

## Circumpolar SRW connectivity over time

1 Incorporating non-equilibrium dynamics into demographic history inferences of a migratory  
2 marine species

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46 ABSTRACT: 250 words

47 Understanding how dispersal and gene flow link geographically separated populations over  
48 evolutionary history is challenging, particularly in migratory marine species. In southern right  
49 whales (SRWs, *Eubalaena australis*), patterns of genetic diversity are likely influenced by the  
50 glacial climate cycle and recent history of whaling. Here we use a dataset of mitochondrial DNA  
51 (mtDNA) sequences ( $n=1,327$ ) and nuclear markers (17 microsatellite loci,  $n=222$ ) from major  
52 wintering grounds to investigate circumpolar population structure, historical demography, and  
53 effective population size. Analyses of nuclear genetic variation identify two population clusters  
54 that correspond to the South Atlantic and Indo-Pacific ocean basins that have similar effective  
55 breeder estimates. In contrast, all wintering grounds show significant differentiation for mtDNA,  
56 but no sex-biased dispersal was detected using the microsatellite genotypes. An approximate  
57 Bayesian computation (ABC) approach with microsatellite markers compared scenarios with  
58 gene flow through time, or isolation and secondary contact between ocean basins, while  
59 modeling declines in abundance linked to whaling. Secondary-contact scenarios yield the highest  
60 posterior probabilities, implying that populations in different ocean basins were largely isolated  
61 and came into secondary contact within the last 25,000 years, but the role of whaling in changes  
62 in genetic diversity and gene flow over recent generations could not be resolved. We hypothesise  
63 that these findings are driven by factors that promote isolation, such as female philopatry, and  
64 factors that could promote dispersal, such oceanographic changes. These findings highlight the  
65 application of ABC approaches to infer connectivity in mobile species with complex population  
66 histories and currently low levels of differentiation.

67 Keywords: southern right whale; approximate Bayesian computation; historical demography;  
68 connectivity; last glacial maximum; non-equilibrium population genetic; *Eubalaena australis*

69 INTRODUCTION

70 Migratory marine species, such as sea turtles, sharks, sea birds and marine mammals, are by  
71 nature highly mobile, and many lack obvious barriers to long-distance movement (e.g., Benson  
72 et al., 2011; Bonfil et al., 2005; Mate & Best, 2011). Despite this, many such species also have  
73 geographically subdivided populations. A key question when managing contemporary  
74 populations of migratory marine species is whether such geographically distinct populations are  
75 linked by current dispersal or gene flow, or are now isolated and experiencing genetic drift. Such  
76 questions are of interest in understanding the evolution of population structure and are also of  
77 importance for management, given the disproportionate number of migratory marine species that  
78 are of conservation concern (Croxall et al., 2012; Dulvy et al., 2014; Hoffmann et al., 2010;  
79 IUCN, 2017). When using genetic data to investigate such questions, it is recognized that  
80 patterns of genetic variation within and among populations result from the interplay of  
81 evolutionary forces through time. Consequently, to understand the potential genetic impacts of  
82 contemporary anthropogenic processes, it is important to ask how the current genetic structure of  
83 a species reflects its history of population dynamics and adaptive challenges (Jobling, 2012).

84         The demographic histories of migratory marine species have been strongly influenced by  
85 oceanographic and climatic processes that shape the distribution of primary productivity and  
86 prey resources (Pastene et al., 2007, Bowen et al., 2016) and suitable habitats (Fontaine et al.,  
87 2010; Munro & Burg, 2017), as well as a species' dispersal strategy and capacity (Bowen et al.,  
88 1994; Munro & Burg, 2017; Pichler et al., 2001; Veríssimo et al., 2017). Life history traits, such  
89 as philopatry (Andreotti et al., 2016; Bowen et al., 2016), social organisation (Baker et al., 1993;  
90 Palsboll et al., 1995; Whitehead, 1998) and mating systems (Palsbøll et al., 2010; Hoelzel, 1999),  
91 also influence patterns of genetic diversity in natural populations of migratory marine species.

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92 Recent anthropogenic impacts, such as direct hunting and habitat degradation, have also affected  
93 contemporary patterns of genetic diversity in such species (e.g., Pinsky & Palumbi, 2014).  
94 However, interpreting the impact of recent anthropogenic activity on longest-lived migratory  
95 marine species, such as baleen whales, is controversial (Alter et al., 2012; Attard et al., 2015).  
96 The long and overlapping generation times of baleen whales (20+ years: Taylor et al., 2007) may  
97 have slowed the loss of genetic diversity during the demographic bottleneck caused by whaling,  
98 which was severe for many species but relatively short-lived.

99         Here we focus on a migratory baleen whale species with a circumpolar distribution (Fig  
100 1, IWC, 2001; Richards, 2009), the southern right whale (SRW: *Eubalaena australis*). During  
101 winter, SRWs typically inhabit shallow, sheltered coastal areas at mid-latitudes, where females  
102 calve and both sexes socialize. During spring, SRWs migrate to offshore summer feeding  
103 grounds in mid- to high-latitudes (IWC, 2001). Given these habitat preferences, we suggest that  
104 the historical demography of SRWs has been influenced by the transition from the last glacial  
105 maximum (LGM) to the Holocene, during which sea levels rose dramatically, primary  
106 productivity increased and Antarctic sea ice cover decreased while becoming more seasonal  
107 (Allen et al., 2011; Bentley et al., 2014; Clark et al., 2009; Denis et al., 2009; Gersonde et al.,  
108 2005; Scourse, 2013). These changes impacted the shallow, near-shore marine environment used  
109 as SRW wintering areas: many such areas would have become unsuitable due to sea level rises  
110 while newer, larger potential wintering areas were created during the expansion of shallow  
111 marine habitat (Scourse, 2013). These disruptions could have plausibly precipitated increased  
112 dispersal rates among SRW wintering grounds, leading to secondary contact between previously  
113 isolated populations.

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114           Furthermore, whaling, and the species' subsequent recovery, may have influenced  
115 connectivity between wintering grounds (Allendorf et al., 2008). Between the 18<sup>th</sup> and 20<sup>th</sup>  
116 centuries, whalers killed an estimated 150,000 or more SRWs, driving a hemispheric population  
117 size decline from ~100,000 whales to possibly fewer than 400 whales by 1920 (IWC, 1986,  
118 2001, 2012; Jackson, et al., 2008). Covert Soviet whaling from 1951-1971, in violation of  
119 international protection from the League of Nations introduced in 1931 (IWC, 1986), further  
120 slowed the species' recovery: the 3,368 SRWs killed (Tormosov et al., 1998) comprised an  
121 estimated 50% of the hemispheric population size at that time (Jackson et al., 2008). Today, the  
122 species has recovered in some parts of its former range. Large aggregations now occur in some  
123 key calving/nursery areas (e.g, Argentina, South Africa, Australia; see Fig. 1), while regular  
124 sightings of small numbers of SRWs occur in other parts of the historical range (Bannister, 1990;  
125 Best, 1990; Carroll et al., 2013; Cooke et al., 2001; Groch et al., 2005; Patenaude et al., 1998).  
126 The latter areas could represent remnant populations (e.g. Chile/Peru: Reilly et al., 2008) and/or  
127 areas that are undergoing recolonization from larger wintering aggregations (e.g. mainland New  
128 Zealand: Carroll et al., 2014). Recolonisation and asymmetric migration rates could have  
129 resulted from the differential rates of recovery shown by SRW wintering grounds (IWC, 2001),  
130 promoting higher levels of connectivity in the aftermath of whaling.

131           Genetic studies of several extant SRW populations, defined by current calving grounds,  
132 using a short fragment of the mitochondrial (mtDNA) control region (275 bp), showed  
133 hierarchical population structure, indicating limited connectivity between the South Atlantic and  
134 Indo-Pacific (Patenaude et al., 2007). Female philopatry was invoked as a major cause of this  
135 pattern, as long-term studies of individually identified SRWs show long-term fidelity to natal  
136 wintering grounds (e.g., Carroll et al., 2016; Rowntree et al., 2001). Subsequent studies

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137 integrating stable isotope and genetic data of contemporary populations, suggest some degree of  
138 maternally-directed learning of both wintering and summer feeding grounds (Carroll et al., 2015;  
139 Valenzuela et al., 2009).

140 Here we build on previous work using mtDNA haplotype sequences from 1,327  
141 individuals (~10% of the current global population) and 17 nuclear DNA microsatellite  
142 genotypes for 222 individuals (~2% of the population), allowing both mtDNA and nuclear DNA  
143 diversity and population structure to be inferred for the first time on a circumpolar scale in the  
144 SRW. This extensive dataset allows us to begin to disentangle contemporary and historical  
145 factors that account for observed patterns of genetic variation, thereby illuminating the complex  
146 population dynamics of this widely distributed species. Specifically, we make inferences about  
147 past and current patterns of gene flow, while taking into account non-equilibrium population  
148 dynamics, and provide information for conservation and management of this species now  
149 recovering from centuries of whaling.

