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1 **Title:** Outlier SNPs detect weak regional structure against a background of genetic
2 homogeneity in the Eastern Rock Lobster, *Sagmariasus verreauxi*

3

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32

33 **Abstract**

34 Genetic differentiation is characteristically weak in marine species making assessments
35 of population connectivity and structure difficult. However the advent of genomic
36 methods have increased genetic resolution, enabling studies to detect weak, but
37 significant population differentiation within marine species. With an increasing number
38 of studies employing high resolution genome-wide techniques, we are realising the
39 connectivity of marine populations is often complex and quantifying this complexity
40 can provide an understanding of the processes shaping marine species genetic structure
41 and to inform long-term, sustainable management strategies. This study aims to assess
42 the genetic structure, connectivity and local adaptation of the Eastern Rock Lobster
43 (*Sagmariasus verreauxi*), which has a maximum pelagic larval duration of 12 months
44 and inhabits both subtropical and temperate environments. We used 645 neutral and 15
45 outlier SNPs to genotype lobsters collected from the only two known breeding
46 populations and a third episodic population — encompassing *S. verreauxi*'s known
47 range. Through examination of the neutral SNP panel, we detected genetic homogeneity
48 across the three regions, which extended across the Tasman Sea encompassing both
49 Australian and New Zealand populations. We discuss differences in neutral genetic
50 signature of *S. verreauxi* and a closely-related, co-distributed rock lobster, *Jasus*
51 *edwardsii*, determining a regional pattern of genetic disparity between the species,
52 which have largely similar life histories. Examination of the outlier SNP panel detected
53 weak genetic differentiation between the three regions. Outlier SNPs showed promise in
54 assigning individuals to their sampling origin and may prove useful as a management
55 tool for species exhibiting genetic homogeneity.

56 **Introduction**

57 Researchers and resource managers traditionally believed that genetic homogeneity was
58 the only genetic structure possible for a marine species with a pelagic larval duration
59 (PLD) in the order of months to years. As the ocean has few physical barriers, species
60 with longer PLDs have the potential to disperse over larger geographical scales (Shanks
61 et al. 2003; Siegel et al. 2003), enhancing gene flow between geographically isolated
62 populations. Early population genetic studies, limited to a small number of neutrally
63 evolving genetic markers, often lacked statistical power to detect population divergence
64 (Ouborg et al. 1999; Allendorf 2017) characteristic of many marine species (Allendorf
65 et al. 2010); reinforcing the assumption of high connectivity between populations in the
66 marine environment. However, with the advent of powerful genomic techniques, large
67 panels of Single Nucleotide Polymorphisms (SNPs) have increased genetic resolution,
68 enabling studies to detect weak, but significant population differentiation within marine
69 species (Benestan et al. 2015; Araneda et al. 2016; Villacorta-Rath et al. 2016).

70

71 Using high resolution genomic methods, such as RADSeq (Baird et al. 2008; Peterson
72 et al. 2012) and DArTSeq (Sansaloni et al. 2011), enables analyses to differentiate
73 between neutrally evolving SNPs and “outlier” SNPs — loci with higher genetic
74 divergence than expected under neutral conditions (Perez-Figueroa et al. 2010). The
75 higher genetic divergence detected in these loci is potentially caused by environmental
76 selection, however it should be noted that outlier loci may also be detected due to Type
77 I error or demographic processes, such as range-expansions and pre- or post-zygotic
78 isolation (Bierne et al. 2011). Nevertheless, outlier loci are often more powerful than
79 neutral SNPs in delineating genetic structure and reliably assigning individuals to

80 sampling regions in species exhibiting genetic structure (Freamo et al. 2011; Milano et
81 al. 2014; Araneda et al. 2016; Villacorta-Rath et al. 2016). Furthermore, if outlier SNPs
82 can be linked to biological function, they may provide useful insight into the ecological
83 drivers of adaptation within their environment.

84

85 With an increasing number of studies employing high resolution genome-wide
86 techniques, we are realising that the connectivity of marine populations is often
87 complex: influenced by a multitude of factors including local oceanographic features,
88 life-history factors and historical environmental changes (Zardoya et al. 2004). Species
89 that occupy the same geographical location, are closely related and/or have similar life-
90 history traits can exhibit markedly different patterns of genetic structure (Ovenden et al.
91 2013; Holland et al. 2017; Momigliano et al. 2017), indicating that the traditional
92 assumption of high population connectivity is inappropriate for marine species.

93 Understanding and quantifying the complexity of connectivity in the marine
94 environment is important on an evolutionary scale to understand processes that shape
95 the genetic structure in marine species, but also on a contemporary scale to inform long-
96 term, sustainable conservation and management strategies (Hauser and Carvalho 2008;
97 Ovenden et al. 2013; Bernatchez et al. 2017).

98

99 Population structure and connectivity in the Eastern Rock Lobster, *Sagmariasus*
100 *verreauxi*, is currently poorly understood. This species supports commercial fisheries in
101 New South Wales (NSW), Australia (NSW Department of Primary Industries 2007) and
102 in the North Island of New Zealand (NZ; Kensler and Skrzynski 1970). Separate
103 management strategies exist for both countries based on the results of an early genetic

104 assessment, which used six mitochondrial regions, indicating separate genetic
105 populations in NSW and NZ (Brasher et al. 1992). While *S. verreauxi* are yet to be
106 assessed with high resolution genetic markers, SNPs recently confirmed a trans-Tasman
107 genetic break in the co-distributed, closely related, commercially important Southern
108 Rock Lobster, *Jasus edwardsii* (Villacorta-Rath et al. 2016). Oceanographic models
109 indicate that trans-Tasman gene flow for both species of lobster is possible due to their
110 long PLDs (Chiswell et al. 2003); microsatellite studies have indicated that for *J.*
111 *edwardsii*, trans-Tasman gene flow occurs at levels low enough to maintain genetic
112 structure (Thomas and Bell 2013). As *S. verreauxi* and *J. edwardsii* have many similar
113 life-history characteristics, such as long pelagic larval durations, high fecundity and
114 restricted breeding times (Table 1), we could expect the subdivision detected for *J.*
115 *edwardsii* to be mirrored in *S. verreauxi* populations. However these lobster species do
116 exhibit some differences in their life-history, such as geographically restricted vs
117 unrestricted breeding locations and large vs small migratory movements (Table 1),
118 which can result in disparate patterns of genetic structure (Ovenden et al. 2009).
119 Comparing and contrasting the genetic structure of closely related, co-distributed
120 species provide insights into the factors responsible for shaping genetic structure in the
121 marine environment (Kelly and Palumbi 2010).

122

123 *Sagmariasus verreauxi* inhabits a wide latitudinal range, covering sub-tropical to
124 temperate environments. The two geographically restricted breeding grounds occur in
125 the subtropical environments of northern New South Wales, eastern Australia
126 (Montgomery 1992) and Cape Reinga, New Zealand (Booth 1986), while a third small,
127 non-breeding population occurs in temperate Tasmania, the southernmost area of

128 Australia (Montgomery et al. 2009; Fig. 1). Distribution across heterogeneous
129 environments, together with limited breeding sites, suggest that spatially varying
130 selection may play a role in shaping the adaptive genetic structure of *S. verreauxi*.
131

132 *Sagmariasus verreauxi* has been caught in Tasmanian waters since 1886 (Saville-Kent
133 1886), as bycatch of the *J. edwardsii* focussed Tasmanian Rock Lobster Fishery.
134 Tasmanian *S. verreauxi* are currently rare and recruitment into the population is
135 irregular. Recruits are believed to originate in NSW waters, and are transported to
136 Tasmania by the southerly flowing East Australian Current (EAC; Gardener et al. 2000;
137 Pecl et al. 2009). However, evidence for this is anecdotal and originates from the
138 observation of a large number of *S. verreauxi* recruits settling on Tasmania's east coast,
139 coinciding with the occurrence of a strong EAC (Gardener et al. 2000). Importantly, no
140 records exist of egg-bearing females occurring within Tasmanian waters (Pecl et al.
141 2009), despite intensive fishing and monitoring practices in the area. Due to predictions
142 of climate change induced EAC intensification (Cai et al. 2005; Ridgway and Hill
143 2012), there is some concern that this species may undergo a population expansion and
144 establish a breeding population in Tasmania in the future, which may have detrimental
145 effects on local *J. edwardsii* populations (Pecl et al. 2009; Robinson et al. 2015). Thus,
146 it is important to clarify the origins of the Tasmanian recruits to gain an understanding
147 of the likely response of this peripheral population to intensification of the southward
148 EAC penetration in the future.

