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Short Communication

Genomic analyses suggest strong population connectivity over large spatial scales of the commercially important baitworm, *Australonuphis teres* (Onuphidae)

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Abstract. Barriers to dispersal can disrupt gene flow between populations, resulting in genetically distinct populations. Although many marine animals have potential for long-distance dispersal via a planktonic stage, gene flow among populations separated by large geographic distances is not always evident. Polychaetes are ecologically important and have been used as biological surrogates for marine biodiversity. Some polychaete species are used as bait for recreational fisheries, with this demand supporting commercial fisheries for polychaetes to service the retail bait market. However, despite their ecological and economic importance, very little is known about the life history or population dynamics of polychaetes, and few studies have used genetic or genomic approaches to understand polychaete population connectivity. Here, we investigate the population structure of one commonly collected beachworm species used for bait on the eastern coast of Australia, namely, *Australonuphis teres*, by using genome-wide single-nucleotide polymorphism data. We sampled *A. teres* from hierarchical nested spatial scales along 900 km of the coast in New South Wales. We identified six genetic groups, but there was no clear geographic pattern of distribution. Our results suggest that there is considerable gene flow among the sampled populations. These high-resolution genomic data support the findings of previous studies, and we infer that oceanographic processes promote genetic exchange among polychaete populations in south-eastern Australia.

Additional keywords: admixture, fisheries, genotype-by-sequencing, management, polychaete, population structure, SNP.

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Introduction

Life history, particularly the larval stage, and environmental influences govern biodiversity and population structure in the marine environment (Thorrold 2006; Chan *et al.* 2018). Understanding population connectivity, size and structure is critical for effective management of marine resources. Pelagic larval duration along with physical and ecological processes can greatly affect the likelihood of successful dispersal and population connectivity for marine species (Thiel and Gutow 2005*a*, 2005*b*; Cowen and Sponaugle 2009; Riginos *et al.* 2011; Kinlan and Gaines 2003). Despite evidence of strong population connectivity in some species (Shulman and

Bermingham 1995; Roberts 1997; Cowen *et al.* 2007), many other marine taxa, even those with apparently high dispersal potential, show surprisingly little evidence for gene flow among disjunct populations (Dibacco *et al.* 2006; Purcell *et al.* 2006; Froukh and Kochzius 2007; Marko *et al.* 2007; Temby *et al.* 2007; Miller *et al.* 2009, 2014; Xuereb *et al.* 2018). There is, thus, a growing recognition that marine systems are not all open and interconnected (Dennis and Hellberg 2010; Karsenti *et al.* 2011; Iacchei *et al.* 2013). Defining the scale of connectivity and determining the factors that influence gene flow are critical for understanding population dynamics and genetic structure of marine species, and for developing effective management strategies to mitigate anthropogenic effects on populations and ecosystems (Giangrande *et al.* 2005; Waples and Punt 2008).

Polychaete worms are common in intertidal ecosystems (Cole *et al.* 2007, 2017), and are good indicators of species richness and community patterns in benthic invertebrate assemblages (Olsgard and Somerfield 2000; Giangrande *et al.* 2005). Indeed, polychaetes have been used as biological surrogates for marine biodiversity (Olsgard *et al.* 2003; Shokri *et al.* 2009). Among benthic groups, polychaetes are one of the best indicators of environmental disturbance, because there are both sensitive and tolerant species across pristine and heavily disturbed habitats (Olsgard and Somerfield 2000). Polychaetes are important members of the marine food chain; they can act as predators, scavengers and grazers of diverse other organisms, or as prey for a variety of bird, fish and crustacean species (Fauchald and Jumars 1979; Jumars *et al.* 2015).

In addition to their ecological importance, many species of polychaetes are an important bait resource for recreational fishers (Cole *et al.* 2018). As with any fisheries resource, management relies on information about stock size and population connectivity (Cowen *et al.* 2007; Fogarty and Botsford 2007). In Australia, recreational and commercial fishers target beachworms directly for bait or for sale into the bait market respectively. Beachworms, including the 'kingworm' or 'stumpy' *Australonuphis teres* (Onuphidae), inhabit high-energy sandy beaches from Maroochydore, Queensland to Lakes Entrance, Victoria (Paxton 1979). Although little is known about their population biology, they are thought to be broadcast spawners, have been recorded to be sexually mature at 420 mm in length (Paxton 1979), and are suspected to breed multiple times a year (Paxton 1986). As adults, dispersal of *A. teres* is relatively limited (Paxton 1979), with large topographic structures (e.g. headlands and river mouths) that separate sandy beaches acting as physical barriers to dispersal.