150 We use approximate Bayesian computation (ABC) to evaluate the relative power of  
151 alternative historical scenarios to explain the phylogeographic pattern of the mtDNA haplotypes  
152 previously described (Patenaude et al., 2007), and the potential impact of whaling on  
153 connectivity. Patenaude et al., (2007) described a mtDNA phylogeographic pattern for SRW  
154 consistent with two competing hypotheses: (A) random lineage sorting in a species with  
155 continuous gene flow or (B) secondary contact between formerly isolated populations (Avice,  
156 2000). Under hypothesis (A), we posit that there was continued gene flow, potentially male-  
157 biased, between wintering grounds after population divergence. Under hypothesis B, we posit  
158 that the wintering grounds in the South Atlantic and Indo-Pacific became isolated following

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159 divergence, but came into secondary contact as a result of the environmental change following  
160 the last glacial maximum (LGM, 16-20,000 years before present: Clark, 2009).

161 We interpret our results in the context of two different conservation management  
162 frameworks. The first framework (Wade & Angliss 1997) defines subpopulations or stocks as  
163 groups for which demographic processes operating within the group are more important for  
164 persistence than immigration from other subpopulations. The second framework (Crandall et al.,  
165 2000) views subpopulations as groups that can be defined on the basis of contemporary and  
166 historical ecological and genetic exchangeability.

167

## 168 MATERIALS AND METHODS

### 169 *Genetic data generation and compilation*

170 For both the microsatellite and mtDNA control region analyses, we used a combination of  
171 previously published data sources (Carroll et al., 2015; Valenzuela et al., 2009) and new data  
172 (Table 1, Supplementary Material 1, Supplementary Table 1). Allele calls were standardized  
173 between laboratories for the microsatellite data, and standard quality control measures were  
174 taken including tests for deviation from Hardy-Weinberg equilibrium and genotyping error rate  
175 estimation (Supplementary Material 1). All sampling areas were nursery grounds except for the  
176 Australian wintering habitat, which is a mixture of migratory corridors and winter nursery areas  
177 (Carroll et al., 2015). Therefore, we make some comparisons using samples from the southeast  
178 and southwest Australian nursery grounds only, and others using the entire Australian wintering  
179 habitat sample.

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### 182 *Estimates of genetic diversity*

183 We estimated standardized allelic richness with *FSTAT v 2.9* (Goudet, 1995), and estimated  
184 observed and expected heterozygosity for each microsatellite locus per sample partition using  
185 *GenoDive v2.0* (Meirmans & van Tienderen, 2004). We estimated haplotype and nucleotide  
186 diversity for the mtDNA sequence data using *Arlequin v3.5* (Excoffier & Lischer, 2010), and  
187 tested for significant differences in these statistics between sample partitions using permutation  
188 tests (Alexander et al., 2016). To obtain comparable estimates of the number of haplotypes  
189 detected between sample partitions, we randomly selected 12 individuals from each partition,  
190 with replacement, 1000 times, to estimate the mean number of haplotypes (and its standard  
191 deviation). We estimated the apparent contemporary  $N_e$  from the microsatellite genotypes using  
192 the bias-corrected version of the linkage disequilibrium method (Waples, 2006), as implemented  
193 in program *NeEstimator v2.01* (Do et al., 2014).

194

### 195 *Investigating contemporary patterns of genetic diversity*

196 We undertook an hierarchical Analysis of Molecular Variance (AMOVA (Excoffier et al., 1992))  
197 for both the mtDNA and microsatellite data in *Arlequin*, with the wintering grounds grouped into  
198 ocean basins, the significance of which was assessed with a permutation test (50,000  
199 permutations,  $\alpha = 0.05$ ). We estimated pairwise genetic differentiation between sample partitions  
200 for the microsatellite loci by calculating overall and pairwise  $F_{ST}$  and Jost's  $D$  statistic (Jost,  
201 2008) using *GenoDive* and for the mtDNA data by calculating overall and pairwise  $F_{ST}$  and  $\Phi_{ST}$   
202 statistics using *Arlequin*. The probability of the observed level of differentiation occurring in a  
203 panmictic population was estimated using the log-likelihood  $G$  test in *GenoDive* (microsatellite)  
204 and the permutation test in *Arlequin* (mtDNA), for a total of 10,000 permutations each.

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205           We used two complementary methods to detect genetic clusters within the microsatellite  
206 data: discriminant analysis of principal components (DAPC) using the R package *adegenet*  
207 (Jombart & Ahmed, 2011) and *STRUCTURE* v2.3.4 (Pritchard et al., 2000). DAPC is a generic  
208 multivariate method that makes few assumptions about the underlying data and seeks to  
209 maximise between-group variation while minimising within-group variation. We ran DAPC with  
210 samples grouped by wintering grounds and by nursery grounds (Australian migratory corridor  
211 samples were excluded). Data were visualised by plotting samples by linear discriminant  
212 coordinates. In contrast, *STRUCTURE* attempts to group individuals into clusters that minimise  
213 deviations from the Hardy-Weinberg equilibrium and linkage disequilibrium. The fit of the data  
214 to  $K$  populations was assessed in *STRUCTURE* under the admixture and correlated allele  
215 frequency model, with and without prior information on the sampling locations of the data  
216 (location prior set as wintering ground). Ten replicates of  $K = 1 - 5$  were conducted, each with  
217 burn-ins of one million iterations and runs of ten million Markov chain Monte Carlo (MCMC)  
218 iterations, and convergence was assessed by visually inspecting the summary statistics (e.g.  $F_{ST}$ ).  
219 We used *CLUMPAK* to summarise the modes or distinct solutions for each value of  $K$   
220 (Kopelman et al., 2015) and assessed the most likely value of  $K$  using the mean log likelihood  
221 from across the ten runs, summarized using *STRUCTURE HARVESTER* (Earl & VonHoldt,  
222 2012). The relationship between population structure and geographic location was quantified  
223 using *ObStruct* (Gayevskiy et al., 2014).

224           We asked whether the phylogeographic pattern originally documented in the mtDNA by  
225 Patenaude et al., (2007) was still evident with our larger dataset by estimating a phylogenetic tree  
226 using *MrBayes* v3.2 (Ronquist et al., 2012) and sequences from all three right whale species (*E.*  
227 *australis*, *E. japonica* and *E. glacialis*). We used *MrBayes* v3.2 to simultaneously select the best

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228 model of evolution and construct a phylogenetic tree, by sampling across the substitution model  
229 space in the Bayesian MCMC analysis itself. The analysis was conducted using the sequences of  
230 the unique SRW mtDNA control region haplotypes and previously published sequences from  
231 North Atlantic (*E. glacialis*) and North Pacific (*E. japonica*) right whales (see Supplementary  
232 File 1 for accession numbers and Supplementary File 2 for the nexus file of SRW sequences  
233 used). We undertook two runs of *MrBayes*, each with two chains that were run for one million  
234 iterations, using the bowhead whale (*Balaena mysticetus*) sequence as an outgroup. We  
235 compared the standard deviation of the split frequencies ( $<0.01$ ) and the potential scale reduction  
236 factor (PSRF, should be close to 1) to detect whether convergence had been reached, and ran the  
237 program for additional iterations if required. We summarized the tree and branch length  
238 information after discarding the first 25% of trees as burn-in and used *MrBayes* to generate the  
239 consensus tree with clade credibility (posterior probability) values. We also constructed a median  
240 joining network (Bandelt et al., 1999) for the haplotypes using *POPART* (Leigh & Bryant, 2015)  
241 to examine the relationships and distributions of haplotypes (with  $\epsilon = 0$ ).

242

### 243 *Estimating contemporary and long-term gene flow*

244 We used the program *BayesAss v3.0* (Wilson & Rannala, 2003) to co-estimate recent migration  
245 rates (past two generations), individual assignment and ancestries, based on microsatellite  
246 genotypes. Initial runs were conducted to calibrate the mixing parameters and to ensure that  
247 acceptance rates were in the optimal range of 0.2-0.6. During this phase we adjusted the allele-  
248 frequency mixing parameter to 0.15 but decided to keep all other parameters at their default  
249 values (0.10). We then conducted five *BayesAss* runs of ten million iterations with initial burn-  
250 ins of one million iterations. Parameters were sampled every 1000 iterations and traces were

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251 visually checked for convergence in *TRACER v1.6* (Rambaut et al., 2014). We report median  
252 migration rates with 95% HPD interval from all runs and the mean assignment probabilities of  
253 individuals across the five runs.

