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

Authors: William S. Pearman[a]*, Sarah J. Wells[b], Olin K. Silander[a], Nikki E. Freed[a], and James Dale[a]

[a] School of Natural and Computational Sciences, Massey University, Auckland 0745, New Zealand

[b] School of Environmental and Animal Sciences, Unitec, Auckland 1025, New Zealand

*Corresponding author: wpearman1996@gmail.com

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. We find, unexpectedly, that well-known biogeographic barriers, the Cook Strait and the East Cape, have little effect on dispersal. However, there is strong evidence of a north-south break in populations structure, suggesting that unidentified biogeographic barriers prevent migration between these regions.

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.

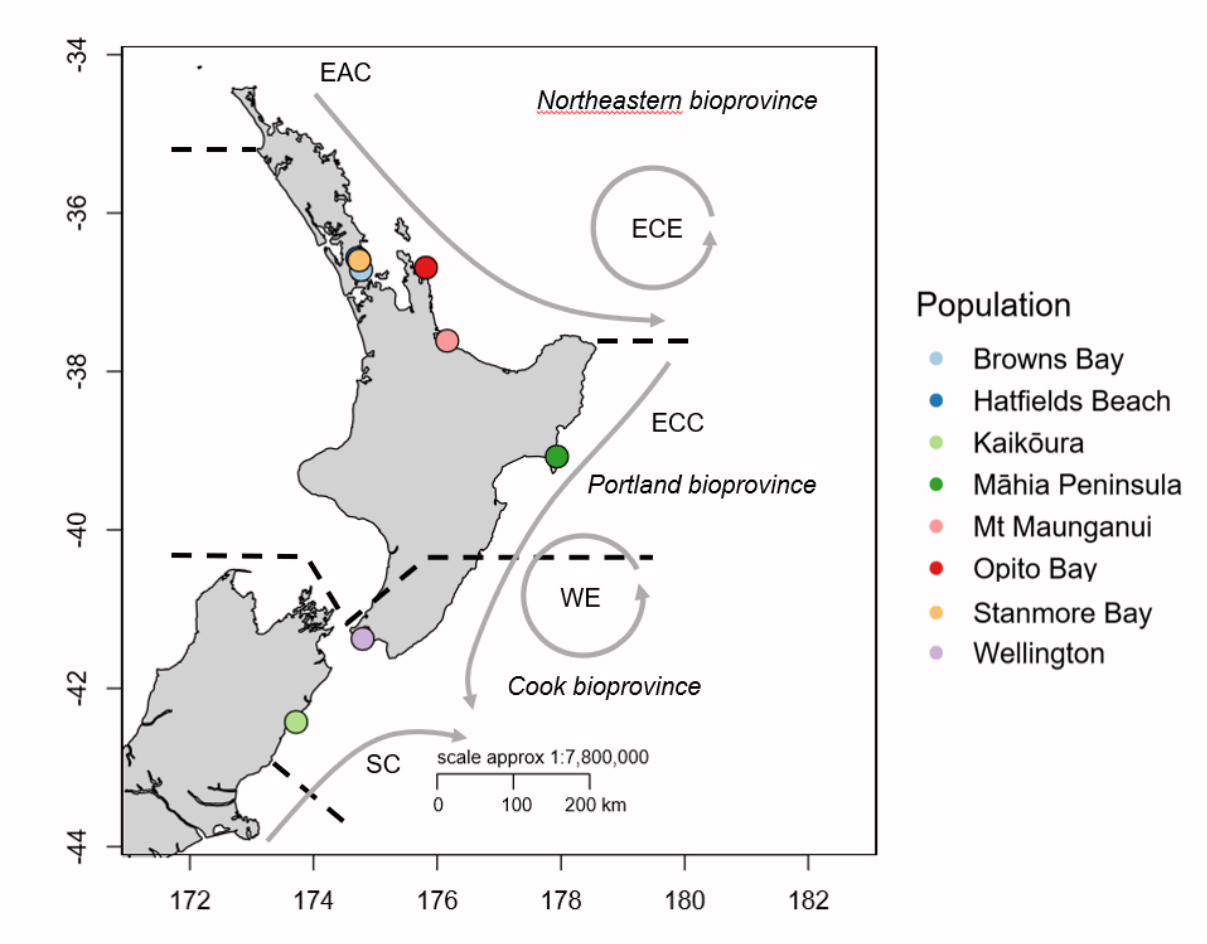
Data Collection and Processing

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

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



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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

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).

