic (v0.36) (Bolger, Lohse, & Usadel, 2014).
203 We selected high quality reads using a Phred-scale average quality score of 20 within 4 bp sliding
204 windows and a minimum size filter of 50 bp. Redundancy among high-coverage reads was reduced by
205 digitally normalising each dataset using Trinity's *insilico_read_normalization.pl* script with a default kmer
206 size of 25 and maximum read coverage of 50 (Grabherr et al., 2011). Overlapping paired reads were
207 merged using FLASH v1.2.11 (Magoč & Salzberg, 2011) with a minimum overlap length of 10 bp. Read
208 mapping, lncRNA identification and all downstream analyses were conducted against a *de novo M.*

209 *galloprovincialis* reference transcriptome obtained from a previously published study (Popovic et al.,
210 2020 for *de novo* assembly details).

211

212 *Identification of lncRNA transcripts*

213

214 Putative lncRNA transcripts were identified following a published bioinformatic pipeline for lncRNA
215 discovery (Gaiti et al., 2015). Transcripts are classified as either protein-coding or non-protein coding
216 using a series of computational tools to perform stepwise filtering, annotation and isolation of transcripts
217 satisfying lncRNA criteria based on (i) homology to known proteins, (ii) the presence of signal peptides,
218 (iii) transcript length, (iv) open reading frame length, and (v) non-coding validation to retain the most
219 likely non-coding candidate transcripts as predicted lncRNAs (details in Supplementary Material).

220

221 *Mapping and identification of SNPs*

222

223 We performed additional filtering of the reference assembly prior to population genomic analyses:
224 Transcripts showing high sequence similarity were clustered using Cd-Hit-Est (Fu, Niu, Zhu, Wu, & Li,
225 2012; Li & Godzik, 2006) with a minimum sequence identity of 95% of the shortest sequence. We
226 removed contigs without a significant blastn hit to the *M. galloprovincialis* draft genome (e-value 10^{-4} ;
227 Murgarella et al., 2016). We also removed transcripts with significant blastn matches (e-value 10^{-3}) to
228 the *M. galloprovincialis* male (Genbank reference: FJ890850.1, AY363687.2) and female (Genbank
229 reference: FJ890849.1, AY497292.2) protein-coding and complete mitochondrial genomes. The
230 resulting 'total' assembly of 143,093 nuclear sequences was used as a reference for Single Nucleotide
231 Polymorphism (SNP) discovery (for analyses of parallelism) among four introduced and three native-
232 range *M. galloprovincialis* populations, *M. planulatus*, and *M. edulis* (Table 1). For comparisons of
233 lncRNA contributions to population structure, we removed all remaining lncRNA loci from this reference
234 assembly, leaving 106,333 transcripts considered as the 'full' transcriptome assembly. RNAseq reads
235 were mapped to each reference assembly (i.e. total, full and lncRNA) using Bowtie2 (Langmead &
236 Salzberg, 2012). PCR duplicates were removed using Picard MarkDuplicates
237 (<http://picard.sourceforge.net>) and indexed BAM files were created with SAMtools. SNPs were called
238 using Freebayes (<https://github.com/ekg/freebayes>), and variants were filtered with VCFtools (Danecek

239 et al., 2011). We removed sites below a genotype quality of 30 and a minimum mean depth coverage
240 of 10 reads, singletons (minor allele count=2 across all populations) and indel variants, and all variants
241 with missing genotype data. Genotypes were statistically phased using beagle v4.1 (Browning &
242 Browning, 2007).

243

244 *Analyses of population differentiation: Full transcriptome and lncRNAs*

245

246 We visualised variation among individual genotypes using Principal Components Analysis (PCA) on
247 SNPs derived from the full and lncRNA assemblies. Because we previously determined that introduced
248 *M. galloprovincialis* in Sydney Harbour and Batemans Bay are introgressed with *M. planulatus*, we
249 included *M. planulatus* samples from Tasmania as a reference parental population, but excluded *M.*
250 *edulis*. The full assembly resulted in 16,906 biallelic SNPs and we identified 471 biallelic SNPs for the
251 lncRNA dataset following filtering. We calculated pairwise *FST* (Weir & Cockerham, 1984) for each
252 dataset using the R package *hierfstat* (Goudet, 2005) and tested for significance using the *boot.ppfst*
253 function (10,000 bootstrap replicates). Given low differentiation between the eastern and western
254 Mediterranean populations (*FST*=0), we combined these populations for subsequent analyses.

255

256 To test the hypothesis that lncRNAs have a role in adaptation following introduction, we examined
257 whether putative lncRNAs contribute to elevated differentiation among native and introduced
258 populations relative to the full transcriptome. Alternatively, if lncRNA transcripts experience evolutionary
259 constraints, we expected that transcripts would contribute significantly less to population structure
260 compared to other expressed transcripts. To assess whether *FST* values were significantly different
261 between full and lncRNA datasets, we randomly resampled 471 variants (i.e. number equivalent to
262 lncRNA SNPs) from the full dataset 1000 times and calculated pairwise *FST* for each iteration to obtain
263 a null distribution of estimates using custom scripts in R. We assessed whether the observed lncRNA
264 *FST* values fell within the 5th or 95th quantiles of the null distribution to determine whether the lncRNAs
265 contributed significantly to elevated or reduced population differentiation, correcting p-values for multiple
266 comparisons at *qvalue*≤0.05 (*'qvalue'* R package; Dabney, Storey, & Warnes, 2010). To explore
267 diversity signatures that may indicate selection acting on lncRNAs, we examined the density of
268 polymorphic sites (proportion of segregating sites per contig averaged across contigs) and contrasted

269 observed and expected heterozygosity and allelic richness (using the smallest population size for
270 rarefaction) for each dataset in *hierfstat*. *PopGenome* (Pfeifer, Wittelsbürger, Ramos-Onsins, & Lercher,
271 2014) allowed us to calculate per locus within-population nucleotide diversity and Tajima's D values
272 (Tajima, 1989) to provide an indirect indication of the number of rare variants. In all subsequent analyses
273 of genetic parallelism (subsections below), we asked whether lncRNAs were among loci showing
274 atypical genetic differentiation following introduction.

275

276 *Patterns of genetic differentiation: Replicated introduced populations*

277

278 To test the hypothesis that *M. galloprovincialis* introductions have undergone parallel differentiation
279 relative to their native genetic backgrounds, we identified highly differentiated loci between introduced
280 and native populations: (i) Batemans Bay and South Africa against Atlantic *M. galloprovincialis* and (ii)
281 California and Sydney Harbour against Mediterranean *M. galloprovincialis*. We calculated pairwise *FST*
282 for each locus (Nei, 1987) using the function *basic.stats()* in *hierfstat* and converted negative *FST* values
283 to zero. To focus analyses on long-term adaptive variation within individual contigs, we considered only
284 SNPs that were shared between populations and also yielded the maximum *FST* value (*maxFST*) for
285 each contig. If more than one shared SNP had a *maxFST* value, we retained a single SNP per contig to
286 limit pseudoreplication of closely linked variants (e.g., Fraïsse et al., 2016). We also repeated parallelism
287 analyses using the *maxFST* value for each contig, irrespective of which SNP yielded the maximum
288 value. Because *FST* measures are contingent on within-population diversity and are influenced by
289 variation in minor allele frequency and sampled population sizes (Berner, 2019), *FST* may not always
290 reflect true allele frequency differences and may have decreased sensitivity at low differentiation levels,
291 such as those characteristic of *Mytilus* populations; we therefore repeated analyses using absolute allele
292 frequency differences between two samples ($\Delta P = |p_1 - p_2|$) to avoid assumptions associated with
293 estimating *maxFST*.

294

295 If introduced populations diverge from their native genetic background in a repeatable manner or share
296 the same history of colonisation (i.e. through stepping-stone migrations), we expected to see positive
297 correlations in genetic differentiation between introduced-native populations, such that the most highly
298 differentiated loci would overlap in different introduced locations. We also examined whether introduced

299 populations originating from divergent genetic backgrounds in California (Mediterranean origin) and
300 South Africa (Atlantic origin) displayed similar differentiation patterns from native reference populations.
301 For all joint comparisons, we used standardised major axis regression to estimate the strength of
302 *maxFST* correlation. We estimated the slope and intercept (elevation) of the regressions using the
303 SMATR R package (Warton, Duursma, Falster, & Taskinen, 2012). We categorised contigs as being
304 highly differentiated in pairwise comparisons if they contained a *maxFST* value within the top 1% of the
305 empirical distribution, whereby contigs within the 99th percentile in both distributions were considered
306 shared outlier contigs.

307

308 To explore whether our results are robust to sampling artefacts associated with small sample sizes and
309 because some of our joint inferences involved pairwise comparisons of the same native population (e.g.,
310 Fig. 2a, Fig. 2b), we undertook a permutation-based test of significance to ascertain the effect of
311 sampling error on the *maxFST* distribution and the influence of small samples size on outlier detection.
312 We took the total number of observed alternative allele counts per locus for each joint comparison and
313 randomly resampled alleles within each locus and across all three populations (i.e. one native population
314 and two introduced populations) of the same sizes as our empirical samples and recalculated *FST* and
315 *deltaP*. This randomisation procedure (1000 permutations) allowed us to obtain the null distribution of
316 summary statistics while (i) holding sample sizes and the number of loci sampled constant at the realised
317 values and (ii) preserving the relationships across all three populations (i.e. one native population and
318 two introduced populations). We recorded locus-specific estimates and used these values to generate
319 marginal cumulative probability distributions to ascertain the probability of obtaining extreme values for
320 some loci in joint comparisons due to random sampling effects.