149

150 In this study, we used double digest Restriction-site Associated DNA sequencing
151 (ddRADSeq) to identify neutral and outlier SNPs in order to assess the genetic

152 structure, connectivity and local adaptation between *S. verreauxi* populations.
153 Specifically, we aimed to clarify whether NSW and NZ *S. verreauxi* populations consist
154 of a single panmictic stock or mirror the genetic structure detected in the closely related
155 *J. edwardsii*. Dependant on the genetic structure detected, we compared and contrasted
156 the times of population divergence and life-history of both rock lobster species in an
157 attempt to understand the biological factors shaping their genetic structure. We also
158 aimed to determine whether evidence of self-recruitment exists for the Tasmanian
159 population and, if not, the most likely source of Tasmanian recruits.

160

161 **Materials and Methods**

162 **Tissue collections**

163 A total of 90 *Sagmariasus verreauxi* tissue samples were obtained from three regions
164 (NSW, NZ, TAS) spanning the species range in 2013 and 2014 (Table 2; Fig. 1). NSW
165 Department of Primary Industries spawning stock and commercial catch surveys
166 provided samples from NSW and the NZ Rock Lobster Industry Council provided
167 samples from NZ. There is no commercial *S. verreauxi* fishery in Tasmania; TAS
168 samples were opportunistically sourced from both fishers and Stanley Seaquarium (a
169 processing facility retaining *S. verreauxi* bycatch in captivity). Tissue samples were
170 taken from either the telson, pleopod or leg and stored in 90% ethanol at -80°C.

171

172 **Molecular techniques**

173 Total genomic DNA was extracted from approximately 20-mg of tissue using a DNeasy
174 Blood and Tissue Kit (Qiagen). DNA samples were divided into two groups for library
175 preparation, with each group including three intra- and three inter-library replicates.

176 Replicate pairs were sourced from a single DNA extraction, but were treated as separate
177 samples during library preparation. Libraries were processed using a modified version
178 of Peterson et al. (2012) ddRADSeq protocol (Supplementary Appendix 1). Libraries
179 were sequenced as 100 base pairs (bp) single end (SE) reads on two lanes of an Illumina
180 HiSeq 2500 by the Australian Genome Research Facility (AGRF; Melbourne,
181 Australia).

182

183 **Preliminary quality control of raw sequencing data**

184 Raw read quality was assessed with FASTQC v0.10.1 (Babraham Bioinformatics
185 2007). Human and bacterial contaminants were identified using KRAKEN v0.10.4
186 (Wood and Salzberg 2014) and subsequently removed. TRIMMOMATIC v0.32 (Bolger
187 et al. 2014) was used to remove reads with an average quality score < Phred 28. Reads
188 matching mitochondrial DNA (mtDNA) were removed with a custom KRAKEN
189 database consisting of *S. verreauxi* mtDNA (Doyle et al. 2015). The remaining data
190 were demultiplexed and trimmed to 75-bp using ‘process_radtags’ from STACKS v1.29
191 (Catchen et al. 2011).

192

193 ***De novo* assembly and SNP calling**

194 *De novo* assembly was conducted using a custom pipeline, RAD-LOCI (Villacorta-Rath
195 et al. 2016, 2017; available at <https://github.com/molecularbiodiversity/rad-loci>), which
196 was developed to deal with paralogous loci retained by other available software. To
197 include sequences with low coverage within individuals but high coverage across the
198 dataset, demultiplexed reads from all samples were initially clustered at 100%
199 similarity, with a minimum cluster depth of 75 sequences — allowing two-thirds of the

200 samples to be represented by at least one read. Reference loci were collated by merging
201 clusters together — allowing a mismatch of three nucleotides — and removing
202 monomorphic clusters (those with less than two variants) and potentially paralogous
203 clusters (those with more than 16 variants). The upper threshold of 16 was chosen as a
204 three-bp mismatch with four possible nucleotide substitutions equates to 64 possible
205 sequence permutations (e.g. 4^3), however during pipeline development the highest
206 number of cluster members identified was 16, hence the upper threshold was set at 16.
207 This step was repeated, using the same thresholds, and clusters containing variants
208 previously associated with a different cluster in the previous filtering round were
209 removed. Variants that mapped to a different cluster in the second filtering round were
210 likely from repetitive or closely related regions. All samples were mapped back to the
211 remaining loci and final filtering removed: i) loci with >20% missing data ii) loci for
212 which a single sample mapped to more than two variants, indicating a repetitive region.
213 Remaining loci were recorded into a RAD-tag catalog and were used as reference
214 sequences to align the filtered sample data with VSEARCH v1.1.3
215 (<https://github.com/torognes/vsearch>) in preparation for SNP calling.

216

217 The genotype likelihoods of putative variant sites were determined using the mpileup
218 command in SAMTOOLS v1.2 (Li et al. 2009), and variants were called using
219 BCFTOOLS v1.2 (Li 2011) with a minimum depth of three reads. To reduce spurious
220 genotyping calls due to low read depth, a likelihood ratio was calculated from the most-
221 and second most-likely Phred scaled likelihood for each genotype. Samples with a ratio
222 of ≤ 10 (equating to 10% error on a Phred scale) were marked as missing data.

223

224 VCFTOOLS v0.1.13 (Danecek et al. 2011) was used for subsequent filtering of variant
225 sites. SNPs which exhibited a significant departure ($p < 0.001$) from Hardy Weinberg
226 Equilibrium (HWE), indels, loci with $>30\%$ missing genotypes, and a global minor
227 allele frequency of <0.05 were excluded from the dataset. Samples with more than 30%
228 missing data across all loci or with an initial sequence read count of less than 1 million
229 were excluded from further analysis. To negate high levels of site linkage within the
230 dataset, only one SNP per locus was retained using the thin option in VCFTOOLS.

231

232 **Analysis of replicates and batch effects**

233 In order to assess batch effects, a principal component analysis (PCA) was conducted
234 on the full SNP panel with the intra- and inter-library replicates using the R package
235 *adegenet* v2.0.0 (Jombart 2008). Locus and allele error rates were calculated for all
236 replicates (Mastretta-Yanes et al. 2015). The replicate from each pair with the highest
237 amount of missing data was removed from further analyses. PCAs were also conducted
238 on the full SNP panel to test for batch effects between sampling years and between
239 juveniles and adults.

240

241 **Detection of markers under selection**

242 The full SNP panel was screened for regional outlier loci using a consensus approach to
243 reduce detection of false positives. Two programs, LOSITAN (Beaumont and Nichols
244 1996; Antao et al. 2008) and ARLEQUIN v3.5 (Excoffier et al. 2005), were run three
245 times each and SNPs identified as divergent in all runs were classified as putatively
246 positively selected. Both programs use a coalescent-based simulation to identify outlier
247 markers by assessing the relationship between F_{ST} and expected heterozygosity, with

248 LOSITAN assuming a neutral island model of migration. Under the assumption of an
249 island migration model, high numbers of false positives can be detected when genetic
250 structure is hierarchical in reality (Excoffier et al. 2009). To mitigate this, ARLEQUIN
251 was run under a hierarchical model, with default settings of 100 demes per ten groups
252 and 50,000 permutations and a finite island model with default settings. LOSITAN runs
253 were performed with 50,000 simulations, neutral and forced F_{ST} , a confidence interval
254 of 0.99 and a false discovery rate of 0.1. SNPs classified as putatively neutral or
255 putatively positive outliers were separated into corresponding SNP panels.