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.

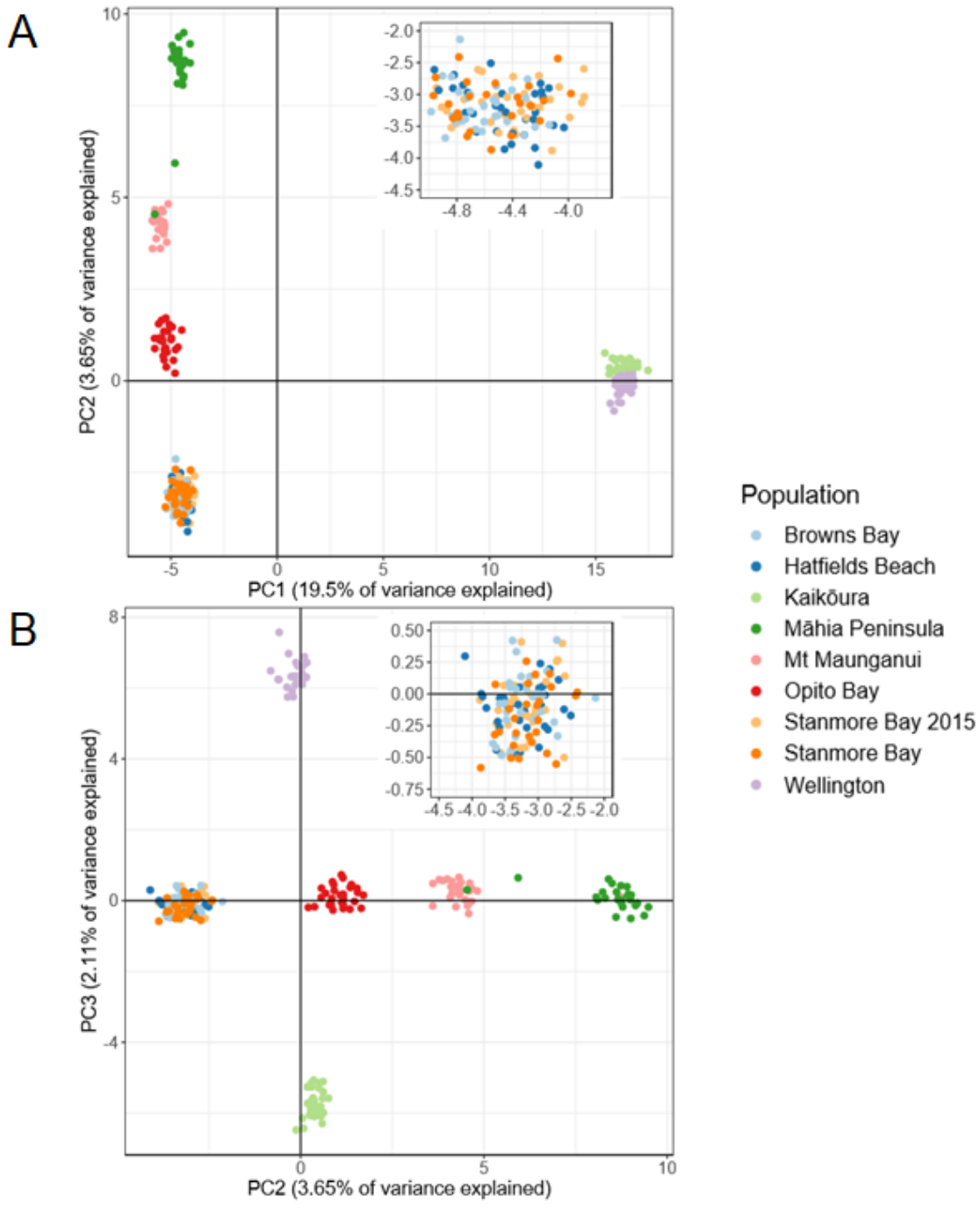

Figure 2. Principal Component Analysis (PCA) indicates strong location-dependent population structure. PC1 (19.5% of the variance) largely differentiates the individuals in southern populations from those in the northern populations (i.e. Wellington and Kaikōura from the rest). PC2 (3.65% of the variance) 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**).