254 We tested for sex-biased dispersal with the R package *hierfstat* (Goudet & Jombart,  
255 2015), looking for differences in  $F_{ST}$  and the variance of corrected assignment indices (vAIC)  
256 between males and females (Goudet et al., 2002). The significance of the difference was tested  
257 using null distributions generated with 1,000 permutations (Goudet et al., 2002).

258 We attempted to estimate long-term gene flow rates using the coalescent based program  
259 *LAMARC v 2.0*, as this program simultaneously estimates migration rates, growth rates and  $\theta$   
260 (Kuhner, 2006). In principle, this method can account for changes in abundance caused by  
261 whaling and also avoid positively biasing diversity estimates by accounting for migration  
262 (Kuhner, 2006). We used the Bayesian option for *LAMARC*, and ran two replicates, each  
263 comprising one chain with 100,000 sampled genealogies, sampled every 50<sup>th</sup> genealogy,  
264 discarding the first 25,000 samples of each search. To improve search performance of the  
265 Bayesian option, we followed the suggestion from the *LAMARC* manual of employing a search  
266 strategy with three heated chains (1.0, 1.1 and 1.3 respectively). We conducted one *LAMARC* run  
267 using all the microsatellite data, as the *LAMARC* manual recommends one longer run with  
268 heating to obtain the best results for the Bayesian option. Given the large size of the mtDNA  
269 dataset, we ran three replicates of *LAMARC*, each with a different set of 100 individuals ( $n = 25$   
270 each for Argentina, South Africa and New Zealand nursery areas and the Australian wintering  
271 habitat), randomly subsampled from the larger dataset without replacement. Long-term and  
272 whaling era migration rates were also estimated with ABC analyses (see below).

273 *Inferring historical gene flow and demographic history of SRWs*

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274 We employed approximate Bayesian computation (ABC) to test competing hypotheses regarding  
275 changes in  $N_e$  and gene flow from observed microsatellite data. These initial scenarios were  
276 generated by previous work characterizing the mtDNA phylogeographic pattern, which has been  
277 described as either consistent with continuous gene flow after divergence or isolation followed  
278 by secondary contact (Patenaude et al., 2007). The mtDNA data were not included in the ABC  
279 analyses as the hypotheses being tested were generated from the mtDNA phylogeny. To test the  
280 hypothesis that whaling could have impacted connectivity between wintering grounds, we  
281 included scenarios in which rates of gene flow rate change in the whaling era. As a type of null  
282 model, we include a scenario with no gene flow after divergence.

283 A total of six scenarios were examined (Figure 2): continuous gene flow following  
284 population divergence at a single migration rate  $M_H$  (Scenario 1) or two migration rates: one  
285 since divergence  $M_H$  and one since the whaling era  $M_W$  (Scenario 2); isolation following  
286 divergence, with either: no subsequent gene flow (Scenario 3); or gene flow at one migration rate  
287 since the whaling era  $M_W$  (Scenario 4), or one migration rate since secondary contact,  $M_C$   
288 (Scenario 5); or two migration rates: one since secondary contact,  $M_C$ , and one since the whaling  
289 era,  $M_W$  (Scenario 6).

290 All scenarios incorporated a reduction in  $N_e$  due to whaling, followed by a recovery (see  
291 Table 2 for prior distributions), and the timing of these events was fixed at nine and two  
292 generations before present, respectively. We assumed an average effective generation time of 25  
293 years (Taylor et al., 2007) and a per-generation mutation rate for the microsatellite loci of  $5 \times 10^{-4}$   
294 (Estoup et al., 2002). For each scenario, 100,000 coalescent simulations were run with  
295 *fastsimcoal2* (Excoffier & Foll, 2011) and 17 summary statistics (Supplementary Table 2), were  
296 calculated in *arlsumstat v3.5.2* (Excoffier & Lischer, 2010). We analysed the results in an ABC

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297 framework with the R package *abc* (Csilléry et al., 2012), using the neural networks algorithm  
298 (Blum & François, 2010) with 1% acceptance ratio to estimate posterior parameters, a method  
299 that is suitable for high-dimensional, correlated summary statistics (Csilléry et al., 2012). Model  
300 selection was conducted by calculating the posterior model probabilities and Bayes factors (BF)  
301 in the *abc* package. BF was calculated for all possible pairs of models and was interpreted  
302 following the scale of Jeffreys (1961; see Supplementary Table 3). The ability of the ABC  
303 approach to distinguish between the best-selected models was assessed using a cross-validation  
304 function in the *abc* package. In addition, we undertook posterior predictive checks using nine  
305 summary statistics not employed in the initial ABC analysis. Posterior predictive checks were  
306 carried out by sampling 1000 combinations of model parameters from the posterior distributions  
307 for scenarios and using these as the input for coalescent simulations in *fastsimcoal2* with the  
308 same settings as used for the initial scenarios. For each of the 1000 simulations per scenario, we  
309 calculated the 95% confidence intervals and determined whether these encompassed the  
310 observed value.

311

## 312 RESULTS

### 313 *Microsatellite genotyping and diversity statistics*

314 In total, 222 individuals were genotyped at an average of 16.2 of 17 microsatellite loci, with an  
315 estimated error rate of 0.7% per allele (for more information see Supplementary Material 1).  
316 Microsatellite-based diversity statistics were broadly comparable across ocean basins and  
317 nursery areas (Table 1). In contrast, the mitochondrial DNA data (Table 1) showed generally  
318 higher levels of diversity in the South Atlantic than in the Indo-Pacific nursery grounds.

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319 Permutations confirmed that this was a statistically significant difference for both nucleotide and  
320 haplotype diversity (at  $\alpha = 0.05$ ).

321 As the samples comprise overlapping generations, the estimates of  $N_e$  based on  
322 microsatellite loci actually reflect the number of effective breeders ( $N_b$ ) that produced the  
323 sample. Estimates of  $N_b$  were broadly similar across ocean basins and Argentinean and South  
324 African nursery grounds (Table 1; Supplementary Table 4). For the two individual Australian  
325 nursery grounds and the New Zealand wintering ground, the estimates of  $N_b$  had undefined upper  
326 boundaries, and for the former this is likely due to the small sample sizes. For the New Zealand  
327 wintering ground, we suggest it is due to the increased variance and lower precision found when  
328 using the bias-corrected linkage disequilibrium method in populations with large  $N_e$  (Waples &  
329 Do, 2010). However, the lower bound has been shown to be reliable in such cases (Waples,  
330 2010), so  $N_b = 192$  is probably a reasonable lower bound for the New Zealand wintering ground.

331

### 332 *Contemporary patterns of genetic diversity*

333 The AMOVA analyses and fixation indices indicated greater variation between ocean basins  
334 (AMOVA:  $F_{ST} = 0.126$  and  $\Phi_{ST} = 0.131$  for mtDNA,  $F_{ST} = 0.024$  for microsatellites, all at  $p < 0.01$ )  
335 than among wintering grounds within ocean basins ( $F_{ST} = 0.052$  and  $\Phi_{ST} = 0.082$  for mtDNA,  $F_{ST}$   
336  $= 0.004$  for microsatellites, all at  $p < 0.01$ ; see Table 3 and Supplementary Table 5 for fixation  
337 indices). Direct comparison of the Indo-Pacific and South Atlantic ocean basins yielded  
338 estimates of divergence for mtDNA at  $F_{ST} = 0.161$  and  $\Phi_{ST} = 0.189$  ( $p < 0.001$ ). The divergence  
339 for microsatellite loci was  $F_{ST} = 0.012$  (95% CI: 0.007, 0.018) and Jost's  $D = 0.041$  (95% CI:  
340 0.024, 0.063, all  $p < 0.001$ ).

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341           Microsatellite loci data clustered by ocean basins, based on the *STRUCTURE* analysis  
342 particularly with location prior set as nursery or wintering ground (Figure 3A, B). This was  
343 supported by log likelihood suggesting the best  $K = 2$ , with cluster corresponding to ocean basin,  
344 and the *ObStruct* analysis showing there was a strong ( $R^2 = 0.95$ ) and significant ( $p < 0.0001$ )  
345 correlation between ocean basin and genetic cluster. When no prior population information was  
346 provided, the highest likelihood was for  $K = 1$  (Figure 3), which is not surprising given that  
347 *STRUCTURE* has little power to resolve population structure  $F_{ST} < 0.02$  (Latch et al., 2006).  
348 However, when  $K = 2$ , the next best fitting  $K$ , was analysed with *ObStruct*, there was a  
349 significant correlation ( $p < 0.0001$ ) between ocean basin and genetic cluster ( $R^2 = 0.45$ ).