321

322 *Patterns of Introgression: Replicated contact zones*

323

324 To evaluate genetic parallelism between independent admixture events in Australia, we quantified locus-
325 specific introgression asymmetries as positive or negative deviations from the average genomic
326 admixture rate, following the approach from Simon, Arbiol, et al. (2020). This allowed us to identify
327 genomic regions either putatively resistant to introgression (positive deviations indicating an excess of
328 introduced *M. galloprovincialis* ancestry) or permeable to introgression by heterospecific native alleles

329 (negative deviations indicating *M. planulatus* ancestry). For each admixed population, we calculated the
330 expected allele frequency of an allele (F_{exp}) as a function of the average population ancestry for the focal
331 admixed population and its frequency in each parental reference population;

332

$$333 F_{exp} = (f_{Introduced} * Q_{Introduced}) + (f_{Resident} * Q_{Resident});$$

334

335 where f is the frequency of the most common allele in the reference native-range population for the
336 introduced species (i.e. $f_{Introduced}$ in Atlantic or Mediterranean *M. galloprovincialis*) and its corresponding
337 frequency in the resident species (i.e. $f_{Resident}$ in native *M. planulatus*); and Q is the average admixture
338 proportion in the admixed population corresponding to each putative parental ancestry component.

339 Given an expected allele frequency, we can calculate the locus-specific deviation from the average
340 genomic admixture rate:

341

$$342 D = F_{obs} - F_{exp};$$

343 where F_{obs} is the observed allele frequency in the admixed population.

344

345 We estimated genome-wide correlations in allelic deviations between independent contact zones to
346 evaluate whether genome-wide departures from the genomic mean were similar between Batemans
347 Bay and Sydney Harbour despite involving divergent *M. galloprovincialis* lineages. If admixture events
348 have led to repeated genetic outcomes, we expected to see positive correlations between allelic
349 deviations in separate localities. The repeatability of admixture can also be assessed by analysing
350 introgression patterns independently within each admixture event. Specifically, if the degree of
351 divergence between incipient species is inversely correlated to introgression rate (Duranton et al., 2018),
352 we predicted that highly differentiated loci between native *M. planulatus* and introduced *M.*
353 *galloprovincialis* lineages would display strong asymmetries in locus-specific introgression (either
354 positive or negative deviations) relative to the average genomic admixture rate. Under the hypothesis
355 of barriers to introgression or other sources of selection favouring either introduced or locally adapted
356 alleles, genome-wide deviations and parental F_{ST} are expected to be correlated, whereby the most
357 divergent loci show an excess of *M. galloprovincialis* ancestry (positive correlations) or tendencies
358 towards resident ancestry (negative correlations). Under neutral expectations (no barriers to

359 introgression) or if highly differentiated loci deviate equally toward introduced or native ancestries
360 (opposing deviations), we would not expect to see correlations with parental *FST*. For each admixed
361 population, we compared allelic deviations against parental *FST* values (between *M. planulatus* and
362 introduced *M. galloprovincialis* lineages) estimated for each SNP locus (*snpFST*). To account for non-
363 independence of loci on the same contig, we fit the data with linear mixed-effects models that included
364 contig identity as a nested random effect using the maximum likelihood method and the `lme()` function
365 in the R package `nlme` (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2013). Both parental *FST* and a
366 Boolean predictor reflecting Mediterranean vs. Atlantic *M. galloprovincialis* differentiation (see below)
367 were included as predictors along with their interaction term.

368

369 For these analyses, population allele frequencies were calculated using VCFtools. We estimated
370 individual ancestry proportions with the program ADMIXTURE (Alexander, Novembre, & Lange, 2009)
371 to obtain average admixture proportions (*Q*) for each population. For ADMIXTURE analyses, we
372 retained positions with up to 20% missing data across all populations, which resulted in 84,150 SNPs
373 across 4941 contigs. We considered four putative ancestries corresponding to Atlantic and
374 Mediterranean *M. galloprovincialis* and *M. planulatus* as a reference parental population, and *M. edulis*
375 as an outgroup taxon. We ran ADMIXTURE with 100 iterations and used the cross-validation procedure
376 with 50 replicates for *K*=4 genetic clusters. Because both Batemans Bay and Sydney Harbour showed
377 >99% average ancestry belonging to *M. planulatus* and a single *M. galloprovincialis* lineage, we only
378 considered two population ancestries for calculating expected allele frequencies.

379

380 It is well established that Atlantic *M. galloprovincialis* and *M. edulis* have a history of secondary contact,
381 and that differential introgression with *M. edulis* contributes significantly to intraspecific outliers and
382 partial reproductive isolation between Mediterranean and Atlantic *M. galloprovincialis* lineages (El Ayari
383 et al., 2019; Fraïsse et al., 2016). Because divergent *M. edulis* genetic elements have been detected in
384 Batemans Bay through secondary admixture with introduced Atlantic *M. galloprovincialis* (Popovic et
385 al., 2020), we explored whether SNPs mapping to contigs strongly differentiating Mediterranean and
386 Atlantic *M. galloprovincialis* lineages (contigs with $\max FST \geq 0.5$) also showed elevated asymmetries in
387 allelic deviations as the most likely candidates for reproductive barriers or local adaptation loci, where

388 locus identity with respect to *M. edulis* introgression was treated as an additional variable in linear mixed-
389 effect models (Boolean indicator for contigs with $\text{maxFST} < 0.5$ or ≥ 0.5).

390

391 **Results**

392

393 *Predicted lncRNA transcripts*

394

395 We predicted 44,096 putative lncRNA transcripts, representing 23.8% of the unfiltered reference *de*
396 *novo M. galloprovincialis* transcriptome. This proportion is similar to high percentages reported for a
397 marine sponge (Gaiti et al., 2015) and plants (garden pea, Kerr, Gaiti, Beveridge, & Tanurdzic, 2017;
398 fern, Atallah, Vitek, Gaiti, Tanurdzic, & Banks, 2018) using the same computational pipeline, although
399 this value is greater than the proportion of lncRNAs (14.6%) identified in the *M. galloprovincialis* digestive
400 gland transcriptome (Gerdol et al., 2014). Despite stringent filtering, our final lncRNA assembly may
401 include untranslated regions, other polyadenylated RNA transcripts that satisfied minimum length
402 requirements (i.e. small regulatory RNAs, tRNAs and rRNAs) or novel *Mytilus* coding peptides with no
403 similarity matches to protein databases.

404

405 *Genetic differentiation: Full transcriptome and lncRNA datasets*

406

407 Principal component analysis of 16,906 biallelic variants from the full assembly revealed genetic
408 separation between introduced populations in California and South Africa (Fig. 1c), with the first and
409 second PC axes explaining 6.51% and 5.69% variance among individual genotypes. This analysis also
410 confirmed genetic structure previously identified between hybridising populations from Batemans Bay
411 and Sydney Harbour, which showed intermediate placement between northern *M. galloprovincialis*
412 populations and Australian *M. planulatus* (Fig. 1c; Popovic et al., 2020). ADMIXTURE analyses
413 indicated shared ancestry between introduced *M. galloprovincialis* in California and Mediterranean
414 populations; individuals sampled in South Africa clustered closely with Atlantic mussels, validating
415 previous inferences regarding the origins of these introductions (Fig. 1b). PCA of genotypic variance
416 confirmed that individuals sampled in California are not hybrids with *Mytilus trossulus*, where
417 introgressed individuals would have shown divergent placement away from the Mediterranean cluster.

418 All populations displayed similar levels of observed heterozygosity, suggesting no reductions in genetic
419 diversity compared to native populations that would indicate large bottleneck effects (Table S1, Table
420 S2).

421
422 lncRNA variant identification and filtering resulted in 200 transcripts with 471 SNPs. Lower expression
423 among lncRNAs compared to coding transcripts (e.g., Quinn & Chang, 2016) may have resulted in the
424 removal of many variants due to low sequence coverage. Overall, PCA of lncRNA variants explained a
425 lower proportion of variance across the first (5.92%) and second (5.10%) PC axes compared to the full
426 transcriptome. For this dataset, only *M. planulatus* sampled in Tasmania and the admixed population in
427 Batemans Bay showed genetic separation from all other populations which did not reflect clustering
428 based on sampling region (Fig. 1c). Pairwise comparisons of population differentiation for the full dataset
429 indicated *F_{ST}* values significantly different than zero for all population pairs, with the lowest values for
430 comparisons between the Mediterranean and California (*F_{ST}*=0.003; Table S3). Compared to the full
431 dataset, lncRNA variants returned lower *F_{ST}* values for most populations pairs (Table S3). Significant
432 reductions in lncRNA *F_{ST}*, however, were only evident for some populations displaying high population
433 structure in the full dataset (e.g., populations from divergent genetic backgrounds and comparisons with
434 Tasmania; Table S3).