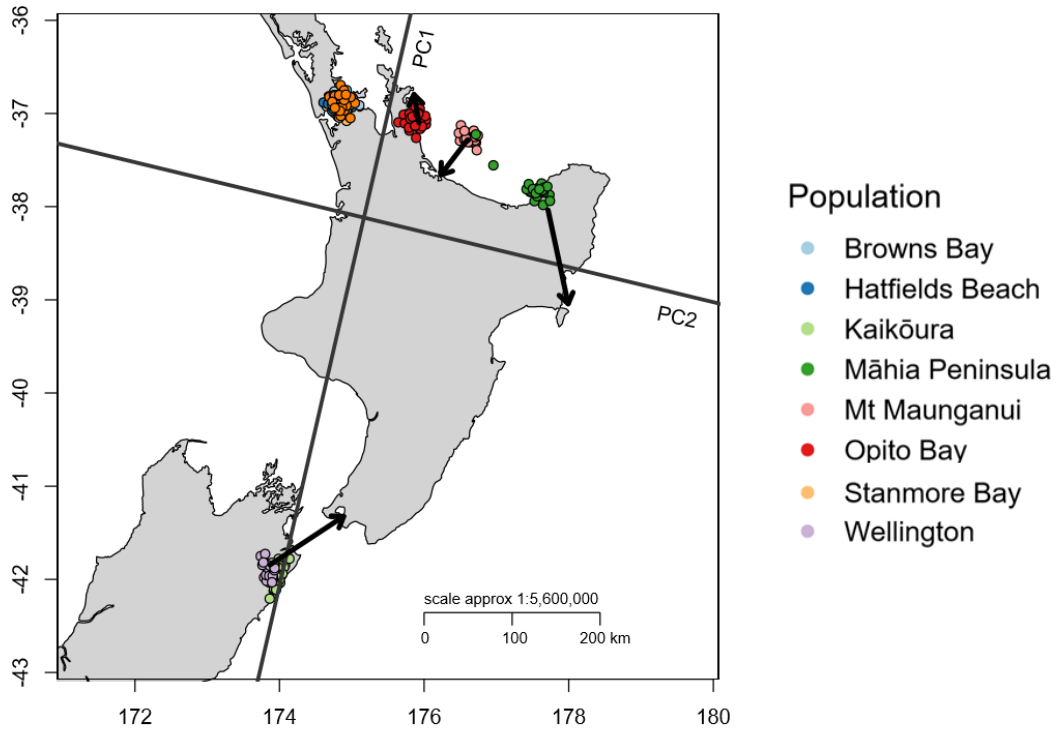

Figure 1. Procrustes transformation of PC1 vs PC2 onto geographical coordinates. The transformation indicates a strong correspondence between sampling location and genotype distance in principal component space. The arrows point to the location where a population is actually found, while clusters indicate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