Despite their ecological and economic importance, few population genetic (and fewer population genomic) studies have yet been conducted for polychaetes. In one genetic study from the USA, the baitworm *Glycera dibranchiata* (Glyceridae) was inferred to have little connectivity among populations within an estuary and between intertidal and subtidal populations (Bristow and Vadas 1991). In contrast, in Australia, a recent study of estuarine polychaetes found little genetic differentiation among populations of the nephtyids *Aglaophamus australiensis* and *Nephtys longipes*, from which the authors inferred that pelagic larval dispersal is probably mediated by ocean currents in these two species (Smith *et al.* 2015). However, this latter research was based only on small fragments of mitochondrial and nuclear loci, which were not of a high-enough resolution to enable assessment of whether population connectivity was ongoing or merely recent. The connectivity of populations of polychaetes along Australian coasts, thus, remains largely unknown, yet, such knowledge is of considerable importance for managing the sustainable harvest of beachworms and other polychaete bait species.

Here, we use genomic approaches to investigate population structure of the polychaete worm *A. teres* at multiple nested spatial scales (i.e. sites separated by kilometres, beaches separated by tens of kilometres, and regions separated by hundreds of kilometres) along 900 km of the New South Wales (NSW) coast in Australia. We generated a single-nucleotide polymorphism (SNP) dataset via genotype-by-sequencing. The three possible findings are as follows: (1) genetic homogeneity in all *A. teres* samples across spatial scales, which would indicate a single panmictic population and considerable gene flow along the coast, (2) genetically distinct populations of *A. teres*, indicating negligible gene flow among populations, or (3) a mixed result, with both similarities and differences among populations, indicating some gene flow. This study is one of the first to use large-scale genomic data to assess population connectivity in polychaetes.

Materials and methods

Field methods for sampling Australonuphis teres

Populations of *A. teres* were sampled in the Eastern Warm Temperate biogeographic zone of the NSW coast. Three bioregions were selected and we designated them as North, Central and South, corresponding to the Tweed–Moreton (28°S–30.5°S), Manning (30.5°S–30.75°S) and Batemans (34.6°S–36.6°S) bioregions respectively. A fully nested design was used to obtain samples of *A. teres*. In each of the three regions (separated by hundreds of kilometres), two beaches (separated by tens of kilometres), each with two randomly chosen sites (separated by kilometres), 45 individuals were collected. The posterior end (the last 20 mm of the body) was removed and placed in 98% ethanol and stored below −18°C for subsequent analysis. Beaches were selected as those where commercial harvesting of beachworms occurs (>0.6 t year^{-1} commercial catch over the previous 2 years). Samples of the population of *A. teres* were obtained through beach sampling, whereby a mesh bag containing a fish frame was dragged along the sand in the swash zone to entice the worms to emerge, and any worms that surfaced were collected by hand.

DNA extraction, library preparation and sequencing

Tissue samples were removed from ethanol, dried and subsampled. DNA was extracted with the Qiagen DNeasy 96 Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The quality and quantity of DNA were evaluated by gel electrophoresis and Qubit fluorometer (Invitrogen, Carlsbad, CA, USA). The 40 highest-yield extractions from each site were selected for sequencing, with a total of 480 individual *A. teres* being used in library preparation.

A genotyping-by-sequencing (GBS) approach to generate sequence data was used, as applied in similarly non-model