435
436 Considering all populations, we observed a lower density of polymorphic sites within lncRNAs (0.00397)
437 compared to the full dataset (0.00453), although mean densities were not significantly different (Welch
438 approximation t-test, *P*=0.07). There were no consistent differences between datasets in within-
439 population observed or expected heterozygosity and allelic richness that would suggest impacts of
440 purifying selection on lncRNAs. Similarly, significant reductions in lncRNA polymorphism (*P_i*, within-
441 population nucleotide diversity averaged across loci) were only evident for the Atlantic population
442 (*P*≤0.01, Table S1). lncRNAs did not show consistently lower Tajima's *D* values or diversity that would
443 suggest stronger selective constraints or the possible action of balancing selection (i.e., positive
444 Tajima's *D*; Table S4).

445

446

447

448 *Repeatability of post-introduction genetic differentiation*

449

450 Filtered datasets of native-introduced population pairs resulted in 11,906 (Sydney Harbour) and 10,088
451 SNPs (California) for Mediterranean-derived populations, and 11,183 (Batemans Bay) and 8,902 SNPs
452 (South Africa) for Atlantic-derived populations. Consistent with recent timescale of presumed *M.*
453 *galloprovincialis* introductions into Australia (since the earliest records of European contact <600 years
454 ago to 100 years ago with the advent of commercial shipping), *maxFST* distributions of shared loci
455 between introduced and native populations were skewed towards low values, with few loci being highly
456 differentiated between populations. Overall, introduced populations originating from Atlantic *M.*
457 *galloprovincialis* were more differentiated from their native-range and showed greater genome-wide
458 variance compared to Mediterranean-derived introduced populations. *maxFST* for individual contigs
459 ranged between 0-0.6 (mean=0.0397, SD=0.0651, n=1634) for South Africa and 0-0.696
460 (mean=0.0529, SD=0.0753; n=1779) for Batemans Bay. Introduced populations in California and
461 Sydney Harbour were less differentiated from Mediterranean *M. galloprovincialis*, with *maxFST* ranging
462 from 0-0.372 (mean=0.0325, SD=0.045, n=1729) in California and 0-0.375 (mean=0.0319, SD=0.0410,
463 n=1873) for Sydney Harbour.

464

465 Joint *maxFST* distributions revealed an effect of interspecific gene flow with *M. planulatus* on levels of
466 differentiation between introduced and native populations. Admixed populations showed greater
467 average *maxFST* against native-range populations from the Atlantic (Batemans Bay) (n=651 loci;
468 standardised major axis regression, elevation=0.00721, P=0.00253, Fig. 2a) and Mediterranean
469 (Sydney Harbour) (n=737, standardised major axis regression, elevation=0.00265, P=0.0115, Fig. 2b),
470 compared to non-hybridising populations. Joint distributions were positively correlated in both
471 comparisons. The *maxFST* correlation between Atlantic-derived populations was moderate, but
472 significant ($R^2=0.532$, $P<0.0001$; Fig. 2a), with highly differentiated contigs ($FST>0.4$) showing similar
473 trends in both introduced populations (labeled in Fig. 2a). Three contigs were classified as shared
474 outliers falling above the 99th percentile of both empirical distributions and had joint *maxFST* values
475 greater than expected by chance ($P<0.001$) based on random permutation tests that were conditional
476 upon empirical samples sizes (Fig. S1). Correlations between Mediterranean-derived populations were
477 also significant ($R^2=0.539$, $P<0.0001$; Fig. 2b), with two contigs classified as shared outliers showing

478 differentiation levels above the 99th percentile in both introductions, although only one outlier was
479 significant based on the simulated marginal P-value threshold ($P < 0.001$) in both comparisons (Fig. 2b,
480 Fig. S1). Joint distributions of *deltaP* estimates and *maxFST* per contig provided concordant results in
481 all comparisons (Fig. S2, Fig. S3).

482
483 To investigate whether genetically divergent introductions may lead to similar genetic outcomes in the
484 absence of hybridisation with native congeners, we tested for correlations in genetic differentiation
485 between non-introgressed populations in California and South Africa against respective native reference
486 populations (Fig. 2c). Joint *maxFST* comparisons resulted in fewer shared loci ($n=318$), a weak genome-
487 wide correlation (standardised major axis regression, elevation=0.0065, $P=0.0043$; $R^2=0.129$,
488 $P < 0.0001$) and no shared outliers (Fig. 2c). In all comparisons, lncRNAs were poorly differentiated and
489 none were differentiation outliers (Fig. 2). Incomplete and unordered scaffolds in the *M. galloprovincialis*
490 draft genome assembly (Murgarella et al., 2016) precluded inferences regarding the genomic positions
491 and the possibility of linkage between shared outlier contigs.

492
493 *Repeatability of introgression patterns between contact zones*

494
495 Mussels from Batemans Bay showed average ancestry proportions belonging to 35.2% Atlantic *M.*
496 *galloprovincialis* and 64.1% *M. planulatus*, whereas Sydney Harbour were composed of 73.3%
497 Mediterranean *M. galloprovincialis* and 26.7% *M. planulatus* (Fig. 1b). Joint comparisons of allelic
498 deviations revealed heterogeneity in locus-specific introgression in both admixed populations, with some
499 SNPs showing concordant positive or negative deviations; but there was no strong evidence for
500 parallelism in genome-wide introgression patterns ($R^2=0.0003$, $P=0.02$) (Fig. 3).

501
502 In Batemans Bay, parental *FST* (between *M. planulatus* and Atlantic *M. galloprovincialis*) predicted
503 locus-specific allelic deviations in the direction of an excess of *M. galloprovincialis* ancestry (+D:
504 slope=0.128, $F_{1,7421}=190.180$, $P < 0.0001$, Fig. 4a) with positive genome-wide deviations from the
505 average admixture rate (intercept=0.0264, $F_{1,7421}=798.096$, $P < 0.0001$). Loci with *maxFST* ≥ 0.5 between
506 Mediterranean and Atlantic populations had significantly higher deviation values (intercept=0.0463,
507 $F_{1,7421}=4.002$, $P=0.0455$; but no difference in slope, $P=0.817$) (Fig. 4a). Additionally, among three contigs

508 (Contig15136, Contig34278, Contig33253) showing parallel genetic responses between Atlantic-derived
509 populations (Fig. 2a), two are highly differentiated between parental Atlantic *M. galloprovincialis* and *M.*
510 *planulatus* and show negative deviations in Batemans Bay, pointing to possible selection against
511 introduced alleles (Fig. 4a). Consistent *M. edulis* introgression contributing to intraspecific outliers
512 between *M. galloprovincialis* lineages (Fraïsse et al., 2016), SNPs with $maxFST \geq 0.5$ between
513 Mediterranean and Atlantic populations were largely fixed within *M. edulis* and show high allele
514 frequency differentials ($\Delta P > 0.6$) for the *M. edulis* major allele (Fig. S4).

515
516 In contrast, allelic deviations in Sydney Harbour showed no effect of parental *FST* (between *M.*
517 *planulatus* and Mediterranean *M. galloprovincialis*) (slope=-0.0181, $F_{1,8678}=3.059$, $P=0.0803$), although
518 the mean genome-wide deviation was positive (intercept=0.0149, $F_{1,8678}=226.816$; $P<0.0001$) (Fig. 4b).
519 Loci diagnostic of Mediterranean and Atlantic lineages showed significant negative deviations from the
520 average admixture rate (intercept=-0.00344, $F_{1,8678}=4.76994$, $P=0.0290$), but there was no difference in
521 slope compared to all loci ($P=0.928$) (Fig. 4b).

522
523 In both admixed populations, the average deviation across SNPs localised to lncRNA transcripts was
524 not significantly different than zero (Batemans Bay: $n=15$ SNPs, mean=0.332, $P=0.148$; Sydney
525 Harbour, $n=15$ SNPs, mean=0.0124, $P=0.432$). Consistent with intraspecific comparisons (native-
526 introduced *M. galloprovincialis*), lncRNA variants were generally poorly differentiated between *M.*
527 *planulatus* and native-range *M. galloprovincialis* (Fig. 4).

528 529 **Discussion**

530
531 Replicated species introductions provide opportunities to investigate repeated patterns of adaptation
532 and local introgression across contact zones. In the present study, we clarify aspects of *M.*
533 *galloprovincialis* introduction history, validating evidence for an Atlantic origin for South African *M.*
534 *galloprovincialis* and Mediterranean-derived introductions in California (Daguin & Borsa, 2000) that
535 complements our earlier results uncovering Atlantic and Mediterranean *M. galloprovincialis* admixture
536 Australian mussels (Popovic et al., 2020). Select outlier loci showed repeated changes in allele
537 frequencies from native reference populations, but there was limited evidence for strong genome-wide

538 correlated shifts in allele frequencies between introduced populations. These results suggest that
539 parallelism affects parts of the genome, with differentiation occurring predominantly within protein-
540 coding regions, as lncRNA loci were minimally differentiated in pairwise comparisons. Comparing two
541 independent hybrid populations, loci did not show parallel shifts in genome-wide introgression patterns
542 from neutral expectations, implying different admixture dynamics when introduced lineages are
543 genetically distinct. Interestingly, we observed that some loci with putatively *M. edulis*-derived alleles
544 were especially resistant to introgression in Batemans Bay. This result is consistent with pre-introduction
545 introgression shaping contemporary admixture whereby local interspecies introgression reinforces
546 isolation between populations within species (Duranton et al., 2018; Foote et al., 2019; Fraïsse et al.,
547 2016; Simon, Fraïsse, et al., 2020, this issue). Together, our findings suggest that both selective
548 processes and the demographic histories experienced by introduced lineages can influence the
549 repeatability of post-introduction evolution.

