

1 Title: Population structure and dispersal across small and large spatial scales in a direct
2 developing marine isopod

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11 **Abstract**

12 Marine organisms generally develop in one of two ways: biphasic, with distinct adult and
13 larval morphology, and direct development, in which larvae look like adults. The mode of
14 development is thought to significantly influence dispersal, with direct developers having
15 much lower dispersal potential. While dispersal and population connectivity is relatively well
16 understood for biphasic species, comparatively little is known about direct developers. In this
17 study, we use a panel of 8,020 SNPs to investigate population structure and gene flow for a
18 direct developing species, the New Zealand endemic marine isopod *Isocladus armatus*. We
19 find evidence that on a small spatial scale (20 kms), gene flow between locations is
20 extremely high and suggestive of an island model of migration. However, over larger spatial
21 scales (600km), populations exhibit a strong pattern of isolation-by-distance. The
22 intersection of our sampling range by two well-known biogeographic barriers (the East Cape
23 and the Cook Strait) provides an opportunity to understand how such barriers influence
24 dispersal in direct developers. We find that *I. armatus* has high migration rates across these
25 barriers. However, we find evidence of a north-south population genetic break occurring
26 between Māhia and Wellington, although there are no obvious biogeographic barriers
27 between these locations. This study suggests that biogeographic barriers may affect
28 migration in direct development species in unexpected ways.

29 **Introduction**

30 **Life history influences genetic population structure**

31 A species' developmental life history has a significant effect on population connectivity and
32 dispersal. For marine organisms, developmental life histories are generally classified in one
33 of two ways: direct developers, in which larvae resemble adults and do not disperse large
34 distances; and biphasic, in which larvae have different morphologies from adults and
35 generally disperse large distances via ocean currents (Cowen & Sponaugle, 2009; Puritz et
36 al., 2017; Simpson et al., 2014) during a pelagic larval stage. For this reason, direct-
37 developing species tend to show greater population structure than biphasic species (Ayre et
38 al., 2009; McMillan et al., 1992; Pelc et al., 2009; Waples, 1987). However, some species do
39 not conform to this expected pattern (Ayre et al., 2009; Puritz et al., 2017; Shanks, 2009;
40 Winston, 2012).

41 Dispersal (and thus population structure) is also affected by biogeographic barriers, and the
42 effects of these barriers themselves depend on the life history of the organism. For example,
43 off shore ocean currents may have large effects on biphasic species, but little effect on direct
44 developers. Similarly, we would expect that direct developers with limited dispersal potential
45 will be doubly limited if there is no suitable habitat within the range of their average dispersal
46 distance. However, in some cases the lack of nearby suitable habitat does not obviously limit
47 dispersal in direct developers, and but does appear to limits the dispersal of biphasic species
48 (Ayre et al., 2009). This is contrary to predictions based on the expected relationship
49 between life history and dispersal potential. These cases, where direct developers exhibit
50 greater dispersal than otherwise predicted, are not uncommon within intertidal organisms
51 (Ayre et al., 2009; González-Wevar et al., 2018; Wells & Dale, 2018; Yoshino et al., 2018),
52 suggesting that population connectivity cannot be entirely predicted by life history or even
53 the knowledge of biogeographic barriers. As a result, it is important to more carefully quantify
54 population structure in direct developing marine species across a range of spatial scales and
55 biogeographic contexts. This will help to clarify the complex relationships between life
56 history, biogeography, and population structure.

57 **Population Genetics in *Isopoda***

58 Marine isopods offer a highly tractable and attractive system for investigating the dispersal
59 potential and population structure of direct-developing species. Many isopod species occur
60 in large numbers in the easily sampled intertidal zone across extensive geographic ranges.
61 However, the forces acting to maintain population genetic structure in marine isopods are
62 not well understood. Some species exhibit genetic structure over small spatial scales, on the
63 order of tens of kilometres. This is congruent with the hypothesis of reduced dispersal in

64 direct developers, and may be responsible for the widespread occurrence of multiple cryptic
65 species of isopods (*Ligia* and *Tylos spp.*) on the Southern California coastline and in Baja
66 (Markow & Pfeiler, 2010; Hurtado et al, 2010; Hurtado et al, 2013).

67 In contrast, other species of isopods exhibit transoceanic distributions, indicative of
68 historically high dispersal rates. One example is *Sphaeroma terebrans*, which is distributed
69 across both the Atlantic and Indian Oceans. The apparently high dispersal rate and wide
70 distribution of this wood-boring isopod may be result of its reliance on “rafting” for dispersal
71 (a process in which individuals use large rafts of algae or other floating debris to disperse)
72 (Baratti et al., 2011). The contrast between *Sphaeromona* and *Ligia* and *Tylos spp.* suggests
73 that for isopods, life history (i.e. whether species are direct developers or not) may not
74 always be a good predictor of population structure, and that behavioural aspects should also
75 be considered.