350           When grouped by wintering grounds, DAPC separated samples by ocean basins along  
351 linear discriminant 1 (LD1) and by wintering grounds within ocean basins along LD2 (Figure  
352 3C). There was overlap between Indo-Pacific wintering grounds, as described previously  
353 (Carroll et al., 2015), although when grouped by nursery grounds the distinctiveness of the  
354 southwest Australian samples was emphasized (Supplementary Figure 1).

355           As expected, the global mitochondrial phylogenetic tree for the three right whale species  
356 shows distinct clades into which North Pacific, North Atlantic and southern hemisphere  
357 individuals sort cleanly (Supplementary Figure 2). Convergence was indicated as average  
358 standard deviation of split frequencies was 0.005 and the PRSF was 1.00. Within SRWs, the  
359 Indo-Pacific sample contains just 13 haplotypes in a total sample of 769 individuals, while the  
360 South Atlantic sample contains 55 haplotypes (4.2 times as many) in a total sample of 558 (0.73  
361 times as many). The 13 Indo-Pacific haplotypes are broadly distributed through the SRW  
362 genealogy, as are many other common haplotypes (Figure 3D). This is the Type II  
363 phylogeographic pattern, described as pronounced phylogenetic gaps between some branches in



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364 a gene tree, with principal lineages showing no obvious geographic pattern (Awise, 2000) as  
365 previously described (Patenaude et al., 2007) for SRWs. However, the Indo-Pacific samples  
366 could possibly be derived from expansions from a few ancestral sequences, which could imply a  
367 small founding population.

368

### 369 *Estimates of contemporary and long-term gene flow*

370 We pooled Argentina and South Africa to represent the ‘South Atlantic’ and pooled New  
371 Zealand and Australia to represent the ‘Indo-Pacific’ for the *BayesAss* analysis, following the  
372 nomenclature previously used (Patenaude et al., 2007). Inspection of the traces for all five runs  
373 indicated convergence was achieved, with effective sample sizes for all parameters on each run  
374 >450. The migration rate estimates were consistent across runs (Supplementary Table 6) and the  
375 median migration rate (proportion of individuals that are migrants) from the South Atlantic to the  
376 Indo-Pacific was 0.038 (95% HPD 0.006, 0.083) and 0.028 (95% HPD <0.001, 0.068) in the  
377 reverse direction (Supplementary Figure 2). *BayesAss* analysis identified two putative first-  
378 generation and four second-generation immigrants, though mostly with low confidence  
379 (Supplementary Table 7). There was no evidence of sex-biased dispersal between ocean basins,  
380 based on either the  $F_{ST}$  or  $vAIC$  metrics using the microsatellite genotypes ( $p > 0.05$  for all  
381 analyses).

382         The three runs of the coalescent sampler *LAMARC* with different random subsamples of  
383 the mtDNA dataset produced similar patterns and so the results were combined for parameter  
384 estimation using *TRACER*. While the combined effective sample sizes were sufficient (>500),  
385 the traces did not show signs of convergence for all parameters. The *LAMARC* analysis using  
386 microsatellite markers also failed to converge, so we do not present the results.

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### 387 *Historical demography of the SRW*

388 The ABC analysis yielded near-zero posterior probabilities ( $<0.0001$ ) for the demographic  
389 scenario with no gene flow (scenario 3) and those with continuous gene flow (scenarios 1 and 2,  
390 see Supplementary Table 8). In contrast, the posterior model probability and BF estimates (Table  
391 2) strongly support the scenarios simulating secondary contact between previously isolated  
392 populations (scenarios 4 - 6) and we focus on the results of these scenarios in the rest of the  
393 paper (posterior distributions can be found in Supplementary File 3).

394 Of the three models simulating secondary contact, scenarios 5 and 6 showed the best fit  
395 to the data based on posterior model support and BF (Table 2B). The support for scenario 5,  
396 which had one constant migration rate since secondary contact, was marginally greater than for  
397 scenario 6, which had one post-secondary contact and one post-whaling migration rate (Table  
398 2B, Supplementary Figure 5), with a BF = 1.24, which is barely worth mentioning on Jeffreys'  
399 (1961) scale for interpreting BF. The cross validation analysis showed that while scenario 4 was  
400 distinguishable from scenarios 5 and 6, these two latter scenarios were misclassified as each  
401 other  $>30\%$  of the time. This implies that the ABC method was unable to distinguish between  
402 scenarios that differ by events that happened in the recent past ( $<10$  generations) given the  
403 available dataset. In light of this, and the fact that the post-contact and post-whaling migration  
404 estimates for scenario 6 were very similar to each other and to the post-contact estimate from  
405 scenario 5 (all  $<0.03$ ), we suggest that scenario 5 offers the most parsimonious scenario to  
406 explain the observed data (see Supplementary File 3 for graphs of model fit and prior and  
407 posterior distributions).

408 Overall, the evidence is consistent with the hypothesis that secondary contact was  
409 stimulated by environmental changes that occurred near the end of the LGM. Obvious candidates

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410 would include sea-level rise, which was dramatic and changed the spatial distribution of suitable  
411 wintering habitat (Scourse, 2013), potentially triggering increased dispersal in search of better  
412 places to calve and socialize. We were unable to resolve the timing of the initial secondary  
413 contact, as the estimates span 11-960 generations ago (corresponding to 275 – 24,000 years,  
414 assuming a 25-year effective generation time), which includes the beginning of the present warm  
415 interglacial period.

416

## 417 DISCUSSION

418 This first investigation of global diversity and population structure for SRW using both mtDNA  
419 and nuclear DNA markers highlights a complex interplay between forces promoting isolation  
420 (e.g., philopatry and migratory fidelity) and forces promoting connectivity (e.g., climate change).  
421 The ABC results robustly support a period of historical isolation was followed by secondary  
422 contact between ocean basins. As right whales can easily swim thousands of kilometers, both the  
423 isolation and its subsequent breakdown were likely the consequences of behavioural  
424 mechanisms, presumably the same ones that continue to isolate populations today, as reflected in  
425 the heterogeneity of gene-flow estimates across the Southern Hemisphere. The present data and  
426 analyses do not provide sufficient resolution to resolve debates about the impact of whaling on  
427 SRW genetic diversity, but they do bear on a number of general issues in population  
428 management.

429

### 430 *Connectivity through time: impacts of natural and anthropogenic changes*

431 The finding of isolation and secondary contact between the Indo-Pacific and South Atlantic  
432 suggests that SRWs in the two ocean basins had limited connectivity until less than 1,000

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433 generations ago (25,000 years, assuming a 25-year effective generation time). This implies that  
434 for thousands of generations after divergence, the populations were relatively isolated, with the  
435 most parsimonious explanation being behavioural mechanisms such as female philopatry,  
436 discussed in-depth below. The timing of secondary contact supports our hypothesis that the  
437 transition from the LGM to the Holocene precipitated the secondary contact, but other, more  
438 recent factors cannot be ruled out. The impact of profound climatic change, such as the transition  
439 to the Holocene after the LGM, will depend on the ecology of the species. For example, both  
440 Antarctic blue (*Balaenoptera musculus musculus*) and bowhead whales saw decreases in  
441 effective population sizes linked to the decline of their sea ice habitat after the LGM (Attard et  
442 al., 2015; Phillips et al., 2013). By contrast, the emergence of new breeding habitat and  
443 productive foraging areas coincident with deglaciation, reduction in sea ice and increasing  
444 productivity during the Holocene after the LGM, led to postglacial population expansion in a  
445 number of penguin species and southern elephant seals (*Mirounga leonina*) in the Southern  
446 Hemisphere (Younger et al., 2016). Other species have apparently adapted to new conditions;  
447 Pyenson & Lindberg (2011) suggest that the gray whale (*Eschrichtius robustus*) can switch prey,  
448 enabling the species to maintain a constant population size across glacial cycles.

449         The impact of glaciation on connectivity within species is less well studied than its  
450 impact on effective population sizes, but its effects would be expected to depend on dispersal  
451 ability, population density and ecological necessity or opportunity (Bérubé et al., 1998; Phillips  
452 et al., 2011). In the ice-adapted and vagile bowhead whale, heavy sea ice three thousand years  
453 ago did not prove a barrier to connectivity across the Holarctic, based on a comparison of  
454 historical and contemporary mtDNA data (Alter et al., 2012). In contrast, dispersal rates  
455 increased in the Steller sealion (*Eumetopias jubatus*) coincident with an increase in glaciation

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456 that disrupted breeding habitat (when effective population size was high; Phillips et al., 2011).  
457 We suggest that SRWs may have experienced something similar, when their breeding areas were  
458 disrupted by sea-level rise following the LGM, prompting increased dispersal between shifting  
459 constellations of winter breeding grounds.