550

551 *Parallel differentiation among introduced populations at outlier loci*

552

553 Replicated *M. galloprovincialis* introductions from the same native-range source lineage exhibited
554 significant, albeit modest, genome-wide correlations (Fig. 2a, 2b), whereas introductions originating from
555 genetically distinct lineages had much weaker correlations (Fig. 2c). Coincident with genome-wide
556 evidence for parallel divergence, a small number of contigs were repeatedly involved in high levels of
557 differentiation in Atlantic-derived populations (South Africa and Batemans Bay). Three contigs provided
558 especially strong evidence for genetic parallelism following introduction, with high differentiation at the
559 same nucleotide positions ($maxFST > 0.4$) when considering joint outcomes across both population pairs
560 in permutation tests ($P < 0.001$) (Fig. 2a). Suggestively, Contig33253 returned a top blastn hit to the *M.*
561 *galloprovincialis* hsp90-2 gene encoding heat shock protein 90 (HSP90); HSPs and other oxidative
562 stress-related proteins have been shown to evolve under positive selection in *M. galloprovincialis*
563 (Popovic & Riginos, 2020) and may also be targets of repeated selection within introduced environments
564 or during long-distance transport experienced by migrant larvae in the ballast water of container ships.

565

566 Determining the evolutionary mechanisms by which parallel divergence arises across *M.*
567 *galloprovincialis* introductions is challenging, as a number of processes may converge towards similar

568 differentiation patterns (Riquet et al., 2019). Parallel evolution is often interpreted as evidence for similar
569 selection acting on the same genomic regions (Bolnick et al., 2018; Butlin et al., 2014), where standing
570 genetic variation is adaptively reused (Bock et al., 2015; Jones et al., 2012). Genetic repeatability is also
571 modulated by species-specific genetic architecture, either because complexes of adaptive alleles are
572 protected in inversions (Van Belleghem et al., 2018) or because the differential effects of long-term
573 linked-selection are conserved across similar recombination landscapes between species (e.g.,
574 *Ficedula* flycatchers, Burri, 2017; Burri et al., 2015; *Helianthus* sunflowers; Renaut, Owens, &
575 Rieseberg, 2014; *Mimulus* monkeyflowers, Stankowski et al., 2019; *Heliconius* butterflies, Martin et al.,
576 2013). In the context of invasive species, background selection is less efficient at the earliest stages of
577 differentiation (Burri, 2017) (i.e. between incipient native and introduced populations) and has limited
578 power to generate differentiation in the absence of strong barriers to gene flow (Stankowski et al., 2019).
579 Consistent with this premise, genomic islands within low-recombining regions (those experiencing linked
580 selection) also resist introgression between marine populations (e.g., European sea bass, Duranton et
581 al., 2018). Similarly, parallel divergence in the absence of ecological similarities, implicates an influence
582 of recombination on both lineage sorting and introgression rate among other hybridising lineages (e.g.,
583 Pacific cupped oyster, Gagnaire et al., 2018; long snouted seahorse, Riquet et al., 2019). Although
584 genomic resources for *M. galloprovincialis* are insufficient to make inferences about whether loci
585 diverging in parallel coincide with low-recombining regions, our findings suggest that similar selective
586 pressures or genomic constraints linked to recombination landscapes or reproductive isolation may lead
587 to repeatable differentiation in some parts of the genome. In addition, such forces can shape
588 differentiation both in the absence or presence of interspecific gene flow with native taxa (Fig 2).

589
590 Differentiation estimates may be confounded by high allele frequency variance due to small sample
591 sizes that can affect population genetic diversity and *FST* distributions (Bierne et al., 2013; Hoban et al.,
592 2016). While false positive outliers are unlikely to contribute to parallel differentiation by chance (Fraisse
593 et al., 2016; Riquet et al., 2019), permutation analyses allowed us to exclude the effects of small sample
594 sizes as a substantial influence on the observed patterns, indicating highly significant ($P < 0.001$) outliers,
595 even when joint comparisons involved the same native population (Fig. 2a, Fig. 2b). Nevertheless, allele
596 frequency shifts in native reference lineages may have contributed in part to correlated differentiation
597 observed between introduced populations. Similarly, low genetic structure between native and

598 introduced populations that is maintained by high standing genetic diversity and possibly ongoing
599 propagule pressure, precluded our ability to rule out the possibility that shared colonisation histories
600 (stepping-stone introduction routes) have led to parallelism at some loci. Indeed, difficulty in determining
601 the native origins of introduced populations appears to be a ubiquitous issue in marine invasion studies
602 and raises significant challenges for interpreting signals of differentiation associated with introductions
603 (Geller, Darling, & Carlton, 2010; Riquet et al., 2019; Viard et al., 2016).

604
605 Despite largely positive correlations across *M. galloprovincialis* introductions, many loci showed
606 location-specific shifts in allele frequencies, with little overlap in many differentiated contigs for both
607 Atlantic and Mediterranean-derived joint comparisons (e.g., $maxFST \geq 0.2$; Fig. 2a, Fig. 2b). Introduced
608 populations likely experience diverse selective pressures imposed by location-specific abiotic
609 conditions, diverse community assemblages and the presence of semi-isolated native lineages
610 (Guzinski et al., 2018; Riquet et al., 2013). In such cases, parallelism is expected to be reduced when
611 different phenotypes are selected (Bolnick et al., 2018; Thompson, Osmond, & Schluter, 2019).
612 Confidence in how location-specific selection shapes evolution in *M. galloprovincialis* introductions,
613 however, will require additional empirical investigations.

614

615 *Locus-specific introgression patterns differ between hybrid populations*

616

617 Contrasting introgression patterns between hybrid populations in Australia revealed that gene flow can
618 remodel population structure between introduced and native taxa in different ways depending on the
619 introduced genetic background (i.e. Atlantic or Mediterranean source lineages). Specifically, joint
620 comparisons of allele frequency deviations in Batemans Bay and Sydney Harbour indicated
621 heterogeneity in locus-specific introgression rates, with no evidence for genome-wide correlations (Fig.
622 3), highlighting that introgression outcomes are not especially repeatable when divergent genetic
623 lineages are involved. Locus-specific deviations were significantly correlated with parental *FST* in
624 Batemans Bay (Fig. 4a), suggesting that the degree of divergence between hybridising species
625 influences locus-specific introgression rates. Specifically, loci showed genome-wide deviations towards
626 an excess of introduced *M. galloprovincialis* alleles introgressing into the *M. planulatus* native genetic
627 background (Fig. 4a). In contrast, there was no evident relationship for Sydney Harbour mussels,

628 although loci had a slight genomic tendency in the direction of *M. galloprovincialis* ancestry (Fig. 4b).
629 This result is unexpected as Sydney Harbour is a large and busy harbour likely subject to high propagule
630 pressures of non-native larvae compared to the small docks and embayments of Batemans Bay, where
631 we would expect *M. planulatus* to outnumber *M. galloprovincialis* (matching average ancestry
632 proportions of 35.2% Atlantic *M. galloprovincialis*: 64.1% *M. planulatus*); thus, the predominant direction
633 of introgression should be of native alleles into the introduced species background (i.e. negative
634 deviation; Currat, Ruedi, Petit, & Excoffier, 2008).

635
636 Overall, our results support the hypothesis that differential introgression at some loci mirrors the
637 divergence between historically allopatric taxa (Duranton et al., 2018). High rates of gene flow and
638 recent divergence times typifying many marine hybrid zones may promote extensive introgression and
639 divergence swamping between semi-isolated lineages, such that the history of divergence is only
640 preserved at the most highly selected loci (Bierne et al., 2013; Duranton et al., 2018; Riquet et al., 2019).
641 In such cases, extrinsic selection may favour either invading or native alleles, depending on each hybrid
642 zone environment. Alternatively, selection may be intrinsic, maintaining divergence in regions
643 associated with reproductive incompatibilities. In Australian hybrid zones, a lack of concordance in
644 admixture patterns among divergent introduced lineages is consistent with recent empirical work on *M.*
645 *galloprovincialis* introductions along the Atlantic coast of Europe (Simon, Arbiol, et al., 2020), where
646 parallel patterns in allele frequency deviations were only observed when the same parental lineages
647 were compared, whereas correlations were negative or non-significant when admixed populations
648 comprised different *M. galloprovincialis* lineages. Thus, our results and those of Simon, Arbiol, et al.
649 (2020), reveal that genomic backgrounds can strongly influence the outcomes of post-introduction
650 admixture even among very closely related taxa.