76 Here we investigate the New Zealand-wide population genetic structure of the intertidal
77 isopod *Isocladus armatus*. Endemic to New Zealand, this highly colour polymorphic species
78 is found in abundance on semi-sheltered rocky shorelines throughout the country. There is
79 evidence that this direct-developing isopod species can exhibit high dispersal rates (Wells &
80 Dale, 2018). In this case, the authors found no significant population divergence between
81 two sites separated by 11km of coastline. This is indicative of a highly mobile species. On a
82 much larger scale (1,000 kms), however, population structure was evident. It is unclear at
83 precisely what spatial scale this population genetic structure begins to break down, or
84 whether biogeographic barriers affect this.

85 To investigate this, we use genotyping-by-sequencing (GBS) to resolve population structure
86 over a range of spatial scales. By quantifying population genetic structure in this species, we
87 are able to identify the role of geography (both distance and seascape features) in
88 influencing gene flow and dispersal. We find, unexpectedly, that well-known biogeographic
89 barriers, the Cook Strait and the East Cape, have little effect on dispersal. However, there is
90 strong evidence of a north-south break in populations structure, suggesting that unidentified
91 biogeographic barriers prevent migration between these regions.

92

93 **Methods**

94 **Sample Collection**

95 We collected specimens of *Isocladus armatus* in June, 2018, from around the North Island,
96 New Zealand, from locations where *I. armatus* has previously been recorded (Hurley &
97 Jansen, 1977; *INaturalist.org*, n.d.). These sites were at Stanmore Bay, Browns Bay, Opito

98 Bay (Coromandel), Mt Maunganui, Māhia Peninsula, and Wellington (Fig. 1). At each site we
99 collected a minimum of 32 individuals, up to a maximum of 48, and attempted to sample
100 individuals as equally as possible amongst colour morph and sex. Where possible, we
101 collected specimens larger than 5mm in order to ensure sufficient DNA could be extracted
102 for sequencing (see supplementary methods for details). The maximum distance between
103 individuals collected at any site did not exceed 30 m. Samples were stored at -80°C in 100%
104 ethanol until extraction. We have included samples from Wells and Dale 2018 (see [ref] for
105 sampling methods) to increase the number of sampled individuals and the range of location.
106 In addition, the temporal structure of this sampling may yield insight into the short term
107 changes in allele frequencies within a population.

108 **DNA Extraction**

109 We extracted DNA following a modified Qiagen DNEasy Blood and Tissue protocol from
110 Wells and Dale (2018). Briefly, we used 178 µl of 0.5M EDTA and 22 µl of 20% SDS in each
111 extraction (rather than varying volumes by weight of tissue). Additionally, we eluted DNA
112 from the spin column three times, using 50 µl of nuclease-free water for each. We let the
113 eluent sit on the column for 15 minutes before centrifugation for one minute at 7,000 rcf.