256

257 To determine if outlier SNPs were associated with biological functions, a homology
258 search of the 75-bp RAD-tags containing the outlier SNPs was performed against the
259 NCBI nr public database using BLASTn (Altschul et al. 1990) and against the
260 American lobster, *Homarus americanus*, transcriptome (McGrath et al. 2016). A
261 minimum E-value of 10^{-6} was the threshold for a significant hit.

262

263 **Genetic variation**

264 Observed heterozygosity (H_O), unbiased expected heterozygosity (H_{UE}) and unbiased
265 F_{ST} estimator θ (Weir and Cockerham 1984) were calculated for the neutral SNP panel
266 using GENODIVE v2.0b27 (Meirmans and Van Tienderen 2004). Significant
267 departures in H_O and H_{UE} among the three regions were tested using the OSx-statistic
268 (Goudet 1995) with 10,000 permutations. Inbreeding coefficient (F_{IS}) was calculated in
269 ARLEQUIN v3.5 (Excoffier et al. 2005). Significance values for F_{ST} and F_{IS} were based
270 on 10,000 permutations.

271

272 **Population structure and assignment tests**

273 Regional genetic structure was examined in the neutral SNP panel using both a
274 Bayesian clustering method, performed in STRUCTURE v2.3.4 (Pritchard et al. 2000)
275 and Discriminant Analysis of Principal Components (DAPC), performed using the R
276 package *adegenet* (Jombart 2008). Both methods were used to identify the most likely
277 number of genetically distinct clusters (K) and to assign individuals to those
278 populations. For the STRUCTURE analysis, 20 independent runs for each value of K
279 (1-6) were performed, under the assumption of an admixture model and allele
280 frequencies being correlated among populations. Each run had a burn-in period of
281 100,000 followed by 100,000 data iterations. To evaluate the best value of K, the ΔK
282 method (Evanno et al. 2005) was implemented in STRUCTURE HARVESTER (Earl &
283 vonHoldt 2012) and results of individual population assignment was visualised with
284 CLUMPAK (Kopelman et al. 2015).

285

286 Unlike STRUCTURE, DAPC is a multivariate analysis that does not assume an
287 underlying population genetic model (Jombart et al. 2010) and was therefore used to
288 assess both the neutral and outlier SNP panels. The premise of DAPC is to minimise
289 within group variation while maximising variation between the groups. To determine
290 the optimal value of K Bayesian Information Criterion (BIC) was implemented in
291 *find.clusters*, without sampling information. Overfitting of discriminant functions can
292 occur when too many principal components (PCs) are retained. To avoid overfitting a
293 cross-validation approach was used to determine the optimal number of PCs to retain,
294 using 75% of the samples as a training set.

295

296 To establish whether source population(s) for TAS recruits could be identified,
297 assignment tests were performed on the neutral SNP panel using a Bayesian approach
298 (Rannala and Mountain 1997) in GENECLASS2 (Piry et al. 2004). NSW, NZ and
299 approximately half of the TAS samples (n=9), chosen at random, served as reference
300 populations and the remaining TAS samples (n=8) were assigned or excluded. The
301 probability computations were based on the resampling algorithm of Paetkau et al.
302 (2004), recommended for detecting first generation migrants (Piry et al. 2004), with
303 10,000 simulated individuals and an α of 0.01, as recommended by Paetkau et al.
304 (2004).

305

306 In a number of marine population genetic studies outlier SNPs have been shown to
307 produce similar patterns of genetic structure as neutral SNPs, but with higher statistical
308 power (Freamo et al. 2011; Milano et al. 2014; Araneda et al. 2016; Villacorta-Rath et
309 al. 2016). Therefore, we examined whether outlier SNPs were able to successfully
310 assign individuals to their sampling region. The same parameters as described for
311 assigning Tasmanian recruits were used, with the additional likelihood of an individuals
312 genotype occurring within the population of collection (L_{home}). The results of the
313 self-assignment test for the outlier SNPs were cross-validated by splitting the samples
314 randomly into reference populations and individuals for assignment. Three different
315 criteria were assessed for successful assignment: a) the highest probability of
316 occurrence b) 99% probability of occurrence and c) 95% probability of occurrence.

317

318 **Allele sharing distance methods**

319 Allele sharing distances have proven effective in detecting genetic partitioning between
320 regions (Bowcock et al. 1994) and subpopulations (Estoup et al. 1995), when allele
321 frequencies indicate little to no genetic differentiation. To assess subtle population
322 genetic structure undetectable through allele frequency methods, an allele sharing
323 distance (ASD) matrix (Bowcock et al. 1994) was created utilising the full SNP panel in
324 the R-package *adegenet*. A Neighbour Joining (NJ) dendrogram was constructed from
325 the ASD matrix with the R-package *ape* v5.0 (Paradis et al. 2004).

326

327 To test whether alleles were randomly distributed across geographical space, the neutral
328 SNP panel was assessed using a Spatial Analysis of Shared Alleles implemented in
329 SAShA 2 (Kelly et al. 2010). Detection of non-random allele distribution can signify a
330 departure from panmixia. Alleles can either be under-represented in space, indicating
331 subtle genetic partitioning, or over-distributed, suggesting alleles occur further apart
332 than would be expected under a panmictic model. The observed mean allele distribution
333 (OM) was tested for significant departure of the expected mean allele distribution under
334 panmixia (EM), with 1,000 permutations.

335

336 **Gene flow analysis**

337 The direction of gene flow between the breeding grounds in NSW and NZ was tested
338 using the Bayesian strategy implemented in MIGRATE-N v3.6.11 (Beerli 1998; Beerli
339 and Felsenstein 1999, 2001). In order for the MIGRATE-N analysis to be
340 computationally tractable a subset of 50 randomly chosen 75-bp loci were tested under
341 the sequence model with constant mutation rates. A series of initial full migration model
342 simulations were conducted to ensure convergence was obtained. The full migration

343 model described NSW and NZ as genetically distinct populations with bi-directional
344 gene flow. Once replicate runs converged, three additional gene flow models were
345 tested, which included NSW and NZ as genetically distinct populations with
346 asymmetrical gene flow originating from NSW or from NZ and a model describing
347 NSW and NZ as a single genetic population (Table 5). Each model was performed with
348 the parameters set to one long chain with 10,000 genealogies sampled and run
349 concurrently five times. Sampling increment and burn-in was 100 and 100,000,
350 respectively. To determine the most likely migration model log Bayes Factors (LBF)
351 were calculated from the Bezier approximation score and compared for all four gene
352 flow models.

353

354 To examine the directionality and magnitude of contemporary migration and identify
355 possible source populations for Tasmanian recruits all three sampling sites where
356 assessed using the *divMigrate* function (Sundqvist et al. 2016) from the R package
357 *diveRsity* (Keenan et al. 2013), employing both Nei's G_{ST} and Jost's D . Relative levels
358 of migration are calculated in *divMigrate* through assessing the genetic differentiation
359 between two populations and a hypothetical pool of migrants. Source and sink
360 populations can be identified when relative migration rates are larger in one direction
361 than the other direction (Sundqvist et al. 2016).