651
652 *Heterospecific alleles may drive genetic parallelism between Atlantic M. galloprovincialis introductions*

653
654 From our analyses of paired introductions, we find that a small number of contigs were highly
655 differentiated in both Atlantic-derived introduced populations (South Africa and Batemans Bay; Fig. 2a).
656 Among three contigs (Contig15136, Contig34278, Contig33253) showing the strongest evidence for
657 genetic parallelism between Atlantic *M. galloprovincialis*-derived populations, two appear to resist

658 introgression between Atlantic and Mediterranean *M. galloprovincialis* lineages ($\max F_{ST} \geq 0.5$, contigs
659 in green; Fig. 2a). Additionally, contigs with alleles putatively shared with *Mytilus edulis* (Fig. 5; Fig. S4)
660 were highly differentiated between parental Atlantic *M. galloprovincialis* and *M. planulatus* and showed
661 negative deviations in Batemans Bay, pointing to possible selection against introduced genotypes (Fig.
662 4a). In Europe, local introgression from *M. edulis* into Atlantic *M. galloprovincialis* contributes
663 significantly to differentiation at intraspecific outliers between Atlantic and Mediterranean *M.*
664 *galloprovincialis* (Fraïsse et al., 2016). *M. edulis*-derived alleles also appear to resist introgression
665 between Mediterranean and Atlantic *M. galloprovincialis* lineages across a zone of secondary contact
666 in Algeria (El Ayari et al., 2019) and can explain repeated patterns of intraspecific differentiation in some
667 populations throughout the native range (Bierne, David, Boudry, & Bonhomme, 2002; Fraïsse et al.,
668 2016; Gosset & Bierne, 2013).

669
670 The influence of *M. edulis* introgression in naturally occurring native-range hybrid zones of Atlantic and
671 Mediterranean *M. galloprovincialis* (Fraïsse et al., 2016) is echoed in our results among introduced
672 populations. In Batemans Bay, *M. edulis* alleles have undoubtedly accompanied introduced Atlantic *M.*
673 *galloprovincialis* (Popovic et al., 2020); when we restricted analyses of allelic deviations to variants
674 within contigs strongly differentiating *M. galloprovincialis* lineages (contigs with $\max F_{ST} \geq 0.5$,
675 analogous to surveys using ancestry informative loci), parental *F_{ST}* had a significant effect on allelic
676 deviations, with elevated mean departures from the genomic admixture rate (intercept=0.0463,
677 $P=0.0455$) compared to analyses considering all loci (Fig. 4a). This pattern of asymmetric introgression
678 illustrates an intriguing aspect of divergence between Atlantic *M. galloprovincialis* and *M. planulatus*,
679 suggesting that highly divergent *M. edulis* alleles involved in reproductive isolation between *M.*
680 *galloprovincialis* lineages likely contribute to high locus-specific variation in introgression rates and may
681 resist introgression with *M. planulatus*.

682
683 Consistently, we observed nearly fixed differences in two highly differentiated contigs in Atlantic-derived
684 comparisons that are also putative *M. edulis* introgression outliers (Fig. 2a, Fig. 5). Contig15136
685 (encoding ribosomal protein L7a) was almost fixed for thymine (T) at position 965 in *M. edulis* (T) and
686 in the Atlantic (T, except for one individual), while *M. galloprovincialis* and *M. planulatus* were fixed for
687 cytosine (Fig. 5a). A similar pattern was observed in Contig34278, although the SNP frequency shift at

688 site 872 is associated with one of *M. edulis*' alleles (Fig. 5b). The high $maxFST$ values between Atlantic
689 and South Africa (Fig. 2a) also likely involve hybridisation but of a different nature: mixed Atlantic and
690 Mediterranean ancestry proportions in one individual sampled in Cape Columbine, South Africa (Fig. 1),
691 points to the possibility that introgressed genetic variation originating from the Mediterranean native
692 range is likely to inflate $maxFST$, and could also reflect Mediterranean alleles resisting introgression
693 with Atlantic *M. galloprovincialis* (that are heterogeneously introgressed by *M. edulis*), such that similar
694 outcomes are evident in the presence (Batemans Bay) and absence (South Africa) of hybridisation with
695 native congeners. For Sydney Harbor mussels, where partial *M. edulis* ancestry is not involved, parental
696 divergence did not affect the departures of introgressing loci from neutral expectations (Fig. 4b).

697

698 From the circumstantial evidence that we have outlined, it appears likely that historical gene flow from
699 *M. edulis* into Atlantic *M. galloprovincialis* (predating anthropogenic introductions) affects evolutionary
700 dynamics in introduced mussel species, both in the context of hybridisation with the Australian *M.*
701 *planulatus* and the previously undocumented input of Mediterranean *M. galloprovincialis* to the invasive
702 South African population (formerly thought to be exclusively Atlantic *M. galloprovincialis*-derived; Daguin
703 & Borsa, 2000). Similar to the case of European port mussels, pre-introduction introgression with *M.*
704 *edulis* may have contributed to instances of repeatable admixture outcomes between introduced *M.*
705 *galloprovincialis* and the local genetic background (Simon, Arbiol, et al., 2020). However, given the small
706 number of genotyped individuals in this study, we cannot make strong claims regarding introgression
707 rates at individual loci. Sampling variance and genetic drift may lead to spurious allele frequency
708 deviations, especially for loci where divergence between hybridising species is low. Likewise, genetic
709 drift at individual loci may obscure parallel trends if only a few generations of backcrossing have
710 occurred since the initial admixture event and there has been insufficient time for introgression to
711 proceed (e.g., Gagnaire et al., 2018). Further investigations through simulations are warranted to better
712 understand the dynamics of allelic deviation statistics under a spectrum of divergence scenarios and
713 drift processes that may be important during invasive secondary contacts.

714

715 Based on genome-wide patterns, however, our findings in Batemans Bay implicate partial reproductive
716 isolation between Atlantic *M. galloprovincialis* and *M. planulatus*, which may also explain why we
717 observed different outcomes when Mediterranean *M. galloprovincialis* was considered. This results

718 suggests that different sets of incompatibility genes may be important for *M. planulatus* and divergent
719 *M. galloprovincialis* lineages. While several reproductive isolating mechanisms are documented among
720 several pairs of *Mytilus* congeners (i.e. asynchronous spawning, Gilg, Kirby, Sullivan, Knapp, & Hilbish,
721 2007; differences in habitat preference, Gosling & McGrath, 1990, assortative fertilization, Bierne et al.,
722 2002; Dobzhansky-Muller incompatibility substitutions at several loci, Bierne, Bonhomme, Boudry,
723 Szulkin, & David, 2006), we currently have no information on the possible isolating mechanisms
724 (ecological or genomic) between *M. planulatus* and other *Mytilus* species.

725

726 *Genetic differentiation: Long non-coding RNAs*

727

728 Distinguishing among the major transcriptomic components of genetic variation underlying
729 differentiation allowed us to characterise how lncRNAs shape population structure among native and
730 introduced *Mytilus* populations (Fig 1c). LncRNA transcripts contributed significantly less to population
731 genetic structure compared to variants derived from the full transcriptome (Fig. 1c; Table S1) and
732 showed no evidence of high differentiation in analyses of parallelism (Fig. 2) or between congeners (Fig.
733 4). These findings suggest that lncRNA evolution may be constrained within lineages, with expressed
734 protein-coding transcripts being more likely to dominate signatures of recent genetic differentiation.
735 Purifying selection on lncRNAs has been documented among *Drosophila* populations, and is consistent
736 with suspected lncRNA functions in conserved developmental regulatory networks (Gaiti, Degnan, &
737 Tanurdžić, 2018; Perry & Ulitsky, 2016). However, measures of diversity among lncRNAs in *M.*
738 *galloprovincialis* indicated no consistent reductions that would support stronger purifying selection or
739 balancing selection on these transcripts.

740

741 Despite notable progress in understanding the role of lncRNAs in speciation, the evolutionary processes
742 influencing lncRNA transcripts are poorly understood, with mixed evidence supporting both sequence
743 conservation and rapid evolution among lineages (Gaiti et al., 2018). lncRNAs frequently evolve faster
744 than protein coding sequences, as the primary sequence is not constrained by protein function (Hezroni
745 et al., 2015; Pang et al., 2006; Quinn & Chang, 2016; Ulitsky, 2016); however, alternative modes of
746 evolution, such as adaptive changes to secondary and tertiary structures may occur through non-
747 nucleotide substitution mechanisms that cannot be detected by SNP-based measures of genomic

748 differentiation as employed in this study. We acknowledge that lncRNA identification using the total
749 assembly subjected to additional filtering (prior to population genomic analyses) resulted in a reduced
750 number of lncRNA transcripts and polymorphisms. Thus, genotyping errors due to mapping biases or
751 assembly errors in the absence of an annotated reference genome may have decreased detectable
752 population structure and our results should be interpreted with some caution. For *Mytilus* mussels, we
753 also cannot exclude the possibility that non-selective processes have contributed to patterns of lncRNA
754 evolution and diversity observed in this study, including variation in mutation rate or evolutionary
755 constraints linked to genomic synteny that do not operate in a population-specific way, or at least not
756 within timescales relevant for biological invasions.

