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

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Abstract

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

Introduction

Life history influences genetic population structure

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

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

Population Genetics in *Isopoda*

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

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

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

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

To investigate this, we use genotyping-by-sequencing (GBS) to resolve population structure over a range of spatial scales. By quantifying population genetic structure in this species, we are able to identify the role of geography (both distance and seascape features) in influencing gene flow and dispersal.

Methods

Sample Collection

We collected specimens of *Isocladus armatus* in June, 2018, from around the North Island, New Zealand, from locations where *I. armatus* has previously been recorded (Hurley & Jansen, 1977; *INaturalist.org*, n.d.). These sites were at Stanmore Bay, Browns Bay, Opito Bay (Coromandel), Mt Maunganui, Māhia Peninsula, and Wellington (Fig. 1). At each site we collected a minimum of 32 individuals, up to a maximum of 48, and attempted to sample individuals as equally as possible amongst colour morph and sex. Where possible, we

collected specimens larger than 5mm in order to ensure sufficient DNA could be extracted for sequencing (see supplementary methods for details). The maximum distance between individuals collected at any site did not exceed 30 m. Samples were stored at -80°C in 100% ethanol until extraction. We have included samples from Wells and Dale 2018 (see [ref] for sampling methods) to increase the number of sampled individuals and the range of location. In addition, the temporal structure of this sampling may yield insight into the short term changes in allele frequencies within a population.

DNA Extraction

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

Data Collection and Processing

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

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

We required SNPs have a minimum call rate ≥ 0.9, a minor allele count of at least 3, observed heterozygosity > 0.5, minimum depth of > 5X and maximum depth of 50X. If we found multiple SNPs on the same read, then we removed the SNP with lowest replicability (based on the number of technical replicates that resulted in the same allele being called). Finally, where appropriate for further analysis, we removed SNPs outside of Hardy-Weinberg Equilibrium or that we inferred as being under selection. Specific details of why these filters were implemented and how are outlined in the supplementary methods. One individual was excluded from all analyses (BBFA3), as this sample had a very high number of SNPs missing across all loci (93%).