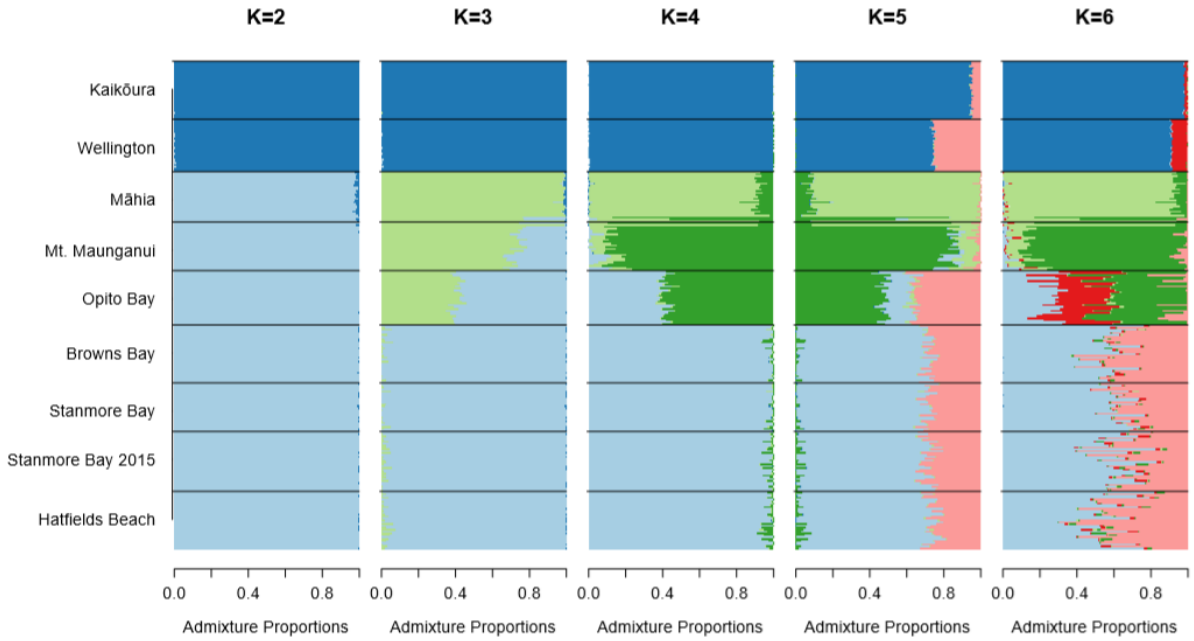

Figure 4. Admixture plots based on Bayesian clustering analyses generated in STRUCTURE. Each horizontal coloured line represents an individual from the locality sampled (indicated on the left). Horizontal black lines designate the junction between population samples. Results are based on 10 replicate 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.