systems in the past, and following Fraser *et al.* (2018*a*) and references therein. Briefly, GBS library preparation followed standard protocols (Elshire *et al.* 2011) with minor modifications (Wilson *et al.* 2019). To each DNA sample, a uniquely barcoded *Pst*I adaptor was added (2.25 ng per sample; Morris *et al.* 2011). Digestion was performed with 4 U *Pst*I-HF (New England Biolabs, MA, USA) in 1 × CutSmart Buffer, and incubation at 37°C for 2 h. Adapters were ligated with T4 DNA ligase in 1 × ligation buffer (New England Biolabs, MA, USA) and incubated at 16°C for 90 min (with 2 min at 37°C every 30 min) and 80°C for 30 min. Purification was performed using a Qiagen MinElute 96 UF PCR Purification Kit (Qiagen, Hilden, Germany), with elution in 25 µL 1 × TE. Polymerase chain reactions (PCRs) were run on 50-µL volumes containing 10 µL purified DNA, 1 × MyTaqTM HS Master Mix (Bioline, Sydney, Australia) and 1 µM each of PCR primers 5′AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATC*T and 5′CAAGCAGAAGACGGCATACGAGATCGGTCTCGGCATTCCTGCTGAACCGCTCTTCCGATC*T (where * indicates phosphorothioation) at 72°C for 5 min, 95°C for 60 s, and 24 cycles of 95°C for 30 s, 65°C for 30 s and 72°C for 30 s, with a final extension step at 72°C for 5 min. Concentrations for each sample were assessed using a LabChip GXII (Caliper Life Sciences, MA, USA) and pooled equimolarly. A 200-base pair (bp) fraction (fragment size 250–450 bp) of the pooled library was separated via electrophoresis on a 1.5% agarose gel. Sequencing of DNA from this size range was performed on one lane of a high-output flowcell in an Illumina NextSeq 500 system (Illumina, CA, USA, 75 bp paired-end). The raw sequence data are available in the NCBI Sequence Read Archive under BioProject: PRJNA512571 (http://www.ncbi.nlm.nih.gov/bioproject/512571).

Data analysis

Sequencing yielded 185 204 387 reads that were, on average, 76 bp long. The quality of the sequences was first assessed using FASTQC (Andrews 2010), and SNPs were extracted using STACKS 2.41 (Catchen *et al.* 2013). All scripts are available as Supplementary Material to this paper.

Raw sequence reads were demultiplexed and quality filtered using the process_radtags module in STACKS. As there is no reference genome, SNP calling was performed using the denovo_map.pl pipeline, using default parameter settings. After removing low-quality individuals, SNPs with less than 60% of individuals sequenced were discarded as likely collapsed repeats. We explored the data following McGaughran *et al.* (2019) in vcftools (Danecek *et al.* 2011) and filtered to have a maximum of 50% of samples with missing genotypes, yielding 853 SNP loci for 273 samples.

The remaining analysis was performed in R, following McGaughran *et al.* (2019), with all scripts used being available in Supplementary Material. We used several packages, including adegenet (Jombart 2008; Jombart and Ahmed 2011), vcfR (Knaus and Grünwald 2017), poppr (Kamvar *et al.* 2014, 2015), devtools (Wickham *et al.* 2019), hierfstat (Goudet 2005), ade4 (Chessel *et al.* 2004; Dray and Dufour 2007; Bougeard and Dray 2018), pegas (Paradis 2010), ggplot2 and ggbiplot (Wickham 2016), radiator (Gosselin 2019) and SeqVarTools (Gogarten *et al.* 2019). We calculated pairwise Nei's distance (Nei 1987) and Weir and Cockerham's Fst (Weir and Cockerham 1984) values at three population levels, namely, region ($n = 3$), beach ($n = 6$) and site ($n = 12$). We looked at the relationship between geographical (all three levels independently) and both measures of genetic differentiation by using a Mantel test. We used principal component analysis (PCA) to visualise patterns in the genetic data.

To further investigate connectivity and population structure, we investigated partitioning of variance at the three hierarchically sampled geographic levels (i.e. region, beach, site) by using an analysis of molecular variance (AMOVA, Excoffier *et al.* 1992), using the R packages poppr (Kamvar *et al.* 2014, 2015), adegenet (Jombart 2008; Jombart and Ahmed 2011) and vcfR (Knaus and Grünwald 2017). To assess statistical significance, a randomisation test was performed using 1000 permutations.

Population-structure analysis was performed using fastSTRUCTURE ver. 2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003, 2007; Hubisz *et al.* 2009). We ran fastSTRUCTURE with default settings for between 1 and 12 populations, chose the model complexity to best explain the structure in the data, and produced plots to visualise the admixture analyses.

Results and discussion

Our GBS dataset contained 853 SNPs for 273 *A. teres* from the eastern coast of Australia. Genetic differentiation among populations in *A. teres* was small or near negligible across the sampling range. Model complexity of the fastSTRUCTURE analysis suggested six genetic populations, but there was no relationship between 'genetic populations' and geographic distribution (Fig. 1). The PCA (Fig. 2) showed no geographic structuring and each component represented less than 4% of the variation.