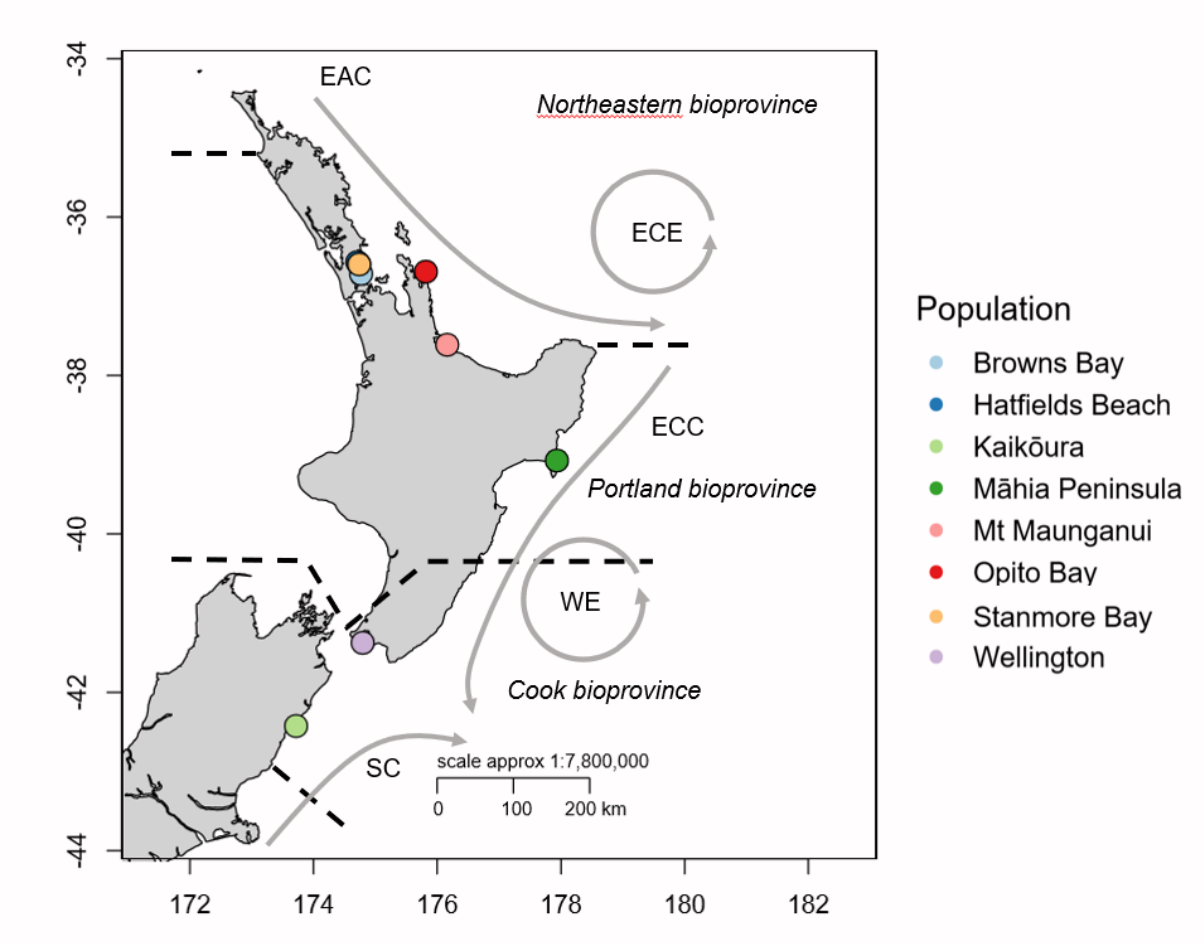

Figure 1. Map of sampling localities within New Zealand (coloured dots). The prevailing ocean currents and biogeographic breaks proposed by Shears et al (2008) are also indicated. Black dashed lines and unabbreviated labels indicate bioprovinces. Grey arrows indicate currents, abbreviated as: EAC (East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

Data Analysis

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

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

We implemented STRUCTURE analyses using STRUCTURE 2.3.4 (Falush et al., 2003) and performed with all populations (including the repeated samples of Stanmore Bay). For these analyses, we assumed an admixture model. We ran the Markov Chain Monte Carlo simulations with 100,000 iterations and a burn-in of 50,000. We conducted ten replicates of each run, and varied K from 2 through 9. We performed final population inference by consolidating the results for each level of *K*, in CLUMPP (Jakobsson & Rosenberg, 2007). Additionally, we performed a separate STRUCTURE analysis on the Auckland populations with the implementation of the locprior model at a *K* of 3, in order to test for fine-grain population structure within Auckland. Due to concerns regarding the inferences made when defining *K,* we chose to present a range of realistic values for *K* (Pritchard et al., 2010; Verity & Nichols, 2016; Lawson van Dorp, Falush 2018).

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

Results

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

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

Table 1. Population F_{st} values. There is evidence of weak population structure within some of the Auckland populations (Hatfields Beach and Stanmore Bay with Browns Bay). However, population structure between all other populations is strong, with a maximal F_{st} of 0.25 between Kaikōura and the 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