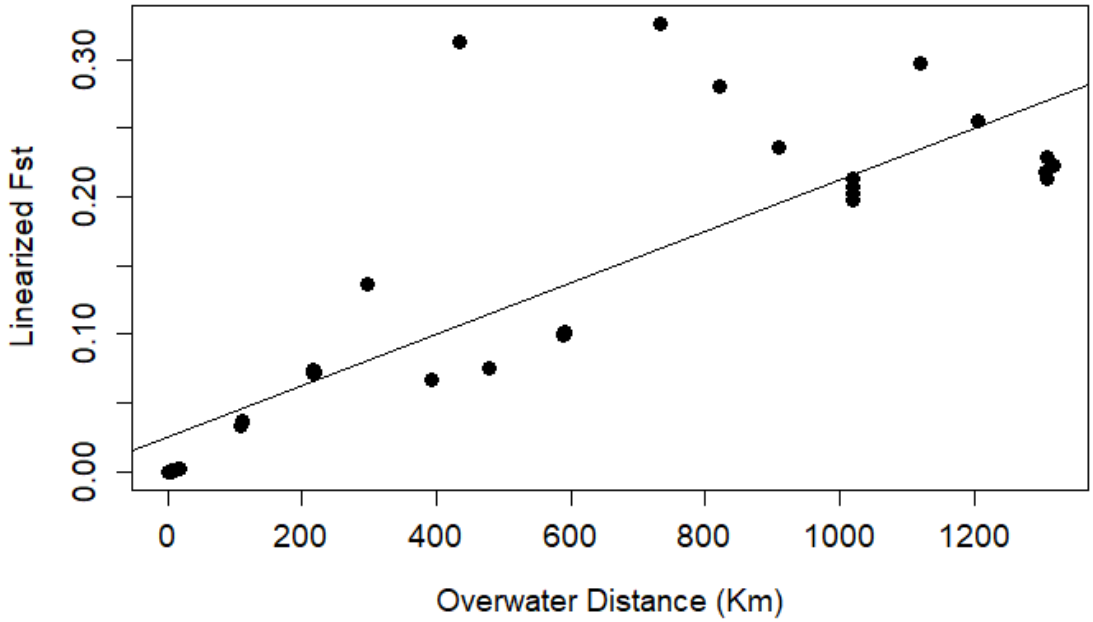

Figure 5. The positive correlation between overwater distance and Slatkin's linearized F_{st}. suggests a pattern of population genetic structure due to isolation-by-distance. The black line indicates the slope of relationship for just the contrasts between the northern populations (points in the lower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

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. Similar clustering of populations in these southern locations has been found for the anemone *Actinia tenebrosa* (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.

References

Amos, W. (2010). Even small SNP clusters are non-randomly distributed: Is this evidence of mutational non-independence? *Proc. Biol. Sci.*, *277*(1686), 1443–1449.

Arranz Martinez, V. (2017). *Connectivity among marine communities: A multi-species approach to determining the major drivers of larval connection between populations of coastal species in New Zealand* [PhD Thesis].

Ayre, D. J., Minchinton, T. E., & Perrin, C. (2009). Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? *Mol. Ecol.*, *18*(9), 1887–1903.

Baratti, M., Filippelli, M., & Messana, G. (2011). Complex genetic patterns in the mangrove wood-borer Sphaeroma terebrans Bate, 1866 (Isopoda, Crustacea, Sphaeromatidae) generated by shoreline topography and rafting dispersal. *J. Exp. Mar. Bio. Ecol.*, *398*(1–2), 73–82.

Beerli, P., & Felsenstein, J. (2001). Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences*, *98*(8), 4563–4568. https://doi.org/10.1073/pnas.081068098

Cowen, R. K., & Sponaugle, S. (2009). Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science*, *1*(1), 443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Dray, S., Dufour, A.-B., & Others. (2007). The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.*, *22*(4), 1–20.

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A Robust, Simple Genotyping-by-Sequencing (GBS) Approach for High Diversity Species. *PLoS One*, *6*(5), e19379.

Evanno, G., Regnaut, S., & Goudet, J. (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology*, 14(8), 2611-2620.

Excoffier, L., Smouse, P. E., & Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics*, *131*(2), 479–491.

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, *164*(4), 1567–1587.

Fraser, C. I., Morrison, A. K., Hogg, A. M., Macaya, E. C., van Sebille, E., Ryan, P. G., Padovan, A., Jack, C., Valdivia, N., & Waters, J. M. (2018). Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. *Nat. Clim. Chang.*, *8*(8), 704–708. https://doi.org/10.1038/s41558-018-0209-7

Gemmell, M. R., Trewick, S. A., Crampton, J. S., Vaux, F., Hills, S. F. K., Daly, E. E., Marshall, B. A., Beu, A. G., & Morgan-Richards, M. (2018). Genetic structure and shell shape variation within a rocky shore whelk suggest both diverging and constraining selection with gene flow. *Biol. J. Linn. Soc. Lond.*, *125*(4), 827–843.

Goldstien, S. J., Schiel, D. R., & Gemmell, N. J. (2010). Regional connectivity and coastal expansion: Differentiating pre-border and post-border vectors for the invasive tunicate Styela clava. *Mol. Ecol.*, *19*(5), 874–885.