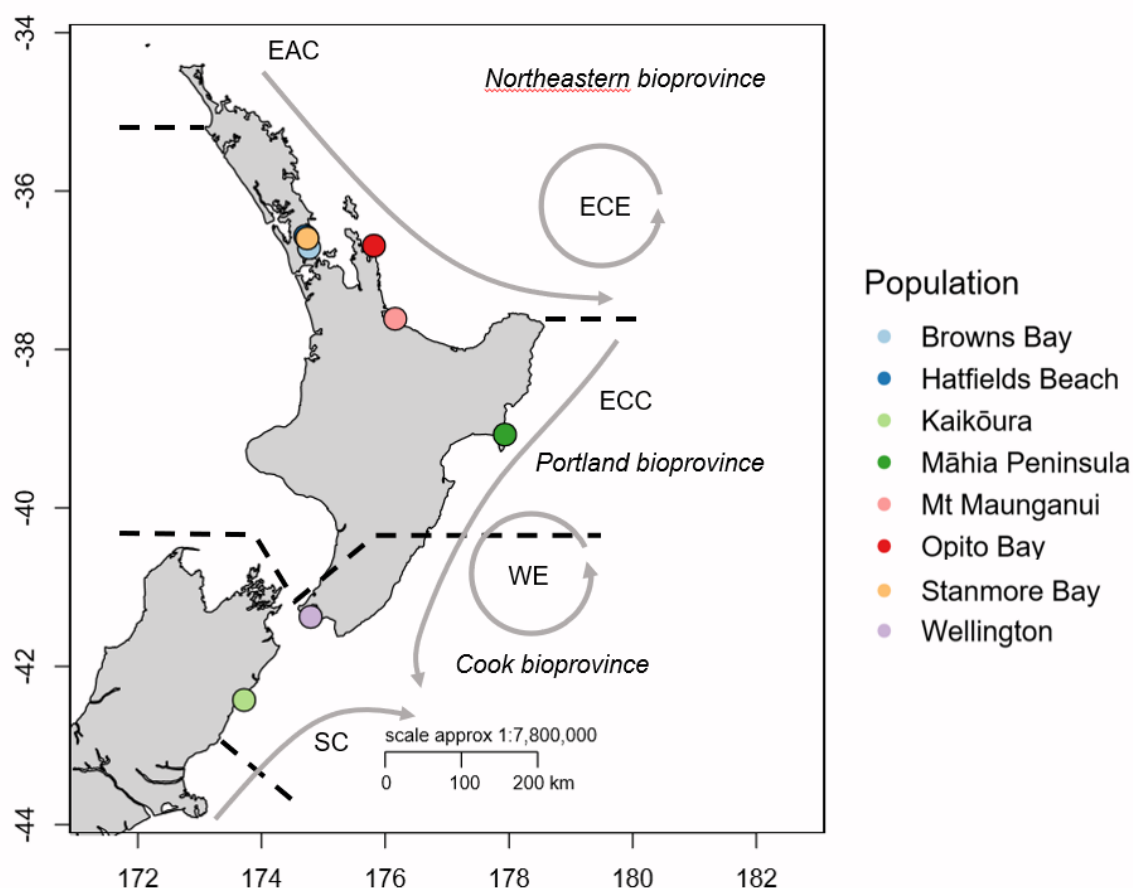
114 **Data Collection and Processing**

115 DNA samples were processed by Diversity Arrays Technology (DArT) Ltd (Canberra,
116 Australia) using a genotyping-by-sequencing (GBS) approach. The methodology behind this,
117 including restriction enzyme choice are described in detail in Wells and Dale (2018). DArT
118 performs SNP calling using a proprietary pipeline. SNPs are only called if both homozygous
119 and heterozygous genotypes can be identified.

120 We analysed the dataset provided by diversityArrays together with the data from Wells and
121 Dale (2018). To ensure the datasets were compatible, we filtered each dataset separately
122 based on the conditions described below using the R packages dartR (Gruber et al., 2018)
123 and radiator (Gosselin, 2019). We then used only the loci shared across both datasets for
124 the remainder of the analyses.

125 We required SNPs have a minimum call rate ≥ 0.9 , a minor allele count of at least 3,
126 observed heterozygosity > 0.5 , minimum depth of $> 5X$ and maximum depth of $50X$. If we
127 found multiple SNPs on the same read, then we removed the SNP with lowest replicability
128 (based on the number of technical replicates that resulted in the same allele being called).
129 Finally, where appropriate for further analysis, we removed SNPs outside of Hardy-Weinberg
130 Equilibrium or that we inferred as being under selection. Specific details of why these filters
131 were implemented and how are outlined in the supplementary methods. One individual was

132 excluded from all analyses (BBFA3), as this sample had a very high number of SNPs
133 missing across all loci (93%).



134

135 **Figure 1. Map of sampling localities within New Zealand (coloured dots).** The prevailing ocean
136 currents and biogeographic breaks proposed by Shears et al (2008) are also indicated. Black dashed
137 lines and unabbreviated labels indicate bioprovinces. Grey arrows indicate currents, abbreviated as:
138 EAC (East Auckland Current), ECE (East Cape Eddy), ECC (East Cape Current), WE (Wairarapa
139 Eddy), and SC (Southland Current).

140

141 Data Analysis

142 We calculated F-statistics using StAMPP (Pembleton et al., 2013). We used F_{st} as the
143 primary measure of genetic differentiation because F_{st} remains relatively robust for biallelic
144 markers such as SNPs (Whitlock, 2011).

145 We conducted principal component analyses (PCA) using the R package adegenet (Jombart
146 & Ahmed, 2011). In order to understand the correspondence between the principal
147 components and geography, we performed a Procrustes transformation of the first two
148 principal components using MCMCpack in R (Martin et al., 2011). Procrustes
149 transformations scale, stretch, and rotate the PCA in order to minimize the differences

150 between two matrices (in this case, the difference between principal components and
151 geographic coordinates).

152 We implemented STRUCTURE analyses using STRUCTURE 2.3.4 (Falush et al., 2003) and
153 performed with all populations (including the repeated samples of Stanmore Bay). For these
154 analyses, we assumed an admixture model. We ran the Markov Chain Monte Carlo
155 simulations with 100,000 iterations and a burn-in of 50,000. We conducted ten replicates of
156 each run, and varied K from 2 through 9. We performed final population inference by
157 consolidating the results for each level of K , in CLUMPP (Jakobsson & Rosenberg, 2007).
158 Additionally, we performed a separate STRUCTURE analysis on the Auckland populations
159 with the implementation of the locprior model at a K of 3, in order to test for fine-grain
160 population structure within Auckland. Due to concerns regarding the inferences made when
161 defining K , we chose to present a range of realistic values for K (Pritchard et al., 2010; Verity
162 & Nichols, 2016).