The lack of strong genetic differentiation was confirmed by pairwise measures of genetic distance between populations showing absent to negligible differentiation among populations along the eastern coast of Australia, using both Nei's genetic distance and Weir and Cockerham's Fst (Table 1).

The Mantel test showed no significant correlation between the geographic and genetic distance matrix, Nei's D −0.153 (*P*-value 0.672) and Weir and Cockerham's Fst −0.115 (*P*-value 0.587), further indicating that there was little genetic differentiation among populations across our sampling range. An AMOVA confirmed limited genetic structure across the sampling range, with most variance being among samples within beaches, and within samples (Table 2).

Using BayeScan ver. 2.1 (Foll and Gaggiotti 2008) to try to partition variance between potentially adaptive and truly neutral loci, we found that 12 SNPs showed an excess of differentiation among the three regions (Fig. 3) and, thus, could be under selection. In the absence of a reference genome, this number of bi-allelic variants is not enough to enable us to meaningfully assess genetic structure from a neutral versus adaptive perspective.

Population genetic structure of sedentary marine species is generally expected to be shaped by the dispersal ability of their larvae (Levin 2006). Long-lived pelagic larvae can connect populations through migration and gene flow, whereas species with non-dispersive larvae might be expected to have genetically differentiated populations (Kesäniemi *et al.* 2012). However, there are notable exceptions to these generic expectations;

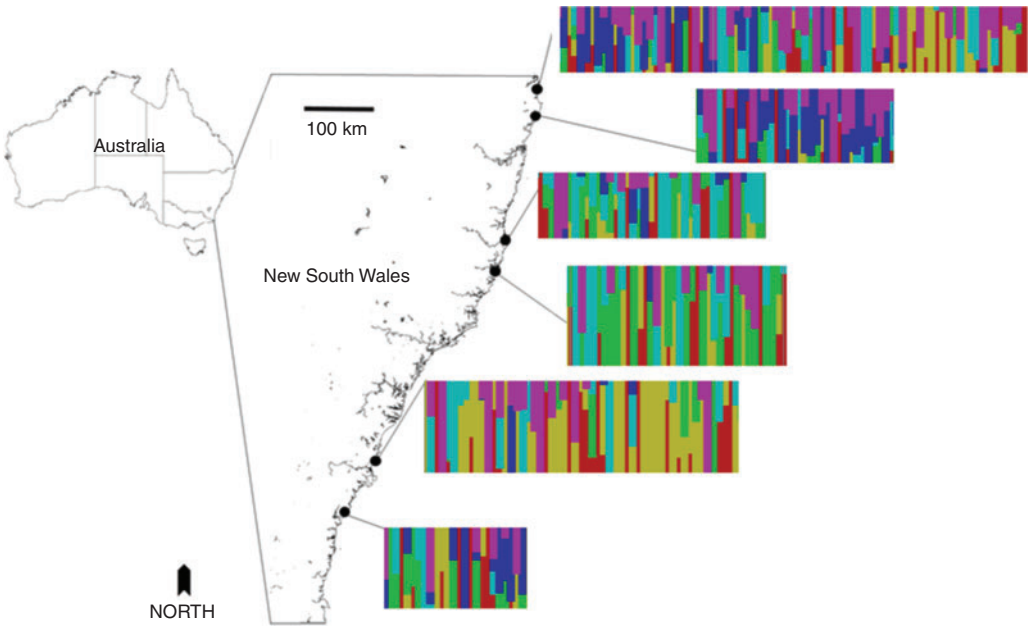

Fig. 1. Admixture analysis of populations of *Australonuphis teres* along the eastern coast of Australia. Individuals are represented as vertical bars in each box, and colours show the six genetic 'groups' inferred. North to south the sites are Wooyung, South Ballina, South West Rocks, Crowdy Head, Seven Mile and Moruya.