460 Our point estimates of migration from the Indo-Pacific into the South Atlantic from  
461 *BayesAss* are tenfold higher than the estimates of post-contact migration from ABC. Whether  
462 this difference reflects a real, very recent increase in migration, or a bias in *BayesAss* estimates,  
463 probably linked to the violation of continuous migration assumption of the program, is not clear.  
464 A recent increase in migration could plausibly be linked to recovery from whaling. Allendorf et  
465 al., (2008) suggested that hunting could either increase directional gene flow into certain  
466 populations, for example, into low density areas, or it could decrease migration with concomitant  
467 reductions in population size and density. Increase in migration linked to population expansion  
468 and recolonisation has been seen in other marine mammals such as the migration from areas of  
469 high to low density implicated in the recovery of populations of gray seals (Brasseur et al.,  
470 2014). As our estimate of recent gene flow in SRW does not appear to be asymmetric, the  
471 change in migration rate could also reflect hunting's impact on behavioural processes across  
472 populations. Hunting appears to effect the timing of migratory events in sockeye salmon  
473 (*Oncorhynchus nerca*) (Quinn et al., 2007), as well as characteristics such as boldness (Leclerc et  
474 al., 2017) that could influence exploratory behaviour (although this is controversial; Mueller et  
475 al., 2014; Rollins et al., 2015). Disruption to breeding behaviour or aggregations could also have  
476 precipitate increased dispersal during or subsequent to the whaling era. For example, the  
477 disruption of humpback whale breeding aggregations is thought to have influenced meta-  
478 population dynamics (Clapham & Zerbini, 2015). This idea, the social aggregation hypothesis,

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479 holds that hunting-induced disruption to the humpback whale's social system led to movement of  
480 animals from low density to high density breeding aggregations as the species recovered from  
481 whaling (Clapham & Zerbini, 2015). Hunting, particularly in the early pre-industrial era, targeted  
482 coastal wintering grounds used by aggregations of SRWs as calving, socializing and breeding  
483 areas (Smith et al., 2012). Disruption of behaviours at wintering grounds by whaling could have  
484 prompted dispersal events in recent generations, just as disruption of wintering grounds by the  
485 expansion of shallow seas during the Holocene could have thousands of years prior.

486         An alternative explanation for a recent increase in migration rates is that the demographic  
487 history of the SRWs violates the assumptions of *BayesAss*, in which case the estimates of  
488 migration rate from this programme could be biased. *BayesAss* considers a constant population  
489 size scenario and implicitly assumes that migration is continuous through time. Linkage or  
490 gametic disequilibrium observed in a population is due to recent migration, which increases  
491 concomitantly with levels of genetic differentiation amongst populations. However, the  
492 demographic history of SRWs, with secondary contact following isolation and the demographic  
493 decline due to whaling, likely increased linkage disequilibrium beyond what is expected under  
494 continuous migration and constant population sizes. This would lead to an overestimate of  
495 migration rates. Simulation studies indicate that if the model assumptions are violated, *BayesAss*  
496 still performs well if migration rates are low ( $<0.01$ ) and  $F_{ST}$  is high ( $>0.10$ ) (Faubet et al., 2007),  
497 however, in the present study  $F_{ST}$  is fairly low ( $F_{ST} = 0.024$ ). Additional empirical and theoretical  
498 work should be directed toward resolving this biologically interesting question, which has  
499 potentially large implications for attempts to predict how SRWs might respond to future climate  
500 change.

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501 More generally, it is important to consider the limitations of methods used to infer  
502 connectivity in non-equilibrium situations. The ABC framework is highly flexible and can  
503 explicitly simulate and compare scenarios involving isolation with gene flow and isolation with  
504 secondary contact scenarios. Previous suggestions that coalescent-based methods may also be  
505 able to differentiate such models based on the timing of migration estimates have proven  
506 incorrect (Gaggiotti, 2011), based on both theoretical (Sousa et al., 2011) and simulation studies  
507 (Strasburg & Rieseberg, 2011). Such investigations would violate the assumption, common to  
508 many coalescent based methods, that immigration rates have been constant throughout the  
509 lifespan of the coalescent tree (Kuhner, 2006; Sousa et al., 2011). Violation of this assumption  
510 may have contributed to the lack of convergence of *LAMARC* analyses in our study, although  
511 other problems have been noted to affect analyses using coalescent-based methods (see Putman  
512 & Carbone, 2014).

513

### 514 *Migratory fidelity and circumpolar population structure*

515 The present analyses confirm previous findings of hierarchical global population structure in  
516 mtDNA haplotype data (Patenaude et al., 2007) using AMOVA and fixation indices and extend  
517 these finding to microsatellite markers (Table 3, Supplementary Table 5). In particular, we  
518 document low but statistically significant differentiation between the Argentinean and South  
519 African nursery grounds at nuclear loci (microsatellite  $F_{ST} = 0.001$ , Jost's  $D = 0.004$ ,  $p < 0.01$ )  
520 (Table 2 and Figure 3), and extends previous findings of stronger differentiation in mtDNA  
521 haplotype data (Patenaude et al., 2007).

522 Reduced connectivity between ocean basins is a common characteristic in cetaceans,  
523 which has been attributed to site fidelity, social structure and resource specialization in toothed

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524 whales, and to migratory fidelity in baleen whales (Bowen et al., 2016). Migratory fidelity, like  
525 other forms of philopatry or site fidelity, is hypothesized to be adaptive as it increased the  
526 chances of finding mates and/or suitable habitat, and may be favoured by natural selection by  
527 enhancing the maintenance of co-adapted gene complexes (Greenwood, 1980; Refsnider &  
528 Janzen, 2010; Stiebens et al., 2013). In addition to many baleen whale species, such as humpback  
529 whales (Baker et al., 2013), natal philopatry is found in all seven sea turtle species (Bowen et al.,  
530 2016), many shark (Chapman et al., 2015) and sea bird species (e.g., Milot et al., 2008), showing  
531 its ubiquity in migratory marine species.

532         We did not find evidence of sex-biased dispersal in SRWs, using indirect genetic  
533 methods based on the microsatellite genotypes. It might be that in SRWs, different genetic  
534 patterns are evident on distinct habitats across a migratory network, reflective of different  
535 patterns of gene flow or dispersal. For example, both males and females show long-term fidelity  
536 to nursery grounds, based on photo-identification and genotype recapture studies (Carroll et al.,  
537 2013; Cooke et al., 2001). Photo-identification studies, tracking individuals, and paternity  
538 analyses, showing recent patterns of gene flow, also indicate limited connectivity between  
539 calving grounds within ocean basins, based on studies from the Indo-Pacific (Carroll et al., 2012;  
540 Pirzl et al., 2009). In contrast, gene flow between individuals that use different calving grounds  
541 could occur on shared migratory corridors, as suggested in Australian migratory habitats based  
542 on a combination of photo-identification and genetic data (Carroll et al., 2015), or on shared  
543 feeding grounds. For example, whales from South African and Argentinean wintering grounds  
544 share summer feeding areas, based on photo-identification and stable isotope data (Best et al.,  
545 1993, Rowntree et al., 2001). This could facilitate mating between whales from different



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546 wintering grounds on migratory corridors or promote the temporary dispersal of whales between  
547 wintering grounds.

548         Sex biased dispersal is not necessarily common in migratory marine species. In a recent  
549 review, Chapman et al., (2015) found residency and site fidelity occurred in both sexes in more  
550 than 50 studies in sharks, although many other studies examined only one sex. In turtles, which  
551 show strong natal philopatry, genetic connectivity is attributed to the occasional wanderer  
552 (Bowen et al., 2016), rather than sex-biased dispersal. Even in a species with a similar life  
553 history pattern with strong female philopatry, the humpback whale, there was no evidence that  
554 dispersal was sex biased on a global scale, based on a large genetic analysis (Jackson et al.,  
555 2014).

556

### 557 *Uncertain impact of whaling-era events in ABC analyses*

558 The ABC analyses could not differentiate scenarios with differences in very recent generations,  
559 including between those scenarios with changes in gene flow linked to the whaling era (e.g.,  
560 between scenarios 5 and 6). This is consistent with findings that recent events are not accurately  
561 detected by the coalescent based methods due to data-driven and theoretical constraints (Boitard  
562 et al., 2016, Wakeley et al., 2016). In the light of this finding, we ran additional analyses and  
563 found that, with the current dataset, the method did not have the power to differentiate between  
564 the scenarios with and without a whaling-related bottleneck (See R code and Supplementary File  
565 3).