163 We tested for Isolation-by-Distance by conducting a Mantel test using the R package vegan
164 (Oksanen et al., 2010). We used Slatkin's linearized F_{st} matrix (transformed using $1/1-F_{st}$
165 (Rousset, 1997)) and an overwater distance matrix for this test. We calculated overwater
166 distance using the marmap (Pante & Simon-Bouhet, 2013) and fossil (Vavrek, 2011) R
167 packages, finding the minimum distance between populations around the coast within a
168 depth range of 150 m.

169

170 **Results**

171 To examine population structure in *I. armatus* populations, we isolated 261 individuals
172 distributed across 8 populations across New Zealand (**Fig. 1**). We obtained DaRT SNP data
173 for these 261 individuals, which identified 78,927 SNP loci as being polymorphic. After
174 stringent filtering (see **Methods** and **Supp. Methods**), 8,020 SNPs remained
175 (**Supplementary Table 2**).

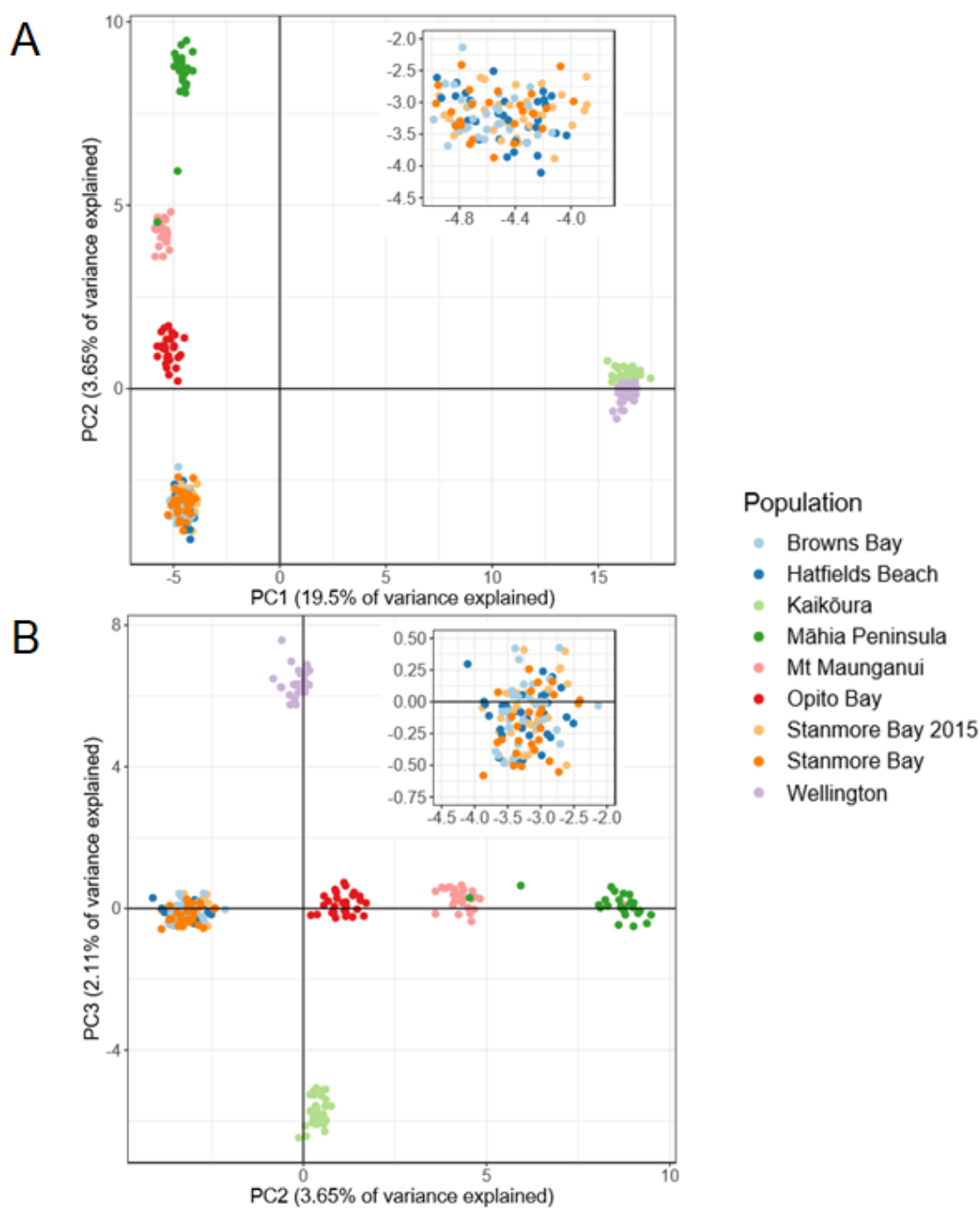
176 We first used this filtered SNP data to test for population structure using F statistics (see
177 **Methods**). We found evidence for structure (likely due to decreased rates of genetic
178 exchange) only between populations at least 19 km apart (Browns Bay and Stanmore Bay),
179 with F_{st} values ranging from 0.06 to 0.25 (**Table 1**).