362

363 **Results**

364 **Sequence filtering and SNP discovery**

365 A total of 417,216,775 SE reads were obtained from sequencing 90 individuals with 9
366 replicated individuals ($n = 99$). Following filtering of raw reads to remove contaminant

367 sequences, poor quality reads, and mtDNA-derived reads, the demultiplexed mean read
368 abundance was 3.5 million reads per sample (± 1.4 million SD; range = 320,694 –
369 1,913,298). These reads were used to create the RAD-tag catalog containing 2,635 RAD
370 loci for SNP calling, from which a total of 3,384 SNPs were identified. After further
371 site- and individual-based filtering, the final full SNP panel contained 756 SNPs, with
372 an average read depth of 16 (± 6.7 SD). Under the hierarchical model ARLEQUIN was
373 unable to complete the outlier analysis as the F-statistics were negative, indicating no
374 hierarchical structure in the data. Consensus outlier analyses of LOSITAN and
375 ARLEQUIN finite island model detected 15 outlier SNPs exhibiting putative positive
376 selection. From the 741 remaining SNPs, 81 were detected to be subject to balancing
377 selection and an additional 15 SNPs had been identified as potential outliers but did not
378 fulfil the requirements of the consensus approach. 645 SNPs were retained in the neutral
379 SNP panel. No significant nucleotide or transcriptome BLAST hits were returned for
380 RAD-tags containing outlier SNPs. A total of 23 individuals, with >30% missing data
381 across all loci, were removed from the dataset, along with one of the replicate samples,
382 resulting in a final sample size of 29, 23 and 17 individuals for NSW, NZ and TAS,
383 respectively (Table 3).

384

385 **Batch effect and replicate analysis**

386 No batch effect from library preparation or sequencing was evident in the PCA of the
387 inter-library replicates, which showed no separation of replicates across the libraries
388 (Supplementary Figure S1). Consistent with this result, the mean locus and allele error
389 rates did not differ between the inter-library replicates. Non-concordant genotyping

390 errors (e.g. different genotyping calls) were present in low abundance: occurring in 9%
391 of SNPs.

392

393 In addition, genetic structure was not attributable to the collection of samples across two
394 sampling years or the different life stages collected. No clear separation between the
395 sampling years, or life stages was evident in the respective PCAs (Supplementary
396 Figure S2a and S2b, respectively).

397

398 **Genetic variation**

399 A founder effect (i.e. a reduction in genetic diversity), characteristic of breeding
400 populations recently colonised by a small number of individuals, was not detected for
401 the Tasmanian population (Table 3). Comparison of H_O and H_{UE} between the NSW,
402 NZ and TAS indicated genetic diversity did not significantly differ between regions (H_O
403 $OS_X = 0.041$, $P = 1.00$; H_{UE} $OS_X = 0.013$, $P = 1.00$). Gene flow between the three
404 regions is evidenced by the lack of regional private alleles detected and the inbreeding
405 coefficient (F_{IS}) not significantly deviating from zero in any region.

406

407 **Population structuring and assignment based on allele frequency methods**

408 No genetic differentiation was detected between regions in any of the analyses
409 performed on the neutral SNP panel. All pairwise F_{ST} values were non-significant,
410 indicating a lack of genetic differentiation between regions (Supplementary Table S1).
411 The Evanno method to determine the optimal value of K identified five genetic clusters,
412 signified by the highest value of ΔK . However, visualisation of the STRUCTURE
413 output, indicates no genetic differentiation between the sampling locations, with all

414 individuals showing similar degrees of admixture of the five genetic clusters
415 (Supplementary Figure S3). The presence of a single genetic stock (K=1) was indicated
416 in the *find.cluster* results as the smallest BIC located was at K=1 (Supplementary Figure
417 S4a). DAPC can only be computed with a minimum K=2, therefore a DAPC was not
418 conducted for the neutral SNP panel. TAS recruits were equally highly likely to be
419 assigned to any one of the three regions (NSW probability = 1.00; NZ probability =
420 1.00; TAS probability = 1.00), based on the neutral SNP panel assignment test. This
421 indicates the regional neutral genetic signatures cannot be distinguished from each
422 other, which is consistent with the lack of genetic differentiation detected with F_{ST} and
423 BIC.

424

425 Weak genetic differentiation among the three regions was detected in the analysis of the
426 outlier SNP panel. While the number of genetic clusters was unable to be defined, BIC
427 indicated the most appropriate number of genetic clusters ranged between 3-5,
428 evidenced by the bend in BIC (Supplementary Figure S4b). The outlier SNPs did not
429 hold enough signal to determine the optimal value of K, however visualisation of each
430 best K with DAPC demonstrated that genetic clusters corresponded to the three
431 geographical regions in K=3 and 4, albeit with some admixture present. The best
432 separation of the three geographical regions, with the least admixture, was exhibited at
433 K=3 (Fig. 2a). One additional cluster was present at K=4 and contained 46% NSW,
434 33% TAS and 25% NZ samples (Fig. 2b). At K=5 genetic clusters relating to the
435 geographical regions were less evident (Fig. 2c).

436

437 Initially, outlier SNPs possessed high power to discriminate between individuals from
438 the three regions as 100% of individuals were successfully assigned to their sampling
439 regions with high probabilities (NSW average probability = 0.993 ± 0.02 SD, $n = 29$;
440 NZ average probability = 0.986 ± 0.03 , $n = 23$; TAS average probability = $0.999 \pm$
441 0.002 , $n = 17$) using the self-assignment approach in GeneClass. However, cross-
442 validating the results using the assignment/exclusion approach indicated a reduction in
443 assignment success (Table 4). Successful assignments based on the highest probability
444 of occurrence returned the highest assignment success rates, while 95% probability gave
445 the lowest. This indicates that while assignments based on the highest assignment
446 probability returned good rates of assignment success, there is often less than 5%
447 difference in assignment probability between the most- and second most-probable
448 location of occurrence.

449

450 **Population structuring based on allele sharing methods**

451 No subtle genetic structure was apparent in the ASD NJ dendrogram based on the
452 neutral SNP panel (Fig. 3a); all branches were of similar length indicating individuals
453 had equal levels of genetic differentiation, regardless of regional origin. However weak
454 genetic partitioning was apparent in the NJ dendrogram based on the outlier SNPs (Fig.
455 3b), with the majority of individuals within a clade originating from the same region
456 (Fig. 3b). Four clades exhibited regional stratification with 73% of NZ individuals
457 belonging to Node 2 and 4, 47% of TAS individuals belonging to Node 3 and 31% of
458 NSW individuals belonging to Node 1.

459

460 The SASHA analysis of the neutral SNP panel detected very small, but significant,
461 difference between the expected and observed mean distance between shared alleles.
462 Shared alleles were found to be dispersed over broader geographical distances than
463 expected under a model of panmixia (OM = 1,137.6 km; EM = 1,132.6 km; $P < 0.001$).

464

465 **Gene flow analysis**

466 The coalescent simulations indicate that the *Sagmariasus verreauxi* breeding stocks
467 located in NSW and NZ consist of a single genetically homogeneous population, as
468 evidenced by the model rankings based on the highest likelihood of occurrence and
469 probability (Table 5). The single genetic population model had a probability 10.6 times
470 higher than that of the next best model of full migration (bi-directional migration from
471 two genetically distinct models). The model found least likely to occur was that of
472 unidirectional gene flow from NZ to NSW.

473

474 Relative contemporary migration rates indicated migration was bi-directionally high
475 between NSW and NZ and between NSW and TAS (Fig. 4). Relative migration rates
476 between NZ and TAS were comparatively lower than the bi-directional rates for NSW.
477 The relative migration rates calculated with Nei's G_{ST} (Fig. 4a) and Jost's D (Fig. 4b)
478 both showed congruence in directionality and magnitude of migration, however relative
479 migration rates with Jost's D indicated less migration between NZ and TAS, than Nei's
480 G_{ST} .

481

482 **Discussion**

483 In this study, we have used genome-wide ddRADseq data to investigate the broad-scale
484 genetic structure, connectivity and local adaptation of *Sagmariasus verreauxi* across its
485 known range. For the neutral SNPs, we found a signature of genetic homogeneity that
486 extended across the Tasman Sea, encompassing the NSW and NZ breeding grounds as
487 well as the putative genetic sink population in Tasmania. This result indicated regional
488 disparity in genetic structure of *S. verreauxi* and the closely related *Jasus edwardsii*, for
489 which a genetic break exists between Australian and NZ populations. Due to the genetic
490 homogeneity detected across the three regions, the source population for the Tasmanian
491 recruits could not be identified. We found no evidence to suggest that self-recruitment is
492 occurring in the Tasmanian population, however we cannot exclude the possibility that
493 self-recruitment in Tasmania is being masked by high gene flow.