González-Wevar, C. A., Segovia, N. I., Rosenfeld, S., Ojeda, J., Hüne, M., Naretto, J., Saucède, T., Brickle, P., Morley, S., Féral, J.-P., Spencer, H. G., & Poulin, E. (2018). Unexpected absence of island endemics: Long-distance dispersal in higher latitude sub-Antarctic Siphonaria (Gastropoda: Euthyneura) species. *Journal of Biogeography*, *45*(4), 874–884. https://doi.org/10.1111/jbi.13174

Gosselin, T. (2019). *thierrygosselin/radiator: Official release*.

Gruber, B., Unmack, P. J., Berry, O. F., & Georges, A. (2018). dartr: An r package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Mol. Ecol. Resour.*, *18*(3), 691–699.

Hurley, D. E., & Jansen, K. P. (1977). The marine fauna of New Zealand: Family Sphaeromatidae (Crustacea Isopoda: Flabellifera). *N.Z. Oceanogr. Inst. Mem.*, *63*, 1–80.

Hurtado, L. A., Mateos, M., Mattos, G., Liu, S., Haye, P. A., & Paiva, P. C. (2016). Multiple transisthmian divergences, extensive cryptic diversity, occasional long-distance dispersal, and biogeographic patterns in a marine coastal isopod with an amphi-American distribution. *Ecology and Evolution*, *6*(21), 7794–7808. https://doi.org/10.1002/ece3.2397

INaturalist.org. (n.d.). https://www.inaturalist.org/

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*(14), 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Jombart, T., & Ahmed, I. (2011). adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. *Bioinformatics*, *27*(21), 3070–3071.

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2014). Poppr: An R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ*, *2*, e281. https://doi.org/10.7717/peerj.281

Keightley, P. D., Ness, R. W., Halligan, D. L., & Haddrill, P. R. (2014). Estimation of the spontaneous mutation rate per nucleotide site in a Drosophila melanogaster full-sib family. *Genetics*, *196*(1), 313–320.

Kilian, A., Wenzl, P., Huttner, E., Carling, J., Xia, L., Caig, V., Heller-uszynska, K., Jaccoud, D., Hopper, C., Aschenbrenner-kilian, M., Evers, M., Peng, K., Cayla, C., Hok, P., & Uszynski, G. (2012). Diversity Arrays Technology: A Generic Genome Profiling Technology on Open Platforms. In *Data Production and Analysis in Population Genomics* (Vol. 888, pp. 67–89).

Kimura, M., & Weiss, G. H. (1964). The Stepping Stone Model of Population Structure and the Decrease of Genetic Correlation with Distance. *Genetics*, *49*(4), 561–576.

Leese, F., Kop, A., Wägele, J. W., & Held, C. (2008). Cryptic speciation in a benthic isopod from Patagonian and Falkland Island waters and the impact of glaciations on its population structure. *Front. Zool.*, *5*, 1–15.

Markow, T. A., & Pfeiler, E. (2010). Mitochondrial DNA evidence for deep genetic divergences in allopatric populations of the rocky intertidal isopod Ligia occidentalis from the eastern Pacific. *Molecular Phylogenetics and Evolution*, *56*(1), 468–473. https://doi.org/10.1016/j.ympev.2009.12.002

Martin, A., Quinn, K., & Park, J. H. (2011). MCMCpack: Markov Chain Monte Carlo in R. *Journal of Statistical Software, Articles*, *42*(9), 1–21.

McGaughran, A., Hogg, I. D., Stevens, M. I., Lindsay Chadderton, W., & Winterbourn, M. J. (2006). Genetic divergence of three freshwater isopod species from southern New Zealand. *J. Biogeogr.*, *33*(1), 23–30.

McMillan, W. O., Raff, R. A., & Palumbi, S. R. (1992). Population Genetic Consequences of Developmental Evolution in Sea Urchins (genus Heliocidaris). *Evolution*, *46*(5), 1299–1312. https://doi.org/10.1111/j.1558-5646.1992.tb01125.x

Mussmann, S. M., Douglas, M. R., Chafin, T. K., & Douglas, M. E. (2019). BA3-SNPs: Contemporary migration reconfigured in BayesAss for next-generation sequence data. *Methods Ecol. Evol.*, *202*, 389.