757

758 *Conclusions*

759

760 Here, we provide comparative evidence for parallel genetic changes in multiple *M. galloprovincialis*
761 populations in the context of anthropogenic introductions and recent secondary contacts. Our study
762 shows that species introductions, both in the presence and absence of gene flow with native congeners,
763 may lead to similar genetic changes, especially for protein-coding loci. The extent of parallel
764 differentiation and admixture patterns between contact zones, however, varied depending on the
765 colonising *M. galloprovincialis* lineage. We observed stronger introgression asymmetries in contigs
766 distinguishing Mediterranean and Atlantic *M. galloprovincialis* lineages compared to genome-wide
767 trends in Batemans Bay, an observation consistent with *M. edulis* alleles influencing introgression
768 barriers between introduced lineages (South Africa) and in secondary contact with native congeners
769 (Batemans Bay). Genomic studies of marine invasive species and especially anthropogenic hybrid
770 zones are still rare (Viard et al., 2016; Viard et al., 2020). The lack of strong reproductive isolation among
771 *M. galloprovincialis* and *M. planulatus* provides a contrast to secondary contact in *Ciona* tunicates
772 (Bouchemousse, Liautard-Haag, Bierne, & Viard, 2016; Viard et al., 2020) and oysters (Gagnaire et al.,
773 2018) where reproductive isolation is strong. Thus, in introduced-native *Mytilus* hybrid zones there is
774 the opportunity to observe the earliest stages of extensive admixture that may lead to consolidation into
775 islands of divergence or to complete genomic swamping. Overall, our findings build on a growing number
776 of investigations (e.g., Duranton et al., 2020; Fraïsse et al., 2016; Simon, Arbiol, et al., 2020; Simon,
777 Fraïsse, et al., 2020) reporting significant impacts of historical introgression on the intrinsic genetic

778 differences between marine lineages, which may also influence the repeatability of recent evolutionary
779 change and the genetic outcomes of human-mediated admixture events.

780

781 **Data Archive**

782

783 RNAseq data is available on the NCBI Sequence Read Archive (SRA) (BioProject ID: PRJNA560413).

784 Raw RNAseq data for newly sequenced populations are deposited to the NCBI SRA (BioProject ID:

785 PRJNA679634). Reference transcriptomes, lncRNA reference assemblies, and genomic datasets that

786 support the findings of this study are openly available in the Dryad digital repository at

787 <https://doi.org/10.5061/dryad.xsj3tx9d9> and the Genomic Observatories MetaDatabase (<https://genome->

788 db.org).

789

790

791

792 **Figure Captions**

793

794 **Fig. 1. (a)** Sampling locations for native (circle) and introduced (triangle) *M. galloprovincialis* populations
795 and *M. planulatus*. Approximated distributions of introduced populations in Australia, California and
796 South Africa are denoted by red (Mediterranean) and purple (Atlantic) indicating known native source
797 lineages, and the *M. planulatus* (MP) range in Australia is shown in yellow. **(b)** ADMIXTURE results for
798 K=4 genetic clusters, including *M. edulis* (ME). Each bar represents an individual belonging to one or
799 more ancestral clusters, corresponding to different colours. **(c)** Principal components analysis (PCA) of
800 *M. galloprovincialis* individuals sampled from geographic locations coloured by geographic location,
801 where *M. planulatus* samples are included as a reference population. Top panel shows a PCA of 16,906
802 variants derived from the full transcriptome assembly and the bottom panel shows a PCA across 471
803 SNPs derived from lncRNA transcripts.

804

805 **Fig. 2.** Joint *maxFST* distributions for pairs of introduced *M. galloprovincialis* populations against native
806 reference populations from the **(a)** Atlantic (elevation=0.00721, P=0.00253; R²=0.532, P<0.0001); and
807 **(b)** the Mediterranean (elevation=0.00265, P=0.0115; R²=0.539, P<0.0001). **(c)** Joint *maxFST*
808 distributions for introduced *M. galloprovincialis* populations from different native origins in South Africa
809 and California (R²=0.129, P=<0.0001). For all plots, the grey dotted line corresponds to the 1:1 slope
810 and the solid line denotes the major axis regression. The red dotted lines show the 99th percentile for
811 both distributions, above which contigs were considered outliers. Solid red lines indicate the probability
812 (P<0.001) of observing outliers due to chance based on permutation tests. Green points correspond to
813 contigs strongly differentiating Atlantic and Mediterranean *M. galloprovincialis* lineages (*maxFST*≥0.5)
814 as putative loci with introgressed *M. edulis* alleles. None of these diagnostic loci were present in
815 comparisons involving Mediterranean populations (Fig. 2b, 2c). Black open circles indicate lncRNA
816 transcripts.

817

818 **Fig. 3.** Joint comparison of allelic frequency deviations from the average genomic admixture rate for
819 hybrid populations in Australia. Mean genome-wide deviations are shown by the dotted lines for
820 Batemans Bay (mean=0.00613) and Sydney Harbour (mean=-0.00320). Loci showing positive
821 deviations from the genomic average indicate an excess of *M. galloprovincialis* ancestry from the

822 Atlantic (purple) and Mediterranean (red) whereas negative deviations indicate ancestry towards *M.*
823 *planulatus* (yellow).

824

825 **Fig. 4.** Locus-specific allele frequency deviations for admixed populations as a function of parental
826 divergence (*snpFST*) between *M. planulatus* (*MP*) and *M. galloprovincialis* (*MG*) lineages from the
827 Atlantic and Mediterranean. **(a)** Significant effects of parental *FST* on allelic deviations in Batemans Bay
828 (grey; slope=0.128, $P<0.0001$) suggest that differential introgression is influenced by the degree of
829 parental divergence, with loci showing positive genome-wide deviations (intercept=0.0264, $P<0.0001$)
830 towards an excess of *M. galloprovincialis* ancestry. SNP variants within contigs differentiating *M.*
831 *galloprovincialis* lineages (green; contigs with $\max FST \geq 0.5$) had significantly higher deviation values
832 (intercept=0.0463, $P=0.0455$; but no difference in slope, $P=0.817$). **(b)** There was no effect of parental
833 *FST* on allelic deviations in Sydney Harbour mussels ($P=0.0803$). The mean deviation for all loci was
834 positive (grey; intercept=0.0149, $P<0.0001$), whereas diagnostic loci showed a slight negative departure
835 from the average admixture rate (green; intercept=-0.00344, $P=0.0290$).

836

837 **Fig. 5.** Frequencies of polymorphic sites along **(a)** Contig15136 and **(b)** Contig34278. Graphs show
838 allele frequencies in reference to the *Mytilus edulis* major allele. Focal SNPs with *maxFST* values for
839 each contig and where signals of parallelism may be attributed to local introgression of *M. edulis* alleles
840 are indicated.

841

842

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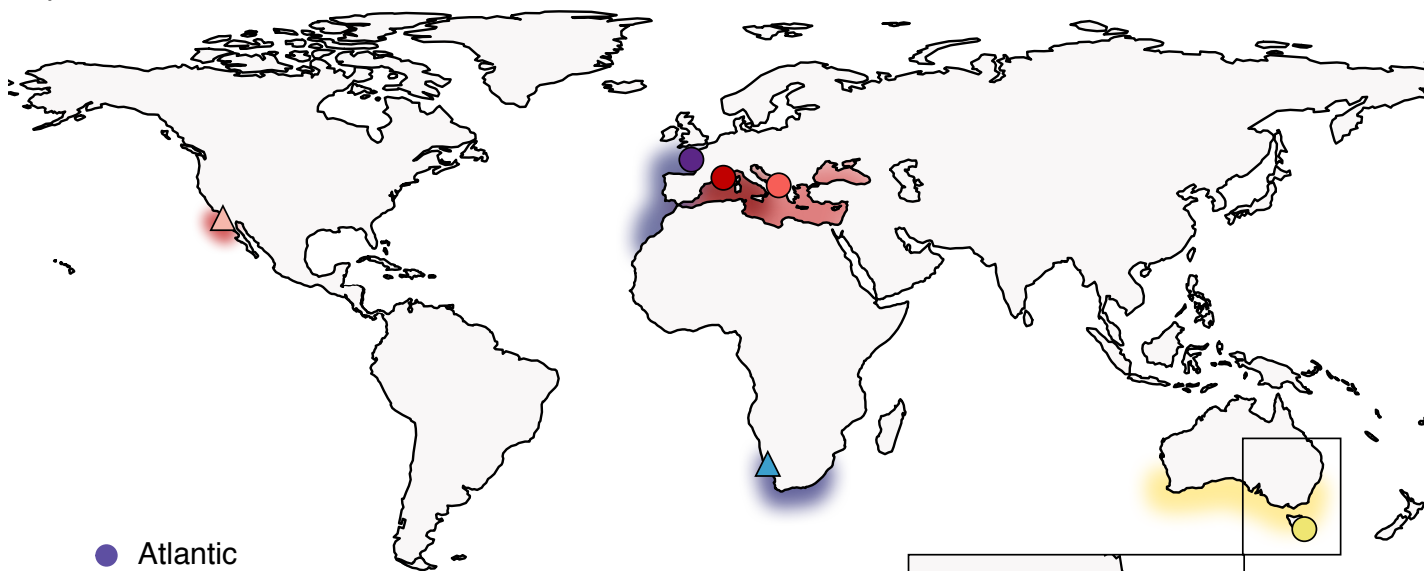
1156

Table 1. Summary of sampling locations.