494

495 Weak regional stratification between NSW, Tasmania and NZ was evident through the
496 examination of only 15 outlier SNPs. While this result suggests that local adaptation
497 may be occurring, we were unable to associate any of the loci with genes and therefore
498 there is a chance that the outliers may be due to Type II error or other demographic
499 processes. Nevertheless, as regional genetic structure with the neutral SNP panel was
500 not detected, we examined the outlier SNP panel to ascertain whether outlier SNPs had
501 increased power to distinguish between regions in a genetically homogeneous species,
502 which has not been examined before. Outlier SNPs showed good regional assignment
503 success based on the highest probability of occurrence. However, there was often less
504 than 5% probability between the first and second most probable locations of occurrence
505 and assignment success rates varied between regions. Nevertheless, this is a promising

506 result and increasing the sampling of SNPs may increase the number of outliers
507 identified and improve regional discrimination in a genetically homogeneous species.
508

509 **Maintenance of neutral genetic homogeneity**

510 Our results of trans-Tasman neutral genetic homogeneity contradict with the results of
511 Brasher et al. (1992), a preliminary genetic study reporting a genetic break between
512 Australian and NZ *S. verreauxi* populations. This discrepancy in results is most likely
513 due to low (N=20) and uneven sampling effort (NZ n= 14, Australian n=6) in the
514 preliminary study, which is known to cause overestimation of genetic stratification
515 calculated via G_{ST} (Caujape-Castells 2010) the genetic distance estimator used in
516 Brasher et al. (1992). Hence it is likely that the genetic break detected in Brasher et al.
517 (1992) is an artefact of the sampling effort, not a biological reality.

518
519 Lack of neutral genetic structure can occur between discrete regions due to gene flow,
520 or alternatively, due to regions retaining effective population sizes (N_e) large enough to
521 overcome the effects of genetic drift, or a combination of both (Hauser and Carvalho
522 2008). From our study, it is not possible to determine the mechanism responsible for
523 maintaining neutral genetic homogeneity, however the detection of overly dispersed
524 alleles is consistent with routine long-distance larval dispersal (Kelly et al. 2010).
525 Furthermore, as genetic differentiation is maintained in the closely related Southern
526 Rock Lobster, *J. edwardsii* (Villacorta-Rath et al. 2016) which has a wider distribution,
527 higher biomass and a longer pelagic larval duration compared to *S. verreauxi*, it is
528 unlikely that genetic homogeneity is being maintained in *S. verreauxi* through a large N_e
529 alone.

530

531 Oceanographic modelling supports the hypothesis of genetic homogeneity in *S.*
532 *verreauxi* being maintained via long distance larval dispersal. Chiswell et al. (2003)
533 demonstrated that it is theoretically possible for 2% of NSW *S. verreauxi* larvae to reach
534 NZ shores within 12 months if they are entrained in the Tasman Front (see Fig. 1 for
535 Tasman Front details). While our historical gene flow analysis was unable to provide
536 the rate or direction of migration due to the breeding populations consisting of a single
537 genetic stock (i.e. NSW and NZ are genetically identical, therefore there is no way to
538 statistically discern patterns of gene flow), this result does not preclude gene flow
539 (Horne and Van Herwerden 2013). Our contemporary gene flow analysis exhibited
540 strong bi-directional gene flow between all three regions, however this is unlikely as
541 there is no evidence that Tasmanian lobsters reproduce. Given that the contemporary
542 gene flow analysis assesses the genetic differentiation between a pool of migrants
543 against two populations, under a scenario where two populations are genetically
544 identical the pool of migrants will exhibit the same degree of genetic similarity to both
545 populations and hence the directionality of gene flow will be deemed to be bi-
546 directional. However, model-based studies have demonstrated that asymmetrical gene
547 flow can cause displacement of the genetic variation within the sink population with
548 that of the source population (Pringle and Wares 2007; Wares and Pringle 2008). Under
549 this scenario the homogeneous genetic signature produced by asymmetrical gene flow
550 will be indistinguishable from bi-directional gene flow.

551

552 Taking into account the local oceanographic features, asymmetrical gene flow from
553 NSW to NZ is the most-likely scenario. It is unlikely that trans-Tasman genetic

554 homogeneity is maintained through bidirectional, or unidirectional gene flow
555 originating from NZ, as a strong Tasman Front undercurrent is required for larvae to
556 transit ~2 000 km within their pelagic larval phase. A Tasman Front undercurrent has
557 been identified at a depth of 800 m (Sutton and Bowen 2014), however this
558 undercurrent is unlikely to be a vector for trans-Tasman spiny lobster dispersal as it is
559 weak and 400 m deeper than the current known maximum depth of spiny lobster larvae
560 (Rimmer and Phillips 1979; Minami et al. 2001; Bradford et al. 2005). Therefore, we
561 propose unidirectional gene flow from NSW to NZ, facilitated by the Tasman Front, is
562 the most likely scenario for *S. verreauxi*.

563

564 The differential population structure observed for *S. verreauxi* and *J. edwardsii* across
565 the Tasman Sea may seem surprising, given their similar life-histories, however patterns
566 of incongruence in regional genetic structure has been found to occur in co-distributed,
567 closely related species of sharks (Ovenden et al. 2009), mackerel (Zardoya et al. 2004)
568 and sea bass (Liu et al. 2006). Explanations for the difference in genetic patterns have
569 been attributed to subtle differences in life-history and/or historical environmental
570 changes resulting in differential timing of population isolation. As the Australian and
571 NZ populations of *S. verreauxi* and *J. edwardsii* were estimated to have physically
572 separated approximately 10 MYA (George 1997) this is unlikely to be the cause of the
573 disparity in genetic structure between the two species. More likely is the difference in
574 fecundity of the two species. *Sagmariasus verreauxi* has a maximum fecundity almost
575 four times higher than *J. edwardsii* (Table 1). This combined with the NSW *S.*
576 *verreauxi* breeding ground being slightly further north than the break off of the Tasman

577 Front could account for more *S. verreauxi* larvae being entrained in the Tasman Front
578 and transported across the Tasman Sea, thus maintaining genetic homogeneity.

579

580 While a genetic break exists for *J. edwardsii* across the Tasman Front, the Tasman
581 Front itself is not a barrier to dispersal as low levels of migration were detected from
582 Australia to New Zealand (Thomas and Bell 2013). The factor that may account for the
583 potential difference of trans-Tasman gene flow between *S. verreauxi* and *J. edwardsii* is
584 the different breeding strategies between the species. *Sagmariasus verreauxi* juveniles
585 undertake a counter current migration to join the geographically restricted breeding
586 grounds with the onset of maturity (Booth 1986), while *J. edwardsii* breed throughout
587 their distribution (Booth and Breen 1994; Booth and Phillips 1994). Therefore, it is
588 possible that *S. verreauxi* larvae are more abundant in an area where trans-Tasman
589 transport is possible, leading to a higher number of *S. verreauxi* recruits successfully
590 traversing the Tasman Sea than *J. edwardsii* recruits, which could account for the
591 genetic disparity between the species.

592

593 **Tasmanian recruits**

594 Assignment tests using neutral SNPs were unable to determine the region of origin for
595 the Tasmanian recruits. Tasmanian recruits were just as likely to be assigned back to
596 Tasmania as the other two regions and due to the absence of a reduction in genetic
597 diversity (i.e. absence of founder effect) in Tasmania, there is no evidence for the
598 occurrence of self-recruitment in Tasmania. Without self-recruitment the Tasmanian
599 population is likely reliant upon immigrants for its persistence.