566         SRWs underwent a centuries-long demographic bottleneck due to whaling, and  
567 simulation studies suggest this reduced mtDNA haplotype number and diversity in the species  
568 (Jackson et al., 2008). Long-term exploitation of other cetacean species first hunted by pre-

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569 industrial whalers is also correlated with declines in genetic diversity (Alter et al., 2012; Waldick  
570 et al., 2002). For example, bowhead whales appear to have lost unique mitochondrial lineages in  
571 contemporary populations compared with historical samples, and this was attributed to habitat  
572 loss during the Little Ice Age and/or whaling (Alter et al., 2012). Any decline in diversity in  
573 nuclear genes like microsatellites is likely to be less severe than declines in mtDNA, given the  
574 larger effective population size. Indeed, high levels of nuclear diversity have been found in some  
575 great whale species, supporting the hypothesis that they have had large, long-term effective  
576 population sizes (e.g. Ruegg et al., 2013). Furthermore, low levels of genetic diversity in pygmy  
577 blue whales (*Balaenoptera musculus brevicauda*) were found to be related to a founder event,  
578 rather than recent whaling, in an ABC study using both mtDNA and microsatellite data (Attard et  
579 al., 2015). These examples highlight the importance of placing recent anthropogenic impacts in  
580 the long-term evolutionary context of a species.

581         The present study provides what appear to be the first estimates of  $N_b$  for SRWs, using  
582 the bias-corrected linkage disequilibrium method (Waples, 2006), which produced similar results  
583 for the South Atlantic ( $N_b = 365$ , 95% CI 241, 712) and Indo-Pacific ocean basins ( $N_b = 331$ ,  
584 95% CI 230, 556). The estimates of  $N_b$  for the Australian, Argentinean and South African  
585 wintering grounds were broadly similar, in the low hundreds. Morin et al., (2012) estimated  $N_b$   
586 for bowhead whale stocks using 22 microsatellite markers and also found estimates in the low  
587 hundreds: the small effective population size was attributed to whaling, but might also be due to  
588 life history traits similar across these related species. Given that the demographic bottleneck in  
589 SRWs happened in recent generations, it is likely that genomic-based methods that estimate  
590 effective population sizes through time using linkage disequilibrium methods (e.g., Hollenbeck

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591 et al., 2016) will be needed to determine the extent to which whaling impacted levels of nuclear  
592 genetic diversity.

593 As with all ABC studies, we could only compare a limited number of distinct hypotheses  
594 (Beaumont, 2010): in the present case, these were suggested by previous analyses of mtDNA  
595 data (Patenaude et al., 2007). Future studies should investigate models that explicitly incorporate  
596 sex-biased dispersal and allow migration rates to vary in response to anthropogenic disturbance  
597 and other environmental variables such as bathymetry. Given that we could decisively reject the  
598 continuous migration scenarios (1-3) in favor of the isolation and secondary contact scenarios (5  
599 and 6) using only 17 polymorphic nuclear markers, future studies using whole-genome data seem  
600 likely to have power to estimate many such parameters.

601

### 602 *Conservation implications of findings*

603 Effective management of migratory species requires consideration of both the overall  
604 migratory network and the different migratory habitats it encompasses. Long term photographic  
605 and genetic monitoring programs show that females return regularly to their natal calving  
606 grounds across decades (Carroll et al., 2013; Rowntree et al., 2001). As recruitment is dependent  
607 upon female reproductive success, the persistence of these calving grounds is likely reliant on  
608 these philopatric females (Awise, 2000), and is unlikely to be supplemented by recruitment from  
609 other calving grounds (Carroll et al., 2011; Clapham et al., 2008). Therefore, SRW calving  
610 grounds seem likely to be substantially demographically independent, which would imply that  
611 they qualify as separate sub-populations under the population concepts advocated by Wade and  
612 Angliss (1997). On an evolutionary scale, female fidelity to wintering grounds will have

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613 contributed to significant differences in mtDNA haplotype frequencies between wintering  
614 grounds, as presented here and in previous studies (Baker et al., 1999; Patenaude et al., 2007).

615         On a broader scale, vertical transmission of migratory preferences to both feeding and  
616 calving or breeding areas suggests an argument for ecological or demographic distinctiveness of  
617 the ocean basins, under the framework advocated by Crandall et al., (2000). While not explicitly  
618 mentioned by those authors, behavioural variability is arguably as valid as morphological  
619 variability when deciding if individuals from different populations are exchangeable. Vertical  
620 transmission of socially learned behaviour, such as learned migratory routes, can shape  
621 adaptation, and by favouring the conservation of migratory traditions, promote isolation between  
622 populations (Brakes & Dall, 2016; Whiten, 2017). Recently it has been suggested that this  
623 ‘second inheritance system’ needs to be integrated into modeling and management of migratory  
624 marine species that face challenges from climate change, as migratory conservatism could limit  
625 responses to a changing environment (Keith & Bull, 2017). Therefore, we suggest that SRWs in  
626 the two ocean basins should be considered distinct population segments. The ABC and genetic  
627 analyses (*STRUCTURE* and  $F_{ST}$  results) reject the null hypothesis of historical and contemporary  
628 genetic exchangeability, and the well-documented behavioural mechanisms are consistent with  
629 the observed levels of genetic differentiation. Our findings also suggest that non-equilibrium  
630 scenarios should be considered in future studies of population structure in migratory marine  
631 species. ABC techniques will make this feasible, even where low levels of differentiation and  
632 complex population histories pose severe challenges for other inference methods.

633

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657

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### 658 CONFLICT OF INTEREST STATEMENT

659 No author has a conflict of interest.

660

### 661 DATA ARCHIVING

662 Supplementary File 1: Data on the mitochondrial DNA sequences compiled and generated for  
663 this study, including haplotype codes, GenBank accession numbers and original citation, where  
664 applicable.

665 Supplementary File 2: Nexus file of the mtDNA haplotypes.

666 Supplementary File 3: Posterior distributions of ABC simulations

667 CircumpolarSRW\_SupportingInfo\_Jan18.docx: Supplementary Materials 1-3, Supplementary  
668 Tables 1-8 and Supplementary Figures 1-5 can be found in the Supporting Information file.

669

670 Microsatellite data will be submitted to dryad upon acceptance and bash and R code used in this  
671 paper can be found at [https://github.com/emmcarr/Circumpolar\\_analysis](https://github.com/emmcarr/Circumpolar_analysis).

672

673

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Circumpolar SRW connectivity through time

1061 Table 1: Summary of the number of samples and diversity statistics for mitochondrial DNA control region (mtDNA) and  
 1062 microsatellite markers (17 loci) for southern right whale nursery areas in Argentina, (ARG), South Africa (SAF), New Zealand (NZ)  
 1063 and southwest Australia (SWA), southeast Australia (SEA), the overall Australian wintering habitat (AUS-WH) and ocean basins  
 1064 (Indo-Pacific; IP and South Atlantic; SA). For mtDNA, the sample size ( $n_m$ ), number of haplotypes ( $n_{hap}$ ), standardised haplotype  
 1065 richness ( $n_{Shap}$ ), haplotype ( $h$ ) and nucleotide ( $\pi$ ) diversities (with standard deviation,  $\pm SD$ ) are shown. For microsatellites, the sample  
 1066 size ( $2n$ ), standardized allele richness ( $k$ ) and observed and expected heterozygosities ( $H_{OBS}$  and  $H_{EXP}$ ) and effective population size  
 1067 ( $N_e$ ; lowest allele frequency 0.02 and jackknifed confidence intervals CI) are shown.