Nagel, M. M., Sewell, M. A., & Lavery, S. D. (2015). Differences in population connectivity of a benthic marine invertebrate Evechinus chloroticus (Echinodermata: Echinoidea) across large and small spatial scales. *Conserv. Genet.*, *16*(4), 965–978. https://doi.org/10.1007/s10592-015-0716-2

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2010). Vegan: Community ecology package. R package version 1.17-4. *Http://Cran. r-Project. Org>. Acesso Em*, *23*, 2010.

Pante, E., & Simon-Bouhet, B. (2013). marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS One*, *8*(9), e73051.

Pelc, R. A., Warner, R. R., & Gaines, S. D. (2009). Geographical patterns of genetic structure in marine species with contrasting life histories. *J. Biogeogr.*, *36*(10), 1881–1890.

Pembleton, L. W., Cogan, N. O. I., & Forster, J. W. (2013). StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Mol. Ecol. Resour.*, *13*(5), 946–952.

Pritchard, J. K., Wen, W., & Falush, D. (2010). *Documentation for STRUCTURE software: Version 2.3*. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.323.9675&rep=rep1&type=pdf

Puebla, O., Bermingham, E., & Guichard, F. (2009). Estimating dispersal from genetic isolation by distance in a coral reef fish (Hypoplectrus puella). *Ecology*, *90*(11), 3087–3098.

Puritz, J. B., Keever, C. C., Addison, J. A., Barbosa, S. S., Byrne, M., Hart, M. W., Grosberg, R. K., & Toonen, R. J. (2017). Life-history predicts past and present population connectivity in two sympatric sea stars. *Ecol. Evol.*, *7*(11), 3916–3930.

463 Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics
464 under isolation by distance. *Genetics*, *145*(4), 1219–1228.

465 Santamaria, C. A., Mateos, M., & Hurtado, L. A. (2014). Diversification at the narrow sea-
466 land interface in the Caribbean: Phylogeography of endemic supralittoral Ligia
467 isopods. *Frontiers in Ecology and Evolution*, *2*.
468 https://doi.org/10.3389/fevo.2014.00042

469 Shanks, A. L. (2009). Pelagic larval duration and dispersal distance revisited. *The Biological*
470 *Bulletin*, *216*(3), 373–385. https://doi.org/10.1086/BBLv216n3p373

471 Shears, N. T., Smith, F., Babcock, R. C., Duffy, C. A. J., & Villouta, E. (2008). Evaluation of
472 biogeographic classification schemes for conservation planning: Application to New
473 Zealand's coastal marine environment. *Conserv. Biol.*, *22*(2), 467–481.

474 Simpson, S. D., Harrison, H. B., Claereboudt, M. R., & Planes, S. (2014). Long-Distance
475 Dispersal via Ocean Currents Connects Omani Clownfish Populations throughout
476 Entire Species Range. *PLOS ONE*, *9*(9), e107610.
477 https://doi.org/10.1371/journal.pone.0107610

478 Smouse, P. E., Long, J. C., & Sokal, R. R. (1986). Multiple Regression and Correlation
479 Extensions of the Mantel Test of Matrix Correspondence. *Systematic Zoology*, *35*(4),
480 627–632. JSTOR. https://doi.org/10.2307/2413122

481 Sponer, R., & Roy, M. S. (2002). Phylogeographic analysis of the brooding brittle star
482 *Amphipholis squamata* (Echinodermata) along the coast of New Zealand reveals
483 high cryptic genetic variation. *Evolution*, *56*(10), 1954–1967.

484 Stevens, M. I., & Hogg, I. D. (2004). Population genetic structure of New Zealand's endemic
485 corophiid amphipods: Evidence for allopatric speciation. *Biol. J. Linn. Soc. Lond.*,
486 *81*(1), 119–133.