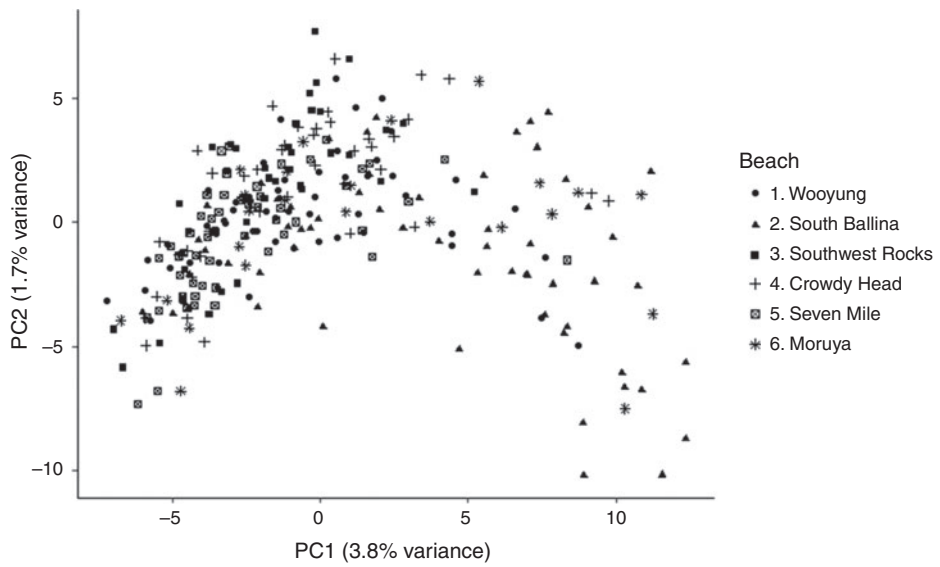

Fig. 2. Principal-component analysis (PCA) of the 853 single-nucleotide polymorphisms (SNPs) in 273 individuals that passed our stringent filtering. PC1 explains 3.8% of the variation and PC2 explains 1.7% of the variation in this dataset. Samples collected from the same beach ($n = 6$) do not cluster together.

for example, congeneric species with similar life-history traits can show dissimilarities in population structure (Temby *et al.* 2007; Miller *et al.* 2009, 2014).

The reproduction and larval development of *A. teres* is not well understood, but *A. teres* have been found with over 100 000 eggs in their body cavity (Paxton 1986), and mature gametes have been found throughout the year, suggesting a long spawning season (Paxton 1979). Exposure to a wide variety of oceanographic and biological processes would occur over this period, potentially influencing larval dispersal distance.

With these polychaetes increasingly being used as bait (Cole *et al.* 2018), there is a growing need to understand their population structure to support sustainable resource-management practices. Our results suggested that despite movement throughout the

Table 1. Pairwise genetic distance between populations (beaches) along the eastern coast of Australia
Nei's D is below the diagonal and Weir and Cockerham's Fst is above the diagonal. CH, Crowdy Head; M, Moruya; SB, South Ballina; SM, Seven Mile; SR, South-west Rocks; and W, Wooyung

	W	SB	SR	CH	SM	M
W	–	0.015	0.003	0.007	0.008	0.011
SB	0.015	–	0.023	0.020	0.033	0.006
SR	0.003	0.023	–	−0.003	0.008	0.005
CH	0.007	0.020	−0.003	–	0.014	0.008
SM	0.008	0.034	0.008	0.014	–	0.021
M	0.010	0.007	0.005	0.007	0.019	–

Table 2. Analysis of molecular variance (AMOVA) results, with *P*-values obtained by permutation tests as in Excoffier *et al.* (1992)

Source of variation	d.f.	Sum of squares	Variance component	Percentage of total variance	*P*-value
Among regions	2.00	814.26	0.36	0.26	0.45
Among beaches within regions	3.00	993.03	1.19	0.86	0.09
Among sites within beaches	6.00	1349.64	1.28	0.93	<0.01
Among samples within beaches	261.00	44 111.64	33.49	24.21	<0.01
Within samples	273.00	27 853.33	102.03	73.75	<0.01
Total	545	75 121.90	138.35	100	