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Region	$n_m$	$n_{hap}$	<i>mtDNA</i>			$2n$	$k \pm SD$	<i>microsatellites</i>		$N_e$ (95% CI)
			$n_{Shap} \pm SD$	$h \pm SD$	$\pi \pm SD$ (%)			$H_{OBS} \pm SD$	$H_{EXP} \pm SD$	
ARG	208	28	8.91 $\pm$ 1.24	0.94 $\pm$ 0.01	2.27 $\pm$ 1.16	92	5.37 $\pm$ 1.49	0.72 $\pm$ 0.03	0.77 $\pm$ 0.03	181 (120, 344)
SAF	350	37	9.03 $\pm$ 1.28	0.94 $\pm$ 0.01	2.47 $\pm$ 1.26	94	5.47 $\pm$ 1.38	0.71 $\pm$ 0.04	0.76 $\pm$ 0.03	239 (142, 656)
SA	558	55	10.04 $\pm$ 1.10	0.97 $\pm$ 0.01	2.52 $\pm$ 1.28	186	5.46 $\pm$ 1.45	0.72 $\pm$ 0.03	0.76 $\pm$ 0.03	365 (241, 712)
SWA	16	5	4.44 $\pm$ 0.63	0.71 $\pm$ 0.09	1.79 $\pm$ 0.10	34	5.16 $\pm$ 1.25	0.80 $\pm$ 0.04	0.78 $\pm$ 0.02	195 (61, $\infty$ )
SEA	12	5	5.71 $\pm$ 0.92	0.82 $\pm$ 0.07	2.17 $\pm$ 1.22	24	5.39 $\pm$ 1.37	0.80 $\pm$ 0.04	0.78 $\pm$ 0.02	317(49, $\infty$ )
AUS-WH	77	10	5.32 $\pm$ 1.06	0.78 $\pm$ 0.03	1.90 $\pm$ 0.99	156	5.47 $\pm$ 1.35	0.78 $\pm$ 0.03	0.78 $\pm$ 0.02	286 (169, 792)
NZ	692	11	3.88 $\pm$ 0.83	0.69 $\pm$ 0.01	1.49 $\pm$ 0.79	102	5.41 $\pm$ 1.47	0.72 $\pm$ 0.03	0.76 $\pm$ 0.03	412 (192, $\infty$ )
IP	769	13	4.10 $\pm$ 0.90	0.71 $\pm$ 0.01	1.60 $\pm$ 0.84	258	5.46 $\pm$ 1.37	0.76 $\pm$ 0.03	0.78 $\pm$ 0.03	331(230, 556)
Total	1327	60	7.91 $\pm$ 1.47	0.89 $\pm$ 0.01	2.21 $\pm$ 1.13	442	5.54 $\pm$ 1.44	0.74 $\pm$ 0.03	0.77 $\pm$ 0.03	-

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## Circumpolar SRW connectivity through time

1073 Table 2: Statistics for the approximate Bayesian computation (ABC) analysis of the historical demography of the southern right whale. A. Prior  
 1074 log-uniform distributions used for ABC analysis and posterior values obtained for the South Atlantic (SA) and Indo-Pacific (IP) ocean basins  
 1075 under Scenarios 4 - 6. Posterior mode and 95% HPDs are reported for migration rates ( $M_C$ : constant migration rate since secondary contact;  $M_W$ :  
 1076 migration rate since whaling era), effective population sizes ( $N_e$ ), and time in generations since secondary contact (CONTACT) and population  
 1077 divergence (DIVERGENCE). Effective population sizes are shown schematically in Figure 2 and are divided into historical or pre-whaling (HIST  
 1078  $N_e$ ), bottleneck (BOT  $N_e$ ) and recovery (REC  $N_e$ ). B. Posterior support, as shown by the posterior model probability, Bayes factor (relative to  
 1079 Scenario 5) and number of posterior predictive summary statistics that encompassed observed value.

A.	Prior	Scenario 4	Scenario 5	Scenario 6
Migration rate since secondary contact ( $M_C$ )				
$M_C$ SA to IP	0.001-0.50	-	0.0281 (0.0087, 0.2068)	0.0114 (0.0023, 0.4259)
$M_C$ IP to SA	0.001-0.50	-	0.0008 (0.0002, 0.0825)	0.0128 (0.0015, 0.4349)
Migration rate since whaling era ( $M_W$ )				
$M_W$ SA to IP	0.001-0.50	0.0164 (0.0034, 0.0717)	-	0.0025 (0.0002, 0.0830)
$M_W$ IP to SA	0.001-0.50	0.0235 (0.0052, 0.2091)	-	0.0025 (0.0013, 0.0718)
Effective population sizes ( $N_e$ )				
HIST $N_e$ SA	1,000-100,000	3,874 (1,057, 80, 909)	3,916 (1,131, 85,781)	3,188 (920, 65,783)
HIST $N_e$ IP	1,000-100,000	4,635 (1,275, 92,942)	3,880 (1,131, 82,748)	3,908 (973, 88,744)
BOT $N_e$ SA	20-2,000	128 (34, 2,447)	90 (23, 2,216)	74 (21, 1,430)
BOT $N_e$ IP	20-2,000	88 (22, 1,936)	88 (23, 1,743)	111 (29, 1,998)
REC $N_e$ SA	1,000-20,000	1,358 (466, 9,433)	888 (344, 8,126)	2,494 (706, 15,728)
REC $N_e$ IP	100-20,000	4,447 (1,179, 24,463)	2008 (814, 10,436)	2,013 (660, 12,851)
Timing (generations)				
CONTACT	10-100,000	Fixed	38 (12, 962)	74 (20, 2,187)
DIVERGENCE	2,000-200,000	189,621 (122,048, 200,959)	194,697 (103,040, 209,241)	198,944 (109,871, 211,017)
B.		Scenario 4	Scenario 5	Scenario 6
Posterior model probability		0.0048	0.5614	0.4338
Bayes factor		117.14	1.00	1.29
Posterior predictive checks		6/9	7/9	7/9

## Circumpolar SRW connectivity through time

1080 Table 3: Genetic differentiation indices between southern right whale southern right whale nursery areas in Argentina, (ARG), South Africa  
 1081 (SAF), New Zealand (NZ) and southwest Australia (SWA), southeast Australia (SEA), and the overall Australian wintering habitat (AUS-WH).  
 1082 Pairwise  $F_{ST}$  based on mtDNA haplotype frequencies (bottom left quadrant) and microsatellite loci (top right quadrant). The 95% confidence  
 1083 intervals for microsatellite-based  $F_{ST}$ , shown in parentheses, was estimated using bootstrapping over loci (999 permutations).

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	ARG-WG	SAF	SWA	SEA	AUS-WH	NZ
ARG		0.001** (0.000, 0.003)	0.021*** (0.013, 0.031)	0.022*** (0.007, 0.021)	0.013*** (0.008, 0.019)	0.012*** (0.006, 0.019)
SAF	0.048***		0.023*** (0.012, 0.034)	0.017** (0.005, 0.031)	0.014*** (0.008, 0.020)	0.013*** (0.007, 0.019)
SWA	0.143***	0.136***		0.013* (0.000, 0.028)	-	0.016** (0.001, 0.035)
SEA	0.104***	0.098**	0.098*		-	0.000 (0.000, 0.003)
AUS-WH	0.123***	0.115***	-	-		0.004** (0.000, 0.010)
NZ	0.190***	0.189***	0.142***	0.000	0.073***	

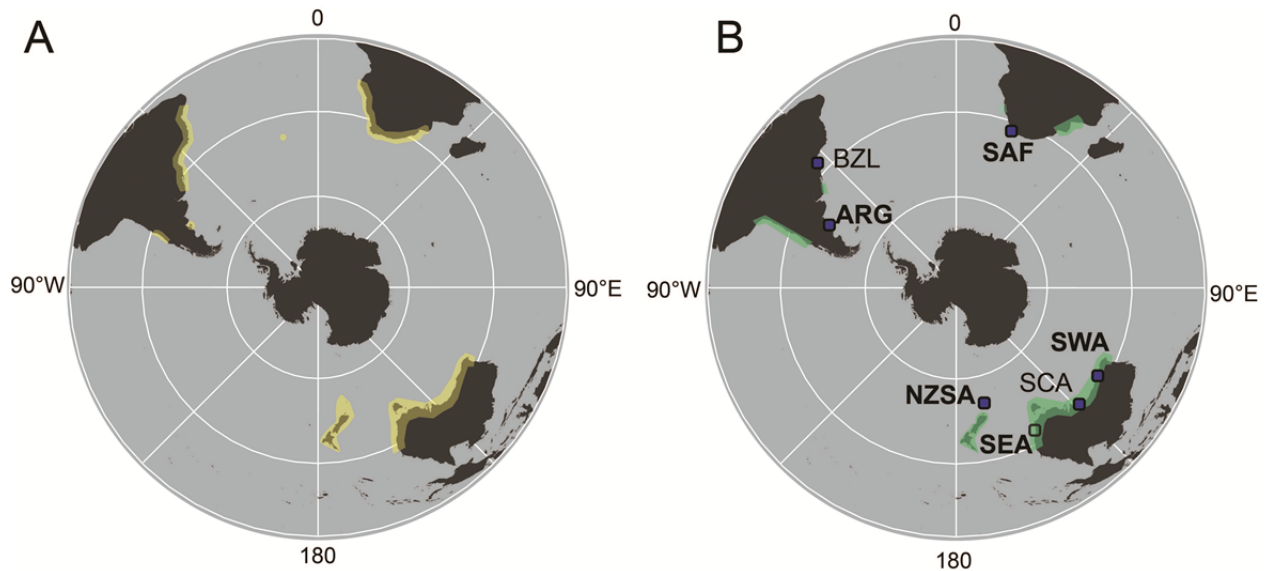
1085 \* $p < 0.05$ ; \*\* $p < 0.01$ , \*\*\* $p < 0.001$