180 **Table 1. Population F_{st} values.** There is evidence of weak population structure within some of the
 181 Auckland populations (Hatfields Beach and Stanmore Bay with Browns Bay). However, population
 182 structure between all other populations is strong, with a maximal F_{st} of 0.25 between Kaikōura and the
 183 Māhia Peninsula. Unless otherwise indicated, all p-values are less than 0.0001.

	Hatfields Beach 2015	Stanmore Bay 2015	Stanmore Bay 2018	Browns Bay 2018	Opito Bay 2018	Mt Maunganui 2018	Māhia Peninsula 2018	Wellington 2018
Stanmore Bay 2015	0 (p=0.65)							
Stanmore Bay 2018	0.001 (p=0.02)	0 (p=0.79)						
Browns Bay 2018	0.002 (p=0.002)	0.002	0.002					
Opito Bay 2018	0.035	0.034	0.034	0.035				
Mt Maunganui 2018	0.067	0.069	0.067	0.068	0.032			
Māhia Peninsula 2018	0.092	0.090	0.091	0.091	0.070	0.063		
Wellington 2018	0.17	0.17	0.24	0.17	0.19	0.22	0.18	
Kaikōura 2018	0.18	0.18	0.19	0.18	0.20	0.23	0.25	0.12

184

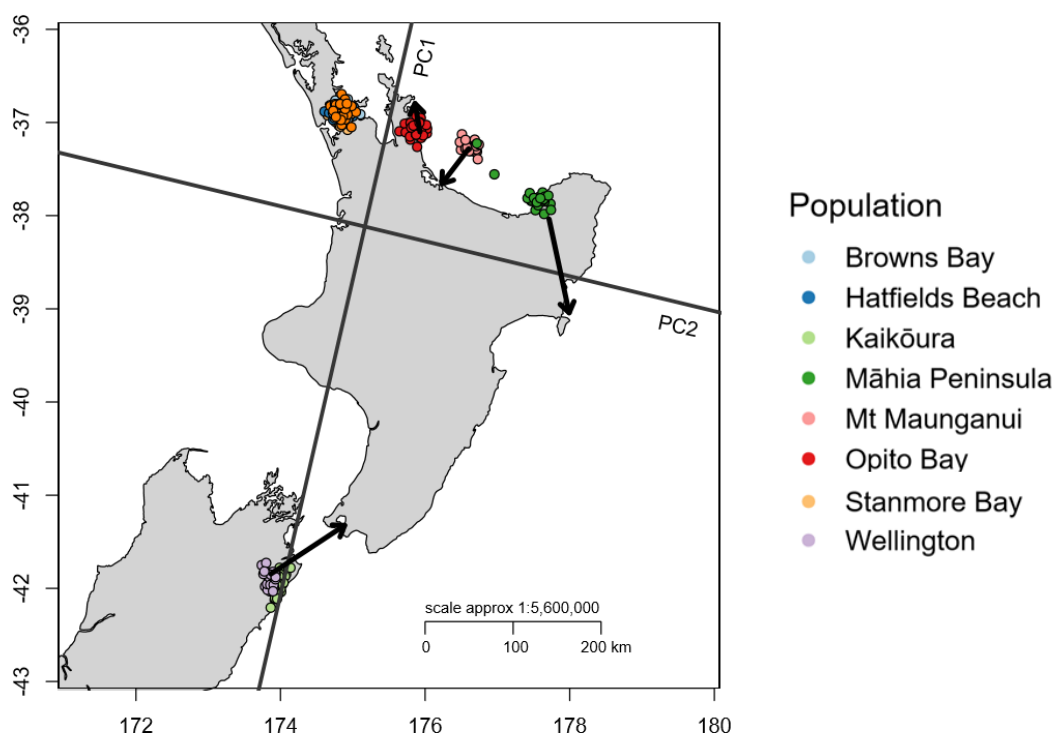
185 We next quantified population structure using principal component analysis, which identifies
 186 the combinations of SNP loci that vary the most between individuals. We found that PC1
 187 accounted for 19.5%, PC2 for 3.65%, and PC3 for 2.11% of the variance in SNP allele
 188 frequency (**Figs. 2A** and **2B**). PC1 primarily delineated the southern Wellington and
 189 Kaikōura populations from the other populations. PC2 primarily differentiated between the
 190 northern populations, and revealed three potential cases of migration between Mt
 191 Maunganui and the Māhia Peninsula (**Fig. 2A**). Finally, PC3 differentiated the southern
 192 populations, Wellington and Kaikoura. All Auckland populations clustered together,
 193 suggesting these individuals form one large population. We found no difference between the
 194 temporal samples from Stanmore Bay, indicating that allele frequency variation over short
 195 timescales is relatively stable.