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

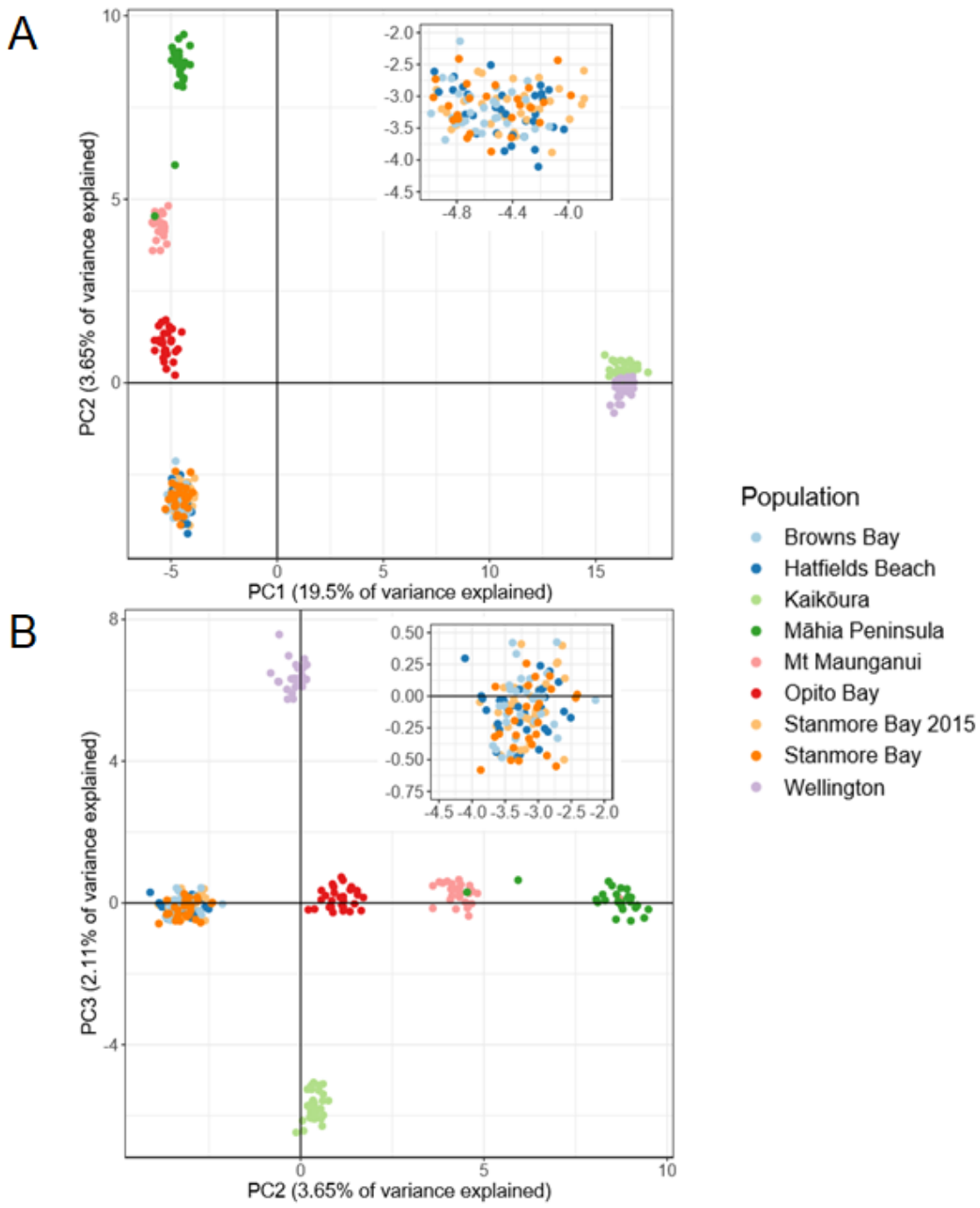

Figure 2. Principal Component Analysis (PCA) indicates strong location-dependent population structure. PC1 (19.5% of the variance) largely differentiates the individuals in southern populations from those in the northern populations (i.e. Wellington and Kaikōura from the rest). PC2 (3.65% of the variance)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