Taxon	Sampling Location	Range	Samples sequenced (RNAseq)
<i>Mytilus edulis</i>	Darling Marine Station, Maine, USA	Native	3
<i>Mytilus galloprovincialis</i>	Primel, France (Atlantic)	Native	5
	Crique des Issambles, France (Western Mediterranean)	Native	5
	Herceg Novi, Montenegro (Eastern Mediterranean)	Native	5
	Scripps Institute of Oceanography, California, USA	Introduced	5
	Cape Columbine, South Africa	Introduced	3
	Yzerfontein, South Africa	Introduced	2
	Sydney Harbour, New South Wales, Australia*	Introduced	9
	Batemans Bay, New South Wales, Australia*	Introduced	9
<i>Mytilus planulatus</i>	Spring Bay, Tasmania, Australia*	Native	5

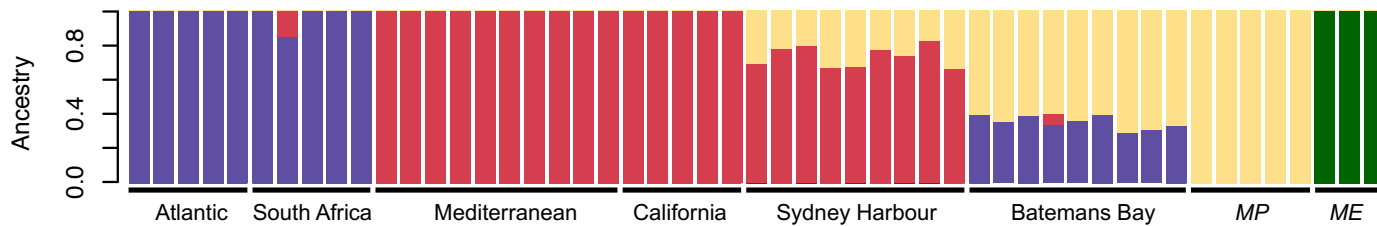
* Species identity and range for *Mytilus* samples is based on genome-wide analyses of species relationships (Popovic et al., 2020).

a)

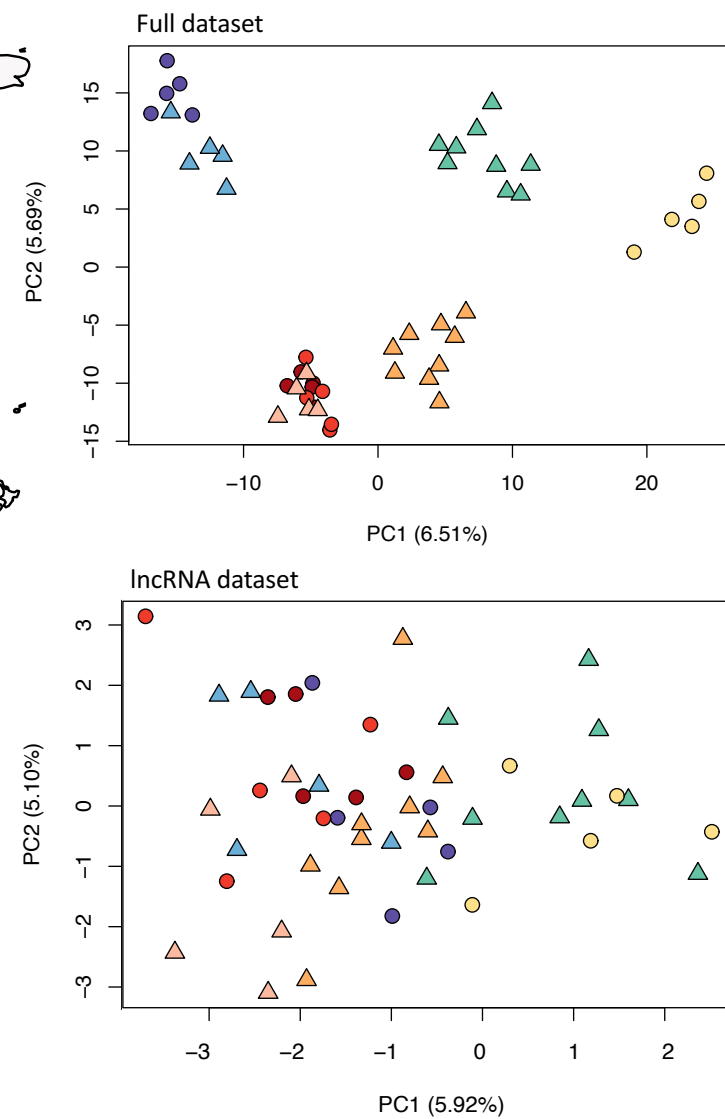


- Atlantic
- ▲ South Africa
- ▲ Batemans Bay
- Mediterranean–West
- Mediterranean–East
- ▲ California
- ▲ Sydney Harbour
- *M. planulatus*

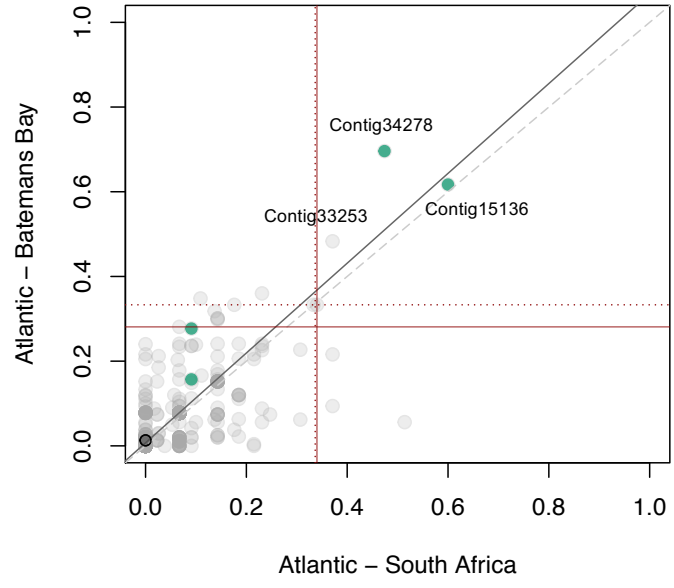
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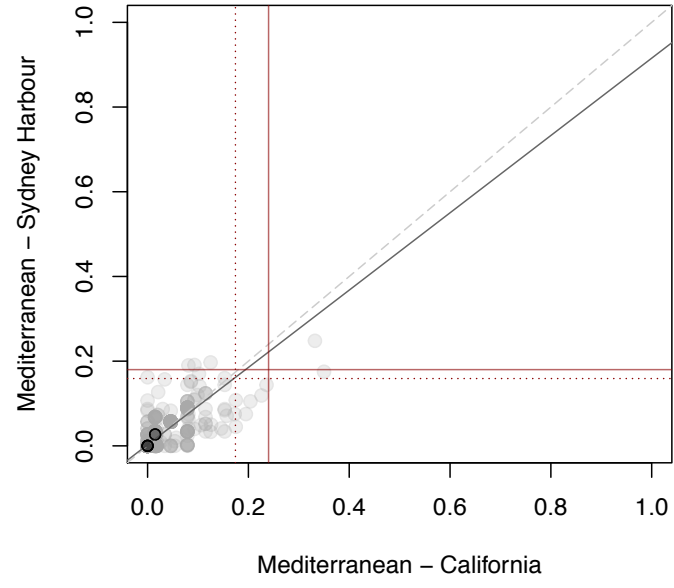
c)



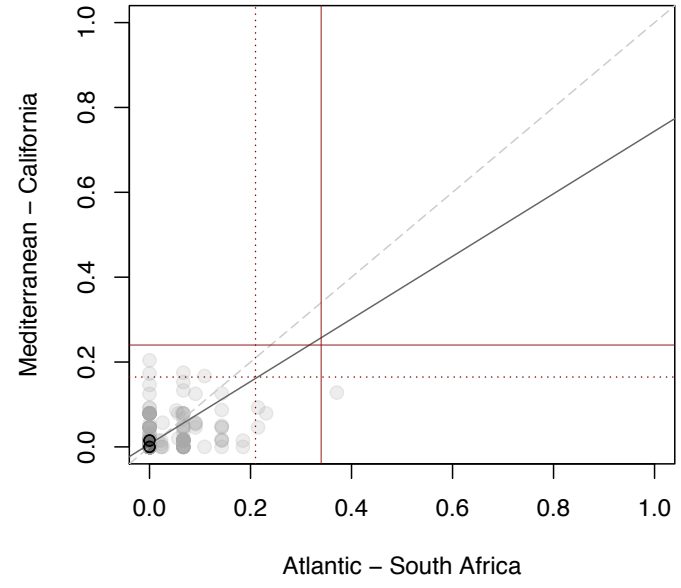
a)