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## Circumpolar SRW connectivity through time

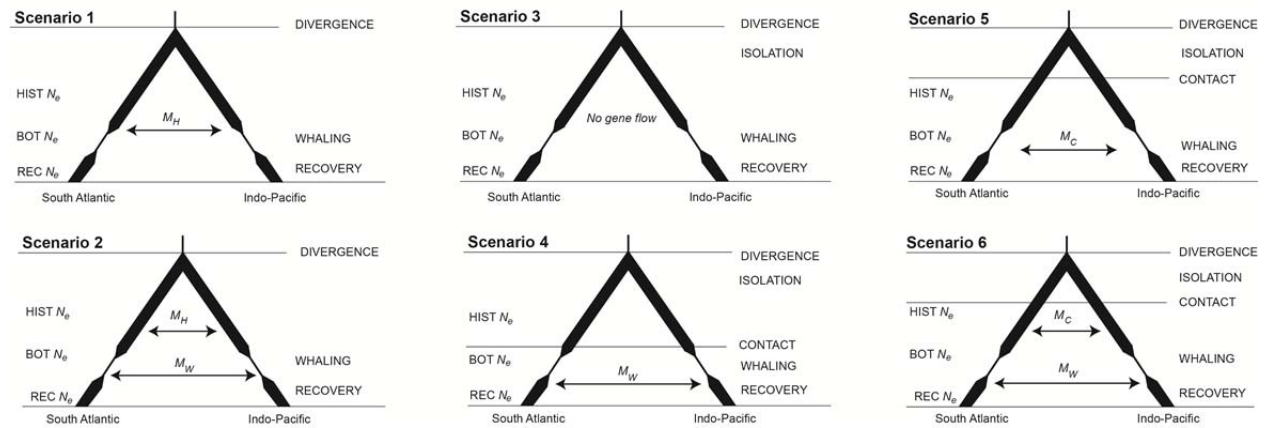


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1090 Figure 1: Map of A. historical and B. contemporary southern right whale winter habitat. The  
1091 contemporary distribution is divided into large wintering aggregations (blue circles) and the  
1092 areas with sporadic sightings (green shading: see Supplementary Material 2 for references).

1093 Samples included in this study are from nursery grounds with bold acronyms: ARG (Argentina),  
1094 SAF (South Africa), SWA (southwest Australia), and NZSA (New Zealand sub-Antarctic), but  
1095 not from the BZL (Brazilian) and SCA (southcentral Australia) nursery grounds, also marked on  
1096 the map. Also included are samples from the SEA nursery ground (southeast Australia, marked  
1097 by black circle) and mainland New Zealand wintering habitat, which are part of the sporadic  
1098 sightings.

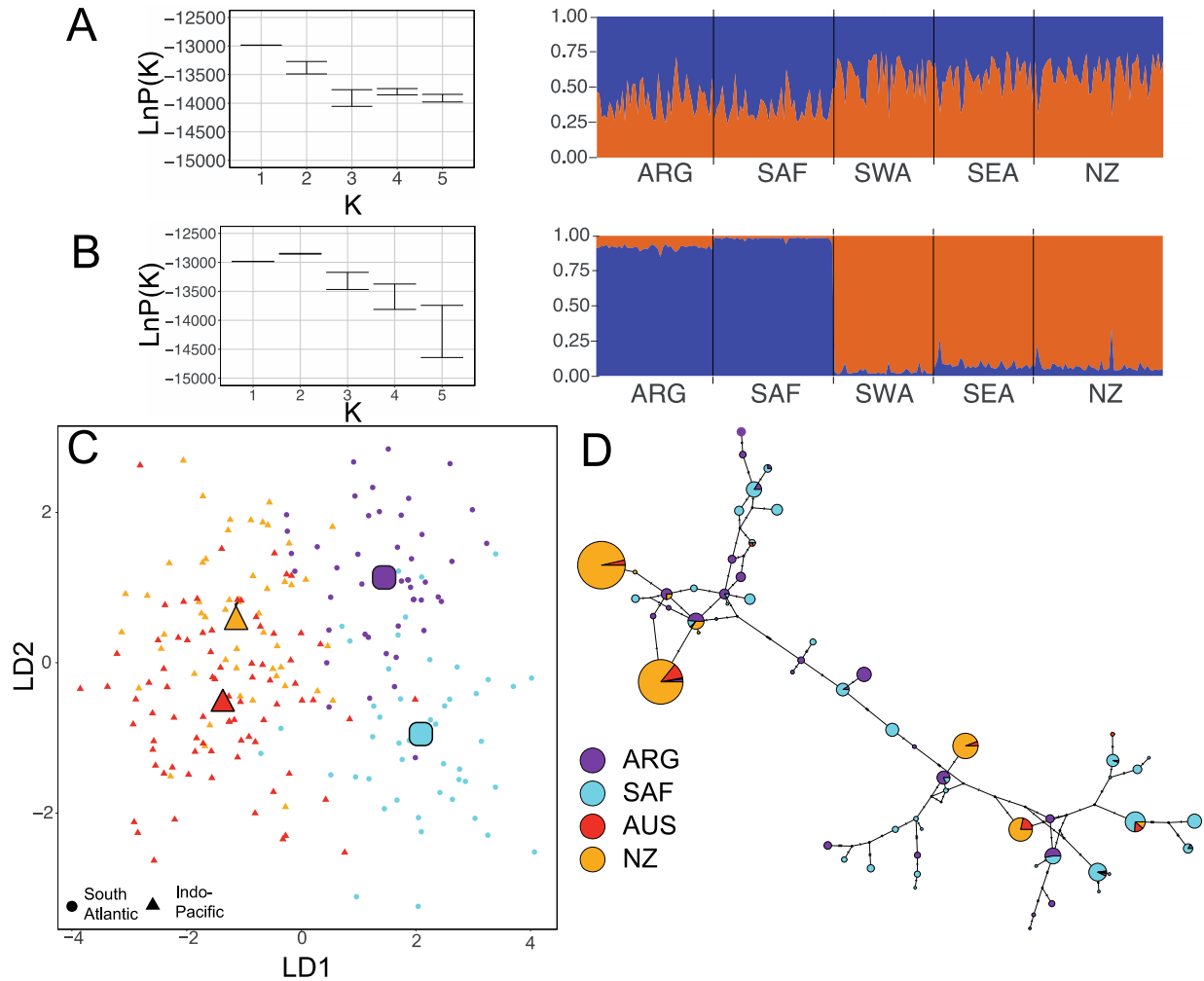
## Circumpolar SRW connectivity through time



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1100 Figure 2: Scenarios compared using the approximate Bayesian computation framework. The six  
 1101 scenarios include continuous gene flow following population divergence with migration varying  
 1102 by scenario; Scenario 1: single migration rate  $M_H$ ; Scenario 2: two migration rates: one since  
 1103 divergence  $M_H$  and one since the whaling era  $M_W$ ; or isolation following divergence, with either:  
 1104 Scenario 3: no subsequent gene flow; Scenario 4: gene flow at one migration rate since the  
 1105 whaling era  $M_W$ ; Scenario 5: one migration rate since secondary contact,  $M_C$ ; or Scenario 6:  
 1106 migration rates: one since secondary contact,  $M_C$ , and one since the whaling era,  $M_W$  (Scenario  
 1107 6). In all scenarios, the populations diverge at time DIVERGENCE and maintain one HIST  $N_e$   
 1108 until whaling, when each population declines to bottleneck population size BOT  $N_e$  during the  
 1109 whaling era and subsequently recover to REC  $N_e$  population size.

## Circumpolar SRW connectivity through time



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1111 Figure 3: Inference of population structure of southern right whale wintering habitats. Samples  
 1112 collected in Argentina (ARG) and South Africa (SAF) are pooled to form the South Atlantic  
 1113 dataset; samples from Australia (AUS) and New Zealand (NZ) are pooled to form the Indo-  
 1114 Pacific dataset. **A and B:** *STRUCUTRE* results (left); mean log likelihood ( $\text{LnP}(K)$ ), for  $K = 1 -$   
 1115 5, and (right) the proportion of each individual's genome that assigns to each cluster when  $K = 2$   
 1116 for (A) standard admixture setting and (B) location prior implemented **C.** Individuals plotted by  
 1117 linear discriminants (LD) from DAPC conducted with samples grouped by wintering ground.  
 1118 The large symbols show the centroid of each wintering ground. **D.** Median joining haplotype

## Circumpolar SRW connectivity through time

- 1119 network of mtDNA haplotypes. Haplotypes are coloured by wintering ground they were sampled  
1120 in, using key shown. Inferred, unsampled haplotypes are shown by small black circles.