600

601 While NZ cannot be completely ruled out as a source for Tasmanian recruits, regional
602 oceanography indicates NSW is the most likely source for Tasmanian recruits due to the
603 southerly flowing East Australian Current (EAC; Ridgway and Hill 2012). The
604 transport of many marine invertebrates from mainland Australia to Tasmania is
605 associated with the EAC, especially recently with the strengthening of the EAC and
606 increased water temperatures that are causing species ranges to shift into Tasmanian
607 waters (Ling et al. 2009; Banks et al. 2010; Johnson et al. 2011; Amor et al. 2014). As
608 NSW is the likely source population, finer scale analysis with higher spatial sampling
609 along the NSW coast should be conducted to examine the existence of isolation by
610 distance or gene surfing patterns, which would indicate range-shifting and self-
611 recruiting (Pierce et al. 2014) in Tasmania. In some cases, fine-scale patterns can be
612 masked at broader scales (Adrian et al. 2017). If this is the case for *S. verreauxi*, self-
613 recruitment within Tasmanian could be obscured by the current regional sampling scale.

614

615 **Outlier SNPs and their utility in assignment tests**

616 Only a few examples exist in the literature of species exhibiting regionally stratified
617 outlier loci against a background of neutral genetic homogeneity (Gagnaire et al. 2012;
618 Pujolar et al. 2014; Gleason and Burton 2016; Jasonowicz et al. 2017), the cause of
619 which is attributed to occurrence of spatially varying selection from a single gene pool.
620 We were unable to associate any biological functions to the RAD loci containing outlier
621 SNPs in this study, however this does not preclude the possibility of spatially varying
622 selection acting through pre- or post-settlement mortality on *S. verreauxi* larvae.
623 Spatially varying selection acts within each cohort, however it can be stable across
624 cohorts if the environmental conditions remain stable (Gagnaire et al. 2012; Pujolar et

625 al. 2014), creating a regional signal of spatial varying selection, as is the case for *S.*
626 *verreauxi*. Alternatively, the genetic structure of *S. verreauxi* could result from an
627 absence of drift-migration equilibrium (Slatkin 1993), where diverged populations with
628 restricted gene flow resemble a single genetic population as there has been insufficient
629 time since population divergence for neutral genetic differentiation to occur.

630

631 Outlier SNPs show promise for assigning individuals to their region of origin when
632 genetic homogeneity is detected through the analysis of neutral SNPs. Our study
633 demonstrates that care is needed in deciding the criteria to base successful assignments
634 on, as different criteria greatly influenced the success rates of individual assignments.
635 Using the highest probability returned the best assignment success, however these
636 results may have been due to chance as differences between probabilities for each
637 location were low. While the assignment success rates were variable between regions
638 and differences between probabilities were low, these factors could be artefacts of the
639 low number (n=15) of outlier SNPs that were detected in this study. The power of
640 outlier SNPs to assign individuals to their geographical origin is a function of the
641 number of outlier SNPs detected, hence more outlier SNPs results in higher assignment
642 power (Benestan et al. 2015). As sequencing technology, such as target capture
643 approaches and whole genome sequencing, develops and becomes more accessible it
644 will be possible to sample more of the genome, providing greater access to highly
645 divergent regions of the genome and outlier SNPS. Even so, with only a small number
646 of SNPs, this study shows that outlier SNPs have the potential to be used for population
647 assignment in species with neutral genetic homogeneity, however further investigations
648 are needed to determine their reliability as a management tool.

649

650 **Management Implications**

651 This study highlights the complexity of elucidating genetic populations to enhance
652 management strategies for a genetically homogeneous species. Quantifying the
653 direction and magnitude of gene flow is essential to determine the level of population
654 connectivity, and more importantly to resource managers, the demographic connectivity
655 between populations. Demographic independence has been suggested to occur when
656 migration rates between populations fall below 10% (Hastings 1993; Waples and
657 Gaggiotti 2006). However, when a species exhibits genetic homogeneity, migration
658 rates are unable to be statistically determined through genetic data alone. We suggest in
659 these cases oceanographic modelling may be needed to estimate potential migration
660 rates between populations. In the case of *S. verreauxi* we hypothesise that the genetic
661 homogeneity between NSW and NZ is caused by asymmetrical gene flow, however
662 biologically realistic (e.g. seeding during egg-hatching months and restricted to the
663 NSW and NZ breeding grounds) oceanographic models are required for further clarity.

664

665 **Conclusion**

666 Our analyses of neutral genetic variation across the known range of *S. verreauxi*
667 suggests that regional genetic structure is homogeneous at neutral SNPs, indicating the
668 lack of a trans-Tasman genetic break. The genetic disparity between the closely related
669 *S. verreauxi* and *J. edwardsii* indicates the importance of quantifying genetic structure
670 for exploited species rather than using the genetic structure and connectivity of a closely
671 related species as a proxy for management decisions. Outlier SNPs detected weak
672 regional partitioning, which could potentially indicate the presence of spatially varying

673 selection between the regions. Due to the weak regional partitioning of the outlier SNPs,
674 they were useful in achieving high individual assignment success between the regions,
675 albeit with low differentiation between probabilities of first and subsequent population
676 assignments. Although further investigations into the reliability of outlier assignment
677 success is needed, these SNPs do show promise in their utility to be used as traceability
678 tools for species exhibiting genetic homogeneity.

679

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685 **Conflict of interest** The authors declare that they have no conflict of interest.

686 **Data accessibility** Reference loci sequences are available through Dryad, doi:

687 **Ethical approval** All applicable international, national and/or institutional guidelines
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690