196

197 **Figure 2. Principal Component Analysis (PCA) indicates strong location-dependent**
198 **population structure.** PC1 (19.5% of the variance) largely differentiates the individuals in
199 southern populations from those in the northern populations (i.e. Wellington and Kaikōura
200 from the rest). PC2 (3.65% of the variance) differentiates between the northern populations.
201 Finally, PC3 differentiates the populations within the southern group. Insets show the
202 Auckland populations, and indicate minimal evidence for structure within within them. Three
203 potential recent migrant individual are apparent, two from the Māhia population (green
204 points) to the Mt Maunganui population (pink points), and one from the Mt Maunganui
205 population to the Māhia population, visible in panel (B) within the green points.
206

207 A Procrustes transformation of the first two components of the PCA onto geographical space
208 revealed that the spacing of each genetic cluster was strikingly concordant with the locations
209 in geographical space, with the exception of Māhia and Wellington (**Fig. 3**).

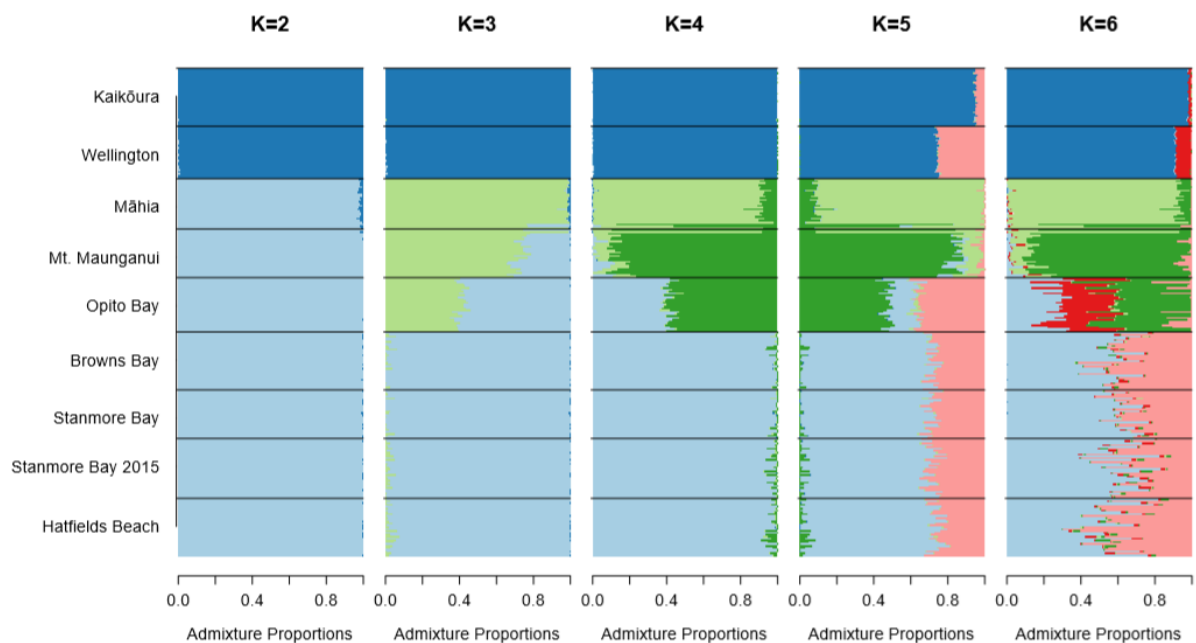


210 **Figure 1. Procrustes transformation of PC1 vs PC2 onto geographical coordinates.**
211 The transformation indicates a strong correspondence between sampling location and
212 genotype distance in principal component space. The arrows point to the location where a
213 population is actually found, while clusters indicate their location in Procrustes-transformed
214 space. The bottom arrow indicates the location of the Wellington population (purple) only.

215

216 As a complementary approach to the PCA in quantifying population structure, we
217 implemented a STRUCTURE analysis. This method implements a model-based clustering
218 approach, which probabilistically assigns individuals to one or more populations under an
219 admixture model. The admixture model assigns different proportions of an individual's
220 genome belonging to different ancestral populations (Pritchard et al., 2010). The
221 STRUCTURE analyses showed similar results to the PCA, with all individuals from the
222 Auckland locations consistently clustering together, while Kaikōura and Wellington also
223 always clustered together across all ranges of K (**Fig. 4**). Again we observed no fine-grain
224 structure within Auckland when sampling location was incorporated into the analysis
225 (through use of the locprior model) (**Suppl. Fig. 3**).

226 As we increased K, additional population genetic structure (history) became apparent. When
227 K=3, Māhia individuals formed a distinct cluster exhibiting high admixture with both Mt.
228 Maunganui and Opito Bay. Increasing K further suggested genetic admixture between all
229 adjacent populations with the exception of Wellington and Māhia. With K=4, there was clear
230 evidence of two Māhia individuals with admixture profiles more similar to Mt. Maunganui
231 individuals, and one Mt. Maunganui individual with a profile similar to Māhia individuals (Fig.
232 5, bottom two individuals in the Māhia sample and top individual in the Maunganui sample,
233 respectively). These correspond to the potential migrants identified in the PCA above.
234 Unexpectedly, with K=5 and K=6, there was evidence of admixture between the
235 northernmost populations (Auckland and Opito Bay) and the southernmost (Wellington and
236 Kaikōura). However, this may be an artefact of overfitting (Evanno et al, 2005).