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

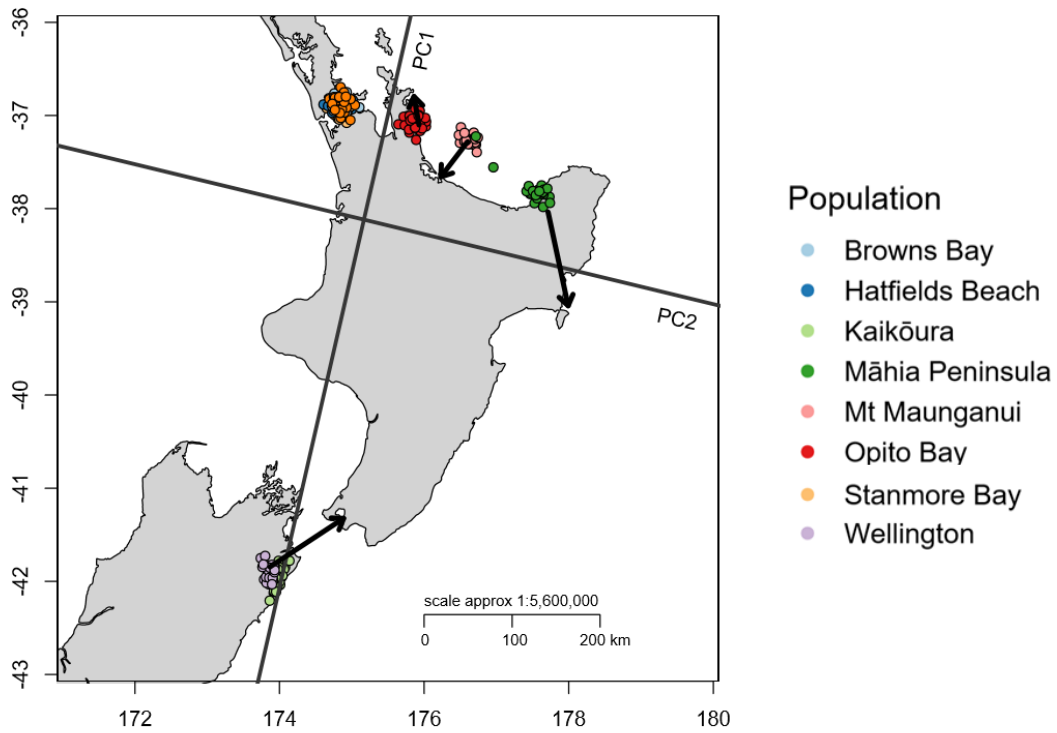

Figure 1. Procrustes transformation of PC1 vs PC2 onto geographical coordinates. The transformation indicates a strong correspondence between sampling location and genotype distance in principal component space. The arrows point to the location where a population is actually found, while clusters indicate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

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

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

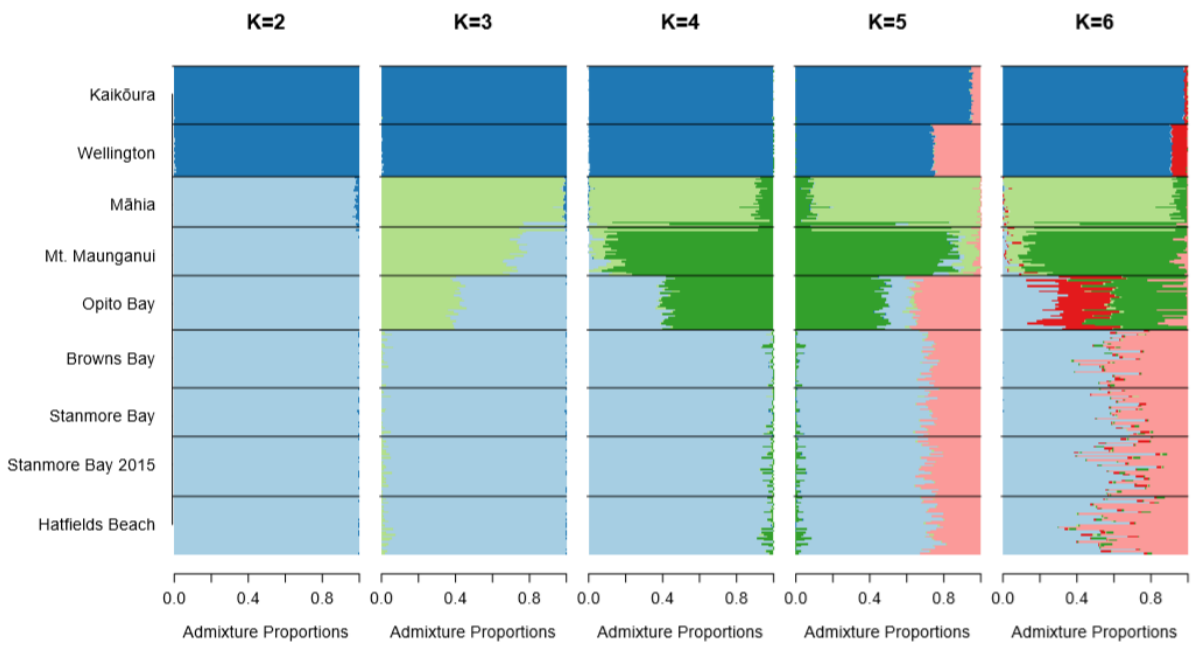

Figure 4. Admixture plots based on Bayesian clustering analyses generated in STRUCTURE. Each horizontal coloured line represents an individual from the locality sampled (indicated on the left). Horizontal black lines designate the junction between population samples. Results are based on 10 replicate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