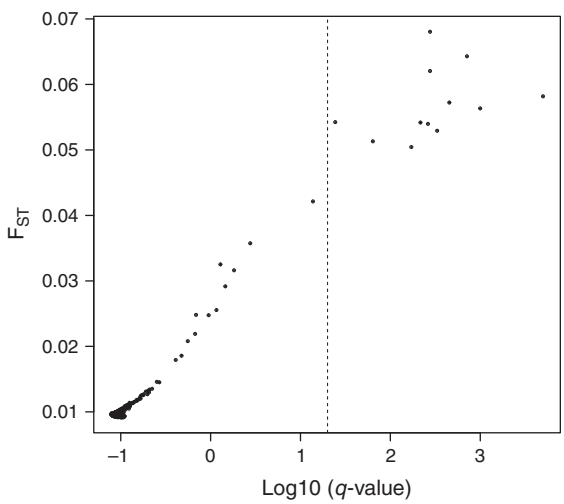

Fig. 3. BayeScan results, showing 12 outlier single-nucleotide polymorphisms (SNPs) among the three regions at *q*-value of <0.05. Dashed line indicates $q = 0.05$.

sample range of this study, each geographic population has a different, but not diagnostic, genetic composition, and there has been bidirectional genetic mixing along the coast. This inference is consistent with previous research along the same region on the eastern coast of Australia, except for benthic estuarine polychaete species, which were inferred to have high levels of gene flow among populations (Smith *et al.* 2015). Although they live in different habitats, *A. teres* and the two estuarine species studied by Smith *et al.* (2015) are likely to be influenced by the same ocean currents.

Most prior studies have found no or little genetic differentiation among polychaete populations (e.g. Shen and Gu 2015; Zaâbi *et al.* 2015; David *et al.* 2016). High levels of gene flow were inferred between populations of two polychaetes, *Laeneereis culveri* and *Capitella nonatoi*, living in lagoons in Brazil, albeit with there being evidence of somewhat restricted gene flow between particular populations (Seixas *et al.* 2018). However, in a similar area, Nunes *et al.* (2017) found strong genetic differentiation between *Phragmatopoma caudata* polychaetes from Florida and those from Brazil, suggesting a biogeographical barrier between these locations. Overall, most research suggests that gene flow can be high in polychaetes, presumably because of planktonic larval dispersal. However, most previous studies have been limited to just one or a few markers, such as, for example, COI (Chatzigeorgiou *et al.* 2015; David *et al.* 2016), 18S rRNA (Shen and Gu 2015; Sun *et al.* 2018), 28S rRNA (Shen and Gu 2015; Sun *et al.* 2018) and ITS (Nunes *et al.* 2017; Sun *et al.* 2018), whereas our study employed a genome-wide approach with hundreds of SNP loci, which enhanced confidence in our inferences.

The eastern coast of Australia appears to have few biogeographical barriers for marine coastal organisms with a high dispersal ability (e.g. Coleman *et al.* 2013; Smith *et al.* 2015; Bellgrove *et al.* 2017). Despite the general southward flow of the East Australian Current (EAC; Coleman *et al.* 2013), some small pelagic invertebrates have been inferred to have travelled 1000 km north from their release site (Ruello 1975; Montgomery 1990). Northward movement probably results from dispersal with counter-currents and local eddies (Coleman *et al.* 2011, 2013). These oceanographic currents could help explain the patchy distribution of *A. teres*, as the eddies, together with other population processes, affect the

spread, deposition and survival of pelagic larvae (Levin 2006; Keane and Neira 2008; Chan *et al.* 2018). Other polychaete worms respond to chemical cues from adults when settling (Hsieh 1994), which could lead to density-dependent processes, including density blocking, limiting gene flow between connected populations (Waters *et al.* 2013; Fraser *et al.* 2018*b*). As the carrying capacity of a beach or site is approached, the rate of successful settlement of additional larvae might diminish, restricting gene flow. In the case of *A. teres*, the presence of six genetic groups could indicate that past structure that has since been eroded by natural disturbance events (e.g. storms), changes in environmental conditions affecting long-term rates of successful larval dispersal (e.g. changes in currents and temperature regimes), anthropogenic disturbance (e.g. periods of heavy harvesting reducing population densities and supporting successful recruitment), or combinations of the above, allowing the observed diverse lineages to establish at each site. Understanding the factors affecting genetic diversity, and minimising anthropogenic processes that could reduce diversity, should be a priority for the ongoing sustainable management of these beachworm populations. This study is one of the first population genomics studies of polychaetes and has demonstrated the power of SNP analyses in resolving fine-scale population structure. Genomic tools can assist with testing evolutionary and ecological questions for polychaetes globally.

Compliance with ethical standards

The authors declare no conflict of interest. The beachworms were sampled following jurisdictional requirements for biological sample collection and all necessary approvals were obtained before commencing this research.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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