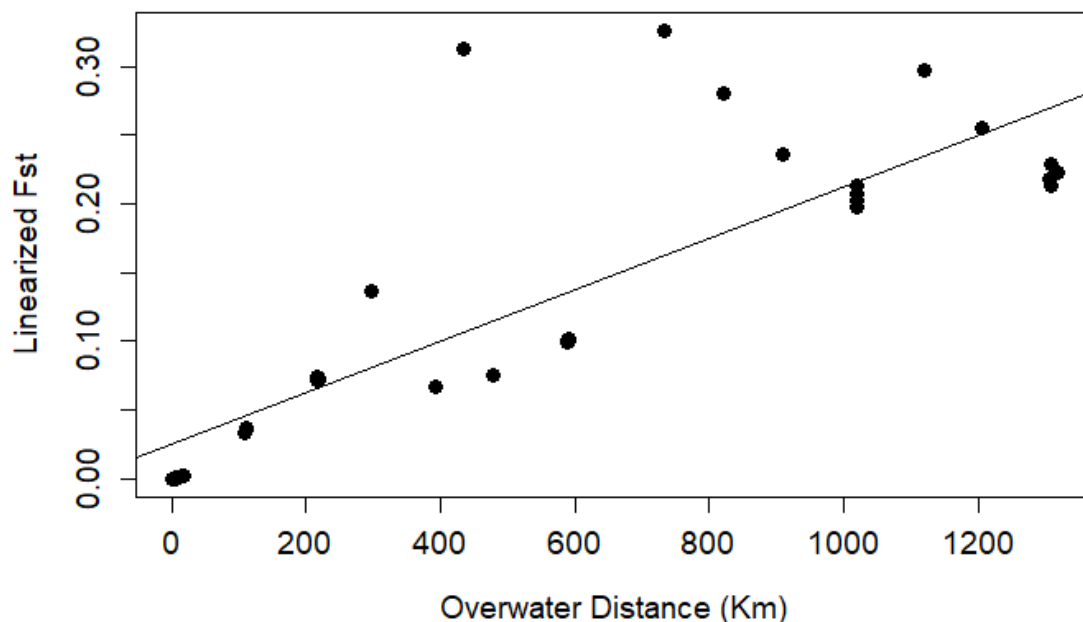


237

238 **Figure 4. Admixture plots based on Bayesian clustering analyses generated in**
239 **STRUCTURE.** Each horizontal coloured line represents an individual from the locality
240 sampled (indicated on the left). Horizontal black lines designate the junction between
241 population samples. Results are based on 10 replicate runs for each K. At K=4 there are two
242 individuals from Māhia with Mt. Maunganui-like admixture profiles (bottom two bars in the
243 Māhia samples), and one individual from Mt. Maunganui with a Māhia-like admixture profile
244 (top bar in the Mt. Maunganui samples).
245

246 For all the analyses above (F_{st} , PCA, and STRUCTURE), there was clear evidence of
247 population structure. In addition, the Procrustes transformation showed high correspondence
248 between PCA distance and geographic distance (i.e. isolation-by-distance, IBD). In order to
249 further confirm this, we used a Mantel test. This test showed a significant positive correlation
250 between Slatkin's linearized F_{st} (used as a measure of population structure) and geographic

251 overwater distance ($r = 0.83$, $P = 0.001$; **Fig. 5**), again supporting IBD. This strong positive
252 relationship remained even after excluding the southernmost populations (Kaikōura and
253 Wellington) ($r = 0.92$, $P = 0.001$), indicating a pattern of IBD across several spatial scales.



254

255 **Figure 5. The positive correlation between overwater distance and Slatkin's linearized**
256 **F_{st} suggests a pattern of population genetic structure due to isolation-by-distance.**
257 The black line indicates the slope of relationship for just the contrasts between the northern
258 populations (points in the lower left quadrant).

259

260 Discussion

261 Here we have quantified population structure in a direct-developing marine invertebrate
262 across a wide range of spatial scales. By employing a GBS approach we aimed to increase
263 our power to detect even low levels of population structure.

264 We found minimal evidence of population structure of *Isocladus armatus* within the Auckland
265 region. Only the F_{st} analysis suggested that there is any population differentiation, between
266 the Browns Bay and other Auckland populations. These are separated by approximately
267 20km, which may be the smallest distance at which population genetic structure starts to
268 occur in this species. Further resolution of this would require more fine-scaled spatial
269 sampling in this region. These results, indicating low levels of population structure, are
270 consistent with previous work in this species (Wells and Dale, 2018), as well as biphasically
271 developing marine invertebrates in the Hauraki Gulf (offshore of the Auckland region), such
272 as the native New Zealand sea urchin *Evechinus chloroticus* (Nagel et al., 2015) and the
273 invasive tunicate *Styela clava* (Goldstien et al., 2010).