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

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

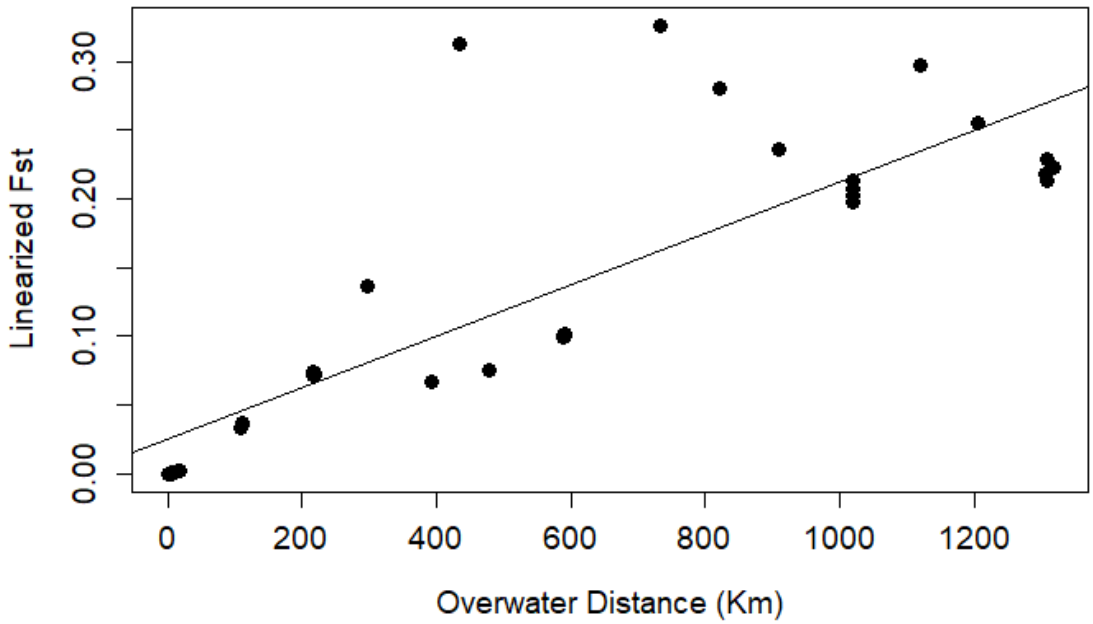

Figure 5. The positive correlation between overwater distance and Slatkin's linearized F_{st}. suggests a pattern of population genetic structure due to isolation-by-distance. The black line indicates the slope of relationship for just the contrasts between the northern populations (points in the lower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

Discussion

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

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

Over larger spatial scales, *I. armatus* exhibited strong patterns of isolation by distance (IBD). The Procrustes-transformed PCA indicated that PC1 and PC2 were highly concordant with the geographic arrangement of populations. To test the hypothesis of IBD more explicitly, we used a Mantel test, which indicated a strong and almost linear correlation between geographic distance and genetic distance, indicative of a stepping stone model of distribution. To try and estimate specific migration rates, we also performed a BayesAss3 analysis (Mussman et al., 2019). However, the parameter estimates from this analysis were internally inconsistent and in some cases had unbounded confidence intervals (see Supplementary Methods). This suggested that additional sampling would be required to accurately estimate these parameters.

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

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

Instead of the expected north-south genetic break at the East Cape, we found a strong north-south break between Māhia and Wellington. This north-south break is congruent with the placement of a proposed biogeographic region border in this area (Shears et al., 2008) (**Fig. 1**). However, Shears et al. also proposed a biogeographic region border at East Cape,

which is inconsistent with our study. Indeed, our study contrasts with two previously proposed hypotheses of strong genetic breaks associated with East Cape and the Cook Strait. Instead, we observe high gene flow over the East Cape, and genetic clustering of Wellington and Kaikōura populations. This contrasts with what has been found for the anemone *Actinia tenebrosa*, which has low gene flow over the East Cape (Veale & Lavery, 2012).

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

Conclusion

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

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