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701

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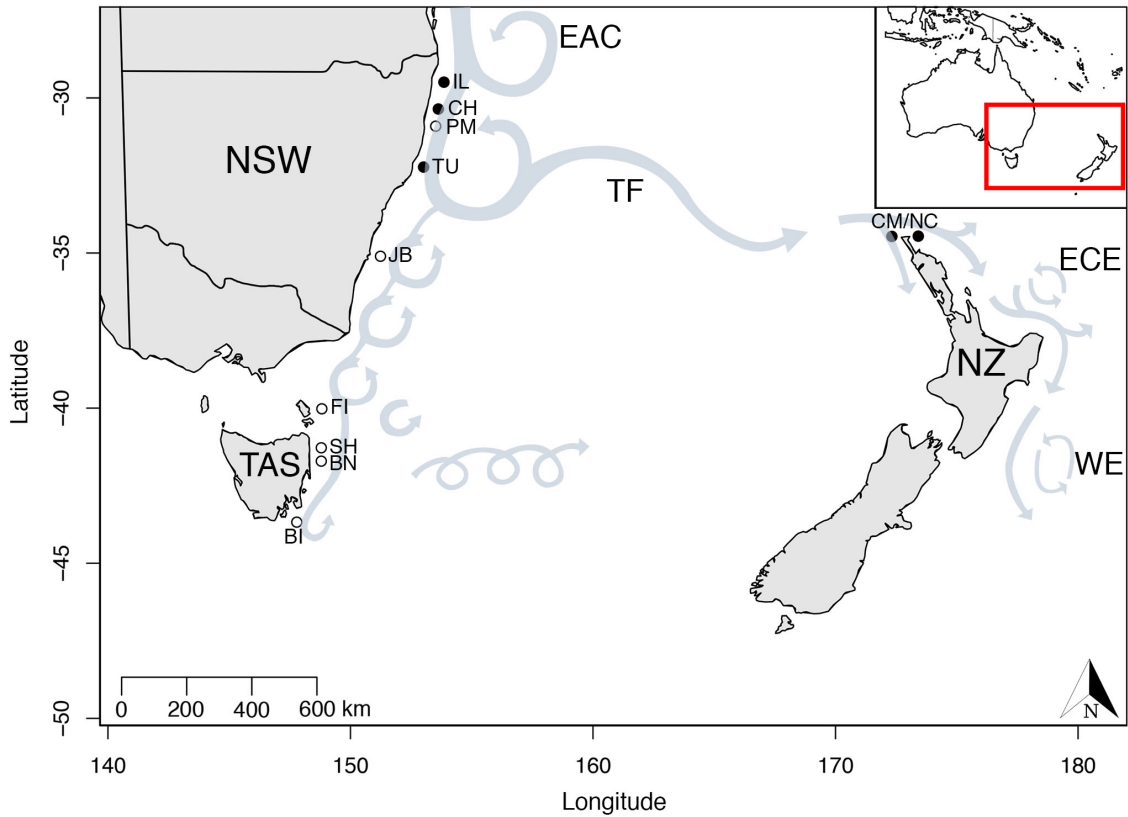
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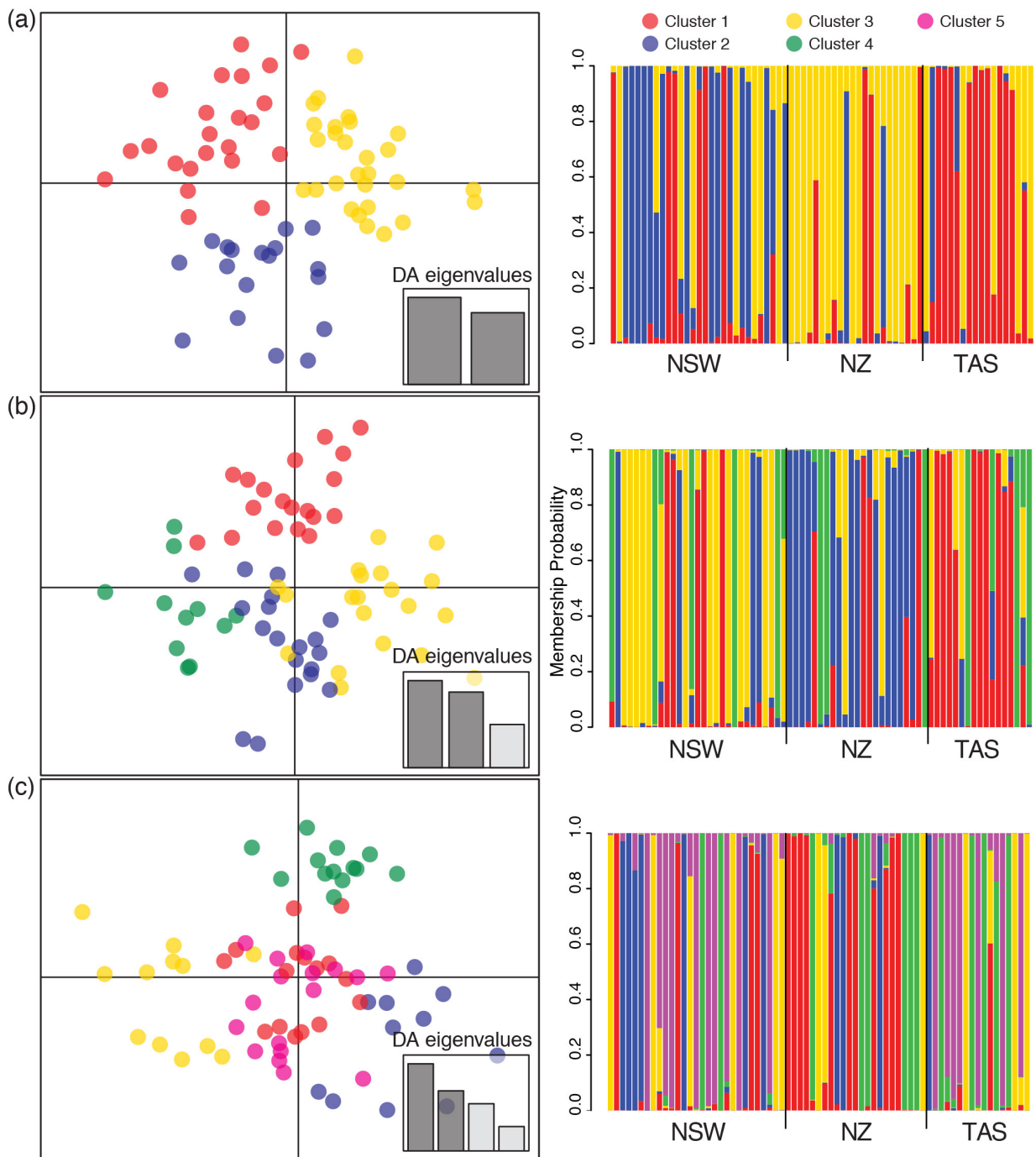
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1009 **Figures**



1010

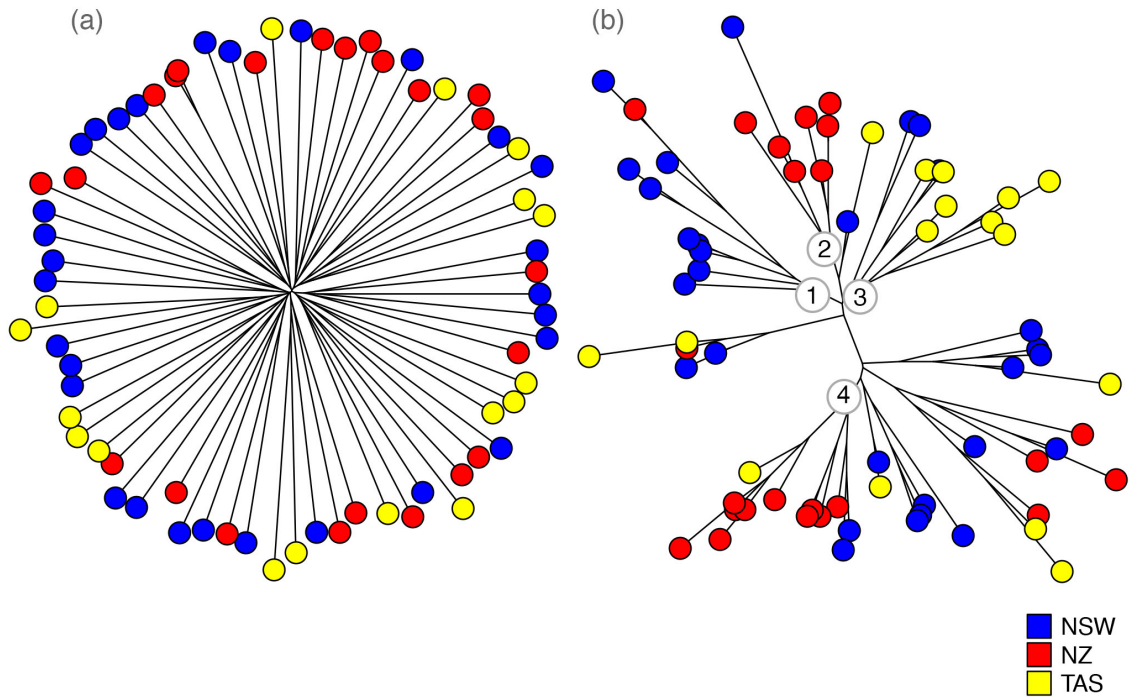
1011 **Fig. 1** Locations of *Sagmariasus verreauxi* sampling sites (listed in Table 2) within
1012 Australia and New Zealand during 2013 and 2014 sampling periods. Black dots denote
1013 sampling sites where only adults were collected. White dots denote sampling sites
1014 where juveniles were collected. The major local oceanographic currents depicted on the
1015 map: EAC, East Australian Current; TF, Tasman Front; ECE, East Cape Eddy; WA,
1016 Wairarapa Eddy. The study region is illustrated in a broader context in the inset map
1017 (red box)