274 Over larger spatial scales, *I. armatus* exhibited strong patterns of isolation by distance (IBD).
275 The Procrustes-transformed PCA indicated that PC1 and PC2 were highly concordant with
276 the geographic arrangement of populations. To test the hypothesis of IBD more explicitly, we
277 used a Mantel test, which indicated a strong and almost linear correlation between
278 geographic distance and genetic distance, indicative of a stepping stone model of
279 distribution.

280 We found evidence for unusually high admixture between Mt. Maunganui and Māhia
281 Peninsula, despite their separation by a well-known biogeographic barrier, the East Cape.
282 Perhaps the strongest evidence for this is the presence of three individuals that appeared to
283 be recent migrants between these populations. In one of these an individual from Māhia
284 population clustered with the Mt Maunganui in the PCA, while the opposite was the case for
285 the second individual. The third individual was found located between the associated PC
286 clusters. These three individuals also clustered with the other population, or were highly
287 admixed, in the STRUCTURE analysis, supporting the migrant hypothesis. The individual
288 with an intermediate genotype, as indicated by both the PCA and STRUCTURE analyses,
289 argues against these results being due to sample contamination.

290 The biogeographic break at the East Cape has been shown to affect population structure in
291 a range of species. This includes direct developers such as the anemone *Actinia tenebrosa*
292 and two species of amphipods (Stevens & Hogg, 2004; Veale & Lavery, 2012). Even
293 population structure in biphasic species with larval stages, such as the pua *Haliotis iris* (Will
294 et al., 2011), and the marine gastropod *Buccinulum vittatum* (Gemmell et al., 2018), are
295 affected by the East Cape. However, in contrast to these other direct developers, this break
296 does not appear to strongly affect *Isocladus armatus*, as F_{st} between Mt. Maunganui and
297 Māhia were no greater than the F_{st} between Mt. Maunganui and the Auckland area
298 populations. In addition, the PCA showed the Mt. Maunganui population as almost exactly
299 intermediate between the Māhia and Opito Bay populations, rather than being more closely
300 allied with the Opito Bay population. Finally, the STRUCTURE analyses also showed
301 admixture between Māhia and Maunganui across all values of K.

302 Instead of the expected north-south genetic break at the East Cape, we found a strong
303 north-south break between Māhia and Wellington. This north-south break is congruent with
304 the placement of a proposed biogeographic region border in this area (Shears et al., 2008)
305 (**Fig. 1**). However, Shears et al. also proposed a biogeographic region border at East Cape,
306 which is inconsistent with our study. Indeed, our study contrasts with two previously
307 proposed hypotheses of strong genetic breaks associated with East Cape and the Cook
308 Strait. Instead, we observe high gene flow over the East Cape, and genetic clustering of

309 Wellington and Kaikōura populations. Similar clustering of populations in these southern
310 locations has been found for the anemone *Actinia tenebrosa* (Veale & Lavery, 2012).

311 One explanation for the strong genetic break may be the presence of cryptic species within *I.*
312 *armatus*, which would drive gene flow to near-zero levels. Within New Zealand, strong north-
313 south divergence between populations of the brooding brittle star, *Amphipolis squamata*, has
314 been suggested to be the result of cryptic speciation (Sponer & Roy, 2002). Cryptic species
315 have been frequently observed in isopods (Hurtado et al., 2016; Leese et al., 2008; Markow
316 & Pfeiler, 2010), and the degree of genetic divergence between the northern and southern
317 group in *I. armatus* is similar to that found between other cryptic species of isopods based on
318 mitochondrial DNA (Leese et al., 2008). The potential for cryptic species is further supported
319 by the observation of an individual from Browns Bay (which was excluded from all analyses)
320 which, despite appearing morphologically similar to *I. armatus*, lacked 93% of SNPs that
321 were present in other samples. While missing data is a common feature of reduced
322 representation datasets, excessively high missingness in GBS data has been associated
323 with divisions between species rather than populations (Tripp et al., 2017).

324

325 **Conclusion**

326 *Isocladus armatus* exhibits a surprisingly high amount of gene flow across small spatial
327 scales. However at distances greater than 20 km the level of population structure is
328 consistent with the expectation of reduced dispersal in direct developing species, and the
329 presence of IBD. Interestingly, the strongest genetic break we observed was between the
330 Māhia Peninsula and Wellington, with populations forming a clear northern and southern
331 grouping either side of this break. This was unexpected, as other well-known biogeographic
332 barriers – the East Cape and the Cook Strait – appeared to have little effect on population
333 genetic structure. Additional fine-scale sampling across this genetic break would help in
334 determining whether differentiation across this break is a result of the existence of cryptic
335 species being present, or the result of a geophysical barrier that prevents dispersal in this
336 region.

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