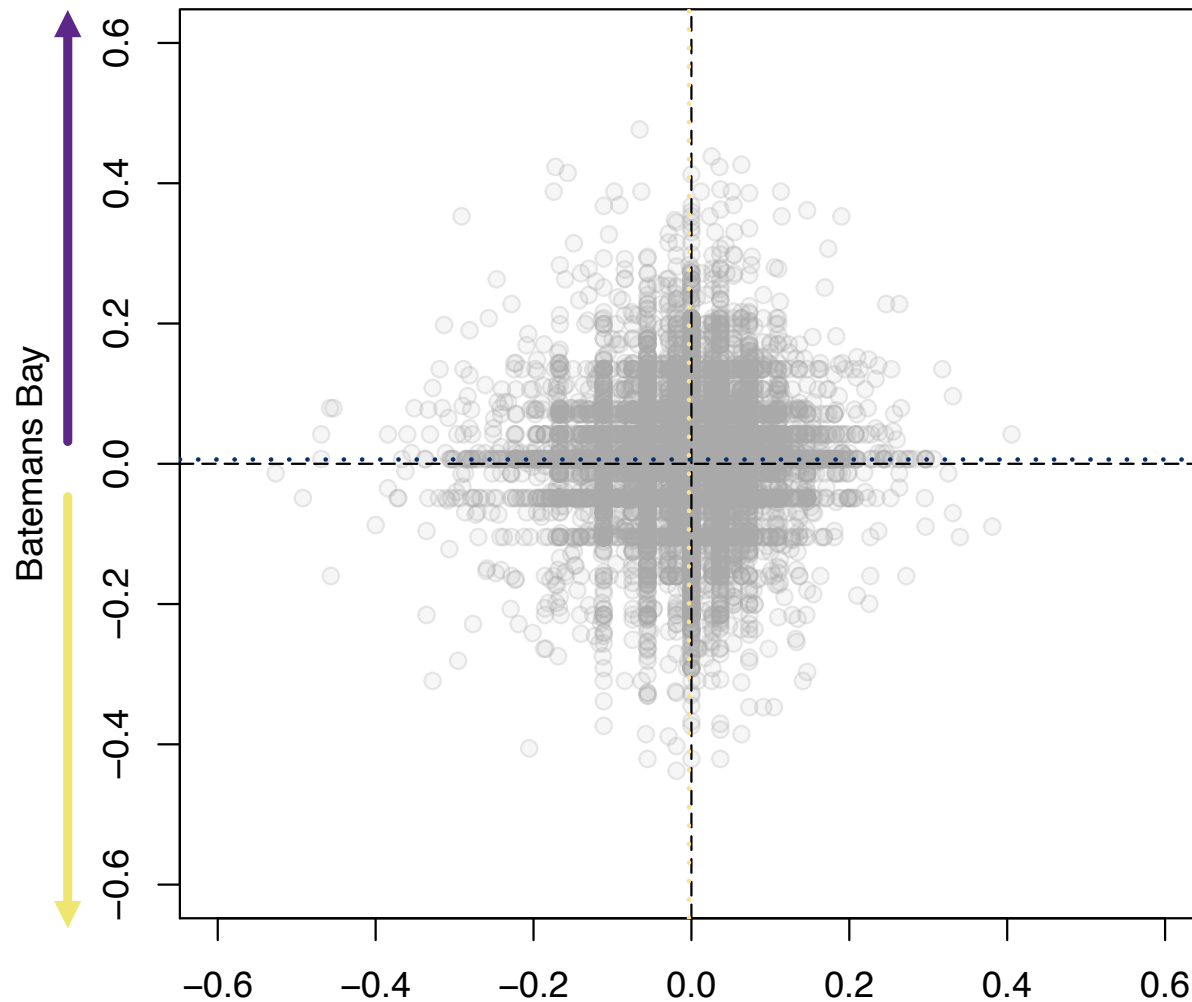
b)



c)



Atlantic MG

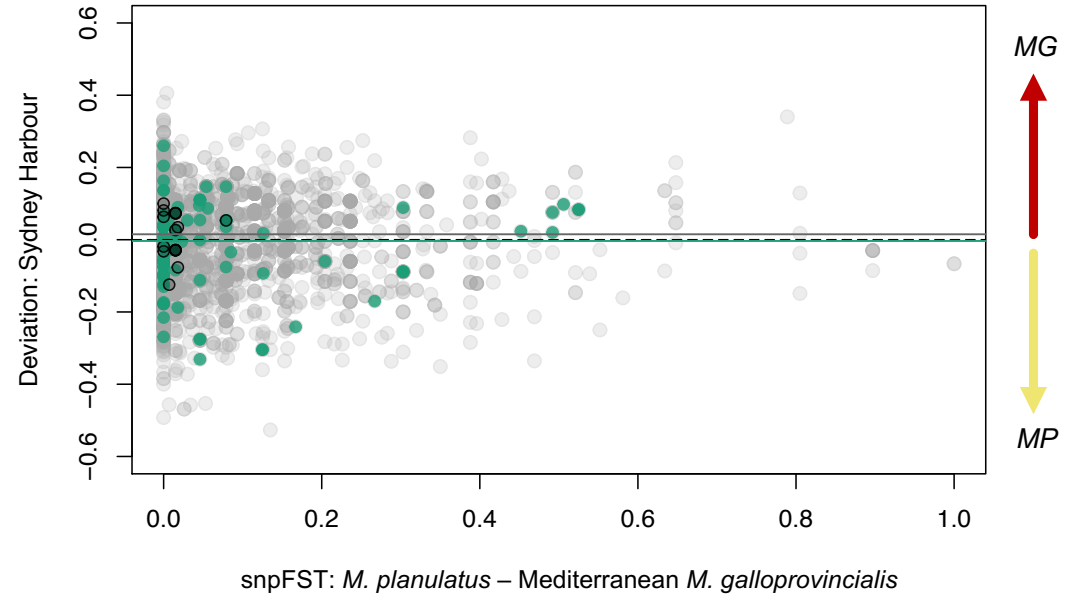
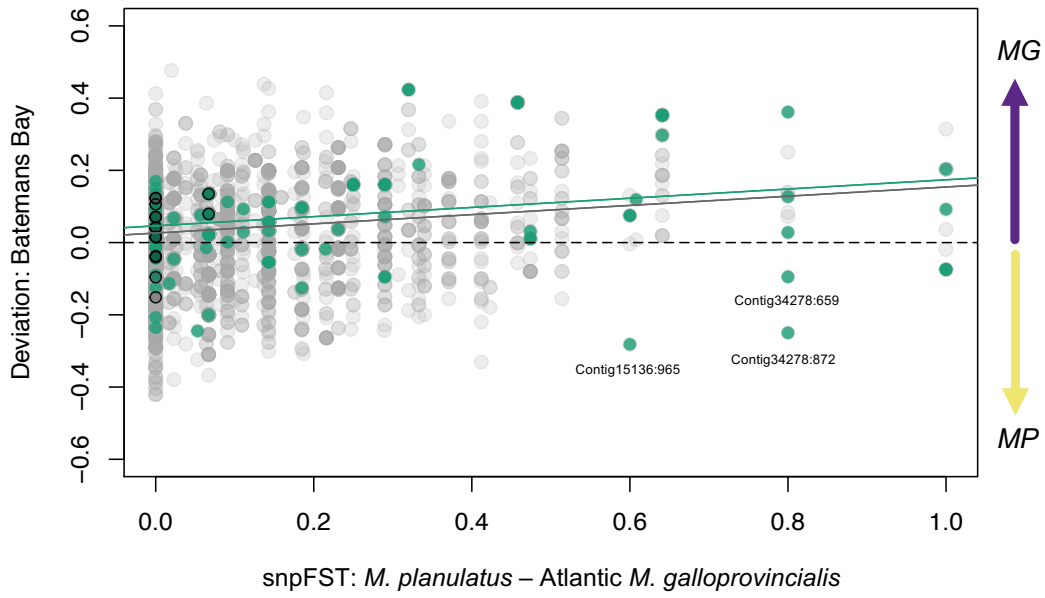


Batemans Bay

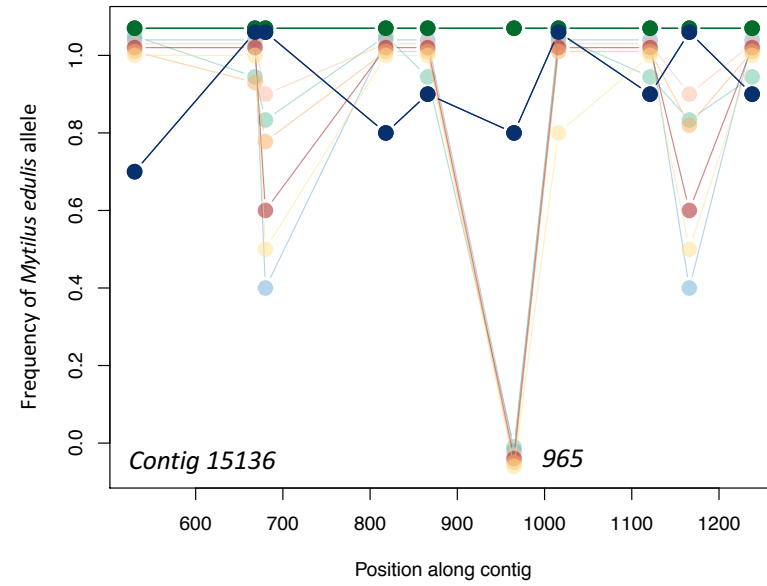
MP

Sydney Harbour

Mediterranean MG



a)



- *M. edulis*
- Atlantic
- Batemans Bay
- South Africa
- California
- Mediterranean
- Sydney Harbour
- *M. planulatus*

b)