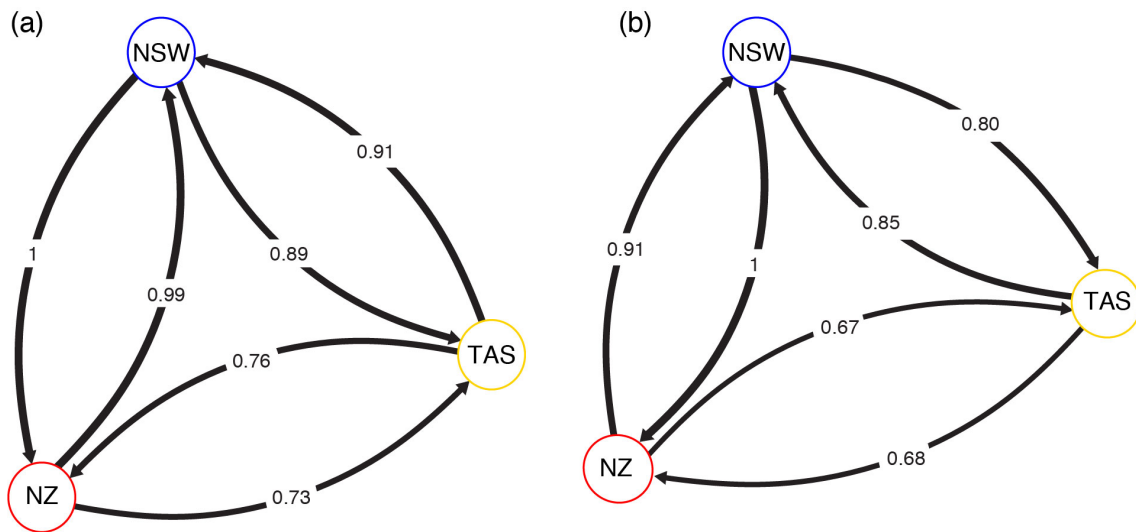
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1019 **Fig. 2** Discriminate Analysis of Principal Components using the outlier SNP panel at
 1020 (a) K=3, (b) K=4 and (c) K=5. Scatterplots (on the left) represent individual samples,
 1021 with the symbols indicating cluster assignment. The concordance between actual
 1022 sampling location (y axis) and cluster assignment based on genotype (x axis; numbers
 1023 correspond to clusters identified in the scatterplot) is presented on the right-side panels.

1024 Each row represents an individual and the colours represent the posterior probability of
 1025 membership to that cluster by the DAPC. NSW, New South Wales, Australia; TAS,
 1026 Tasmania, Australia; NZ, New Zealand



1027
 1028 **Fig. 3** Neighbour joining dendrogram of (a) neutral SNP panel and (b) outlier SNP
 1029 panel based on allele sharing distances. Numbers in circles are the node names, as per
 1030 the text.



1031

1032 **Fig. 4** Relative migration network among all sampling locations, calculated with (a)
1033 Nei's G_{ST} and (b) Jost's D . The arrows indicate direction of migration, while the
1034 numbers and strength of the arrows indicates the relative migration rates. Higher
1035 numbers and thicker lines signify stronger relative migration.

1036 **Table 1** Comparison of the life history characteristics of two rock lobster species, *Jasus*
 1037 *edwardsii* and *Sagmariasus verreauxi*

	<i>Sagmariasus verreauxi</i>	<i>Jasus edwardsii</i>
Physical separation between Australian and NZ populations	~ 10 million years ago (George 1997).	~ 10 million years ago (George 1997).
Distribution	Inhabits coasts of New South Wales, Australia and north east coast of North Island, New Zealand, with a small, episodic population in Tasmania, Australia (Kensler and Skrzynski 1970; Montgomery et al. 2009).	Inhabits all coasts of Southern Australia (including Western Australia, South Australia, Victoria, Tasmania) and New Zealand (Booth 2006).
Breeding locations	Restricted breeding grounds occur along coast of northern New South Wales, Australia and Cape Reinga, New Zealand (Booth 1984; Montgomery 1992).	Breeding occurs in all areas of distribution (Booth and Breen 1994; Booth and Phillips 1994).
Breeding timing	Breeding occurs once/annum between October-January (Booth 1984). Eggs hatch between December to January (Kensler 1967; Booth 1979).	Breeding occurs once/year in June to September (George 2005). Eggs hatch between September and October (Booth and Stewart 1992).
Fecundity	385,000 to 2 million eggs per female (Kensler 1967).	43,918 to 660,156 eggs per female (Green et al. 2009).
Pelagic larval duration	8-12 months (Booth 1986; Montgomery and Kittaka 1994; Montgomery and Craig 2005).	Up to 24 months (Booth and Phillips 1994).
Migration	Recruits settle to the south of the breeding grounds before undergoing a countercurrent migration at the onset of maturity to join the breeding population. Migration distance ranges from 200-1,070km (Booth 1986).	Majority of migrations are small on- and off-shore movements <100km (McKoy 1983; Linnane et al. 2005).
Genetic structure	Australian and New Zealand populations consist of a single genetic stock, with outlier SNPs indicating weak regional differences.	Australian and New Zealand populations and populations within Australia are genetically distinct (Morgan et al. 2013; Thomas and Bell 2013; Villacorta-Rath et al. 2016).

1038

1039 **Table 2** Sampling and sequencing information

Region	Site Code	Site Name	Year	No. samples collected	No. of sequenced individuals:		
					Juveniles	Adults	Unknown
NSW	IL	Iluka	2014	6	-	6	-
	CH	Coffs Harbour	2014	8	1	7	-
	PM	Port Macquarie	2013	7	6	-	-
	TU	Tuncurry	2014	2	1	1	-
	JB	Jervis Bay	2013	7	7	-	-
TAS	FI	Flinders Island	2014	3	1	-	-
	SH	Saint Helens	2014	2	2	-	-
	BN	Bicheno	2013	8	8	-	-
	BI	Bruny Island	2014	1	1	-	-
	SSA	SS Aquarium	2014	16	4	1	-
NZ	CM	Cape Maria van Diemen to North Cape	2013	19	-	3	16
	NC		2014	7	-	4	-

1040

1041 **Table 3** Genetic diversity indices for all sampling regions

Region	Neutral SNP Panel			
	N	H _O	H _{UE}	F _{IS}
NSW	29	0.314	0.300	-0.160
NZ	23	0.347	0.309	-0.309
TAS	17	0.326	0.308	-0.259

1042

1043 Abbreviations: the number of individuals genotyped (N), observed heterozygosity (H_O), unbiased expected heterozygosity

1044 (H_{UE}) and Wright's inbreeding coefficient (F_{IS}).

1045 No F_{IS} values significantly differed from zero.

1046 No significant differences were detected for H_O or H_{UE} among the three regions.

1047 **Table 4** Percentage comparison of successful individual assignments based on a) the
 1048 highest probability, b) probabilities above 0.99 and c) probabilities above 0.95.
 1049 Successful assignments to sampling origin are in bold.

	Percentage of individuals successfully assigned to:				
	NSW	NZ	TAS	> 1 population	Unassigned
Successful assignment based on highest probability					
NSW	71	7	7	14	0
NZ	64	18	9	9	0
TAS	25	0	63	12	0
Successful assignment based on >0.99 probability					
NSW	43	0	0	50	7
NZ	9	18	9	46	18
TAS	13	13	38	25	13
Successful assignment based on >0.95 probability					
NSW	29	0	0	71	0
NZ	9	9	9	73	0
TAS	0	0	13	75	13

1050

1051 **Table 5** Comparison of log Bayes Factors (LBF) inferred from Bezier approximation
 1052 score for different models of migration between NSW and NZ breeding populations

Model	Log(mL)	LBF	Rank	Model Probability
Single genetic population	-8394.13	0	1	0.9137
Full migration	-8396.49	-2.36	2	0.0862
NSW to NZ only	-8415.84	-21.71	3	3.41 x 10 ⁻¹⁰
NZ to NSW only	-8448.69	-54.56	4	1.84 x 10 ⁻²⁴

1053