487 Temunović, M., Franjić, J., Satovic, Z., Grgurev, M., Frascaria-Lacoste, N., & Fernández-
488 Manjarrés, J. F. (2012). Environmental heterogeneity explains the genetic structure
489 of Continental and Mediterranean populations of Fraxinus angustifolia Vahl. *PLoS*
490 *One*, *7*(8), e42764.

491 Teske, P., Papadopoulos, I., Zardi, G., McQuaid, C., Edkins, M., Griffiths, C., & Barker, N.
492 (2007). Implications of life history for genetic structure and migration rates of
493 southern African coastal invertebrates: Planktonic, abbreviated and direct
494 development. *Mar. Biol.*, *152*(3), 697–711.

Tripp, E. A., Tsai, Y.-H. E., Zhuang, Y., & Dexter, K. G. (2017). RADseq dataset with 90% missing data fully resolves recent radiation of Petalidium (Acanthaceae) in the ultra-arid deserts of Namibia. *Ecol. Evol.*, *7*(19), 7920–7936.

Underwood, J. N., Travers, M. J., & Gilmour, J. P. (2012). Subtle genetic structure reveals restricted connectivity among populations of a coral reef fish inhabiting remote atolls. *Ecology and Evolution*, *2*(3), 666–679. https://doi.org/10.1002/ece3.80

Van Wyngaarden, M., Snelgrove, P. V. R., DiBacco, C., Hamilton, L. C., Rodríguez-Ezpeleta, N., Jeffery, N. W., Stanley, R. R. E., & Bradbury, I. R. (2017). Identifying patterns of dispersal, connectivity and selection in the sea scallop, Placopecten magellanicus, using RADseq-derived SNPs. *Evol. Appl.*, *10*(1), 102–117.

Vavrek, M. J. (2011). Fossil: Palaeoecological and palaeogeographical analysis tools. *Palaeontol. Electronica*, *14*(1), 16.

Veale, A. J., & Lavery, S. D. (2012). The population genetic structure of the waratah anemone (Actinia tenebrosa) around New Zealand. *N. Z. J. Mar. Freshwater Res.*, *46*(4), 523–536.

Verity, R., & Nichols, R. A. (2016). Estimating the Number of Subpopulations (K) in Structured Populations. *Genetics*, *203*(4), 1827–1839.

Waples, R. S. (1987). A Multispecies Approach to the Analysis of Gene Flow in Marine Shore Fishes. *Evolution*, *41*(2), 385–400. JSTOR. https://doi.org/10.2307/2409146

Wells, S. J., & Dale, J. (2018). Contrasting gene flow at different spatial scales revealed by genotyping-by-sequencing in Isocladus armatus, a massively colour polymorphic New Zealand marine isopod. *PeerJ*, *6*, e5462. https://doi.org/10.7717/peerj.5462

Whitlock, M. C. (2011). And D do not replace FST. *Mol. Ecol.*, *20*(6), 1083–1091.

Will, M., Hale, M. L., Schiel, D. R., & Gemmell, N. J. (2011). Low to moderate levels of genetic differentiation detected across the distribution of the New Zealand abalone, Haliotis iris. *Mar. Biol.*, *158*(6), 1417–1429.

Wilson, G. A., & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, *163*(3), 1177–1191.

Winston, J. E. (2012). Dispersal in marine organisms without a pelagic larval phase. *Integrative and Comparative Biology*, *52*(4), 447–457. https://doi.org/10.1093/icb/ics040

Yoshino, H., Yamaji, F., & Ohsawa, T. A. (2018). Genetic structure and dispersal patterns in Limnoria nagatai (Limnoriidae, Isopoda) dwelling in non-buoyant kelps, Eisenia

528 bicyclis and E. arborea, in Japan. *PLOS ONE*, *13*(6), e0198451.
529 https://doi.org/10.1371/journal.pone.0198451