Deep--Sea Research I (xxxx) xxxx–xxxx

Contents lists available at ScienceDirect

Deep–Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Population genetic structure of two congeneric deep-sea amphipod species from geographically isolated hadal trenches in the Pacific Ocean

H. Ritchie[a,*], A.J. Jamieson[b,1], S.B. Piertney[a]

[a] Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Aberdeen AB24 2TZ, UK
[b] Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, UK

ARTICLE INFO

Keywords:
Hadal trenches
Amphipoda
Deep sea ecology
Connectivity
Gene flow
Endemism

ABSTRACT

The deep ocean trenches that comprise the hadal zone have traditionally been perceived as a series of geographically isolated and demographically independent features likely to promote local species endemism through potent natural selection and restricted dispersal. Here we provide the first descriptions of intraspecific population genetic structure among trenches from which the levels of genetic connectivity can be examined explicitly. A total of 109 individuals across two species of *Paralicella* amphipods (Lysianassoidea: Alicellidae) were genotyped at 16 microsatellite DNA loci. An analysis of molecular variance identified that 22% of the overall genetic variance was attributable to differences between the species and a further 7% was attributable to differences between populations. The two species showed different patterns of genetic structure, with the levels of genetic differentiation between trenches explained by geographical proximity, the geological ages of the trenches, contemporary bottom current patterns and seabed topography around the Pacific Ocean. Overall, the inferred levels of gene flow among trenches was sufficient to reject the hypothesis that they are evolutionarily independent units.

1. Introduction

The hadal zone is the deepest marine biome, extending from 6000 m to full ocean depth at approximately 11,000 m at the Challenger Deep in the Mariana Trench. It is primarily comprised of 37 trench systems which are formed along subduction zones between tectonic plates, with the majority are located around the Pacific Rim (Jamieson et al., 2010). Trenches break the continuum of the abyssal plains by forming disjunct clusters of ultra-deep habitat "islands". The hadal zone accounts for over 45% of the total vertical depth of the marine environment (Jamieson, 2015) and it is characterised by high hydrostatic pressure, cold temperatures, low food availability and an absence of natural light (Wolff, 1960). Despite being considered an "extreme" environment the hadal zone is host to a diverse range of flora and fauna, notably the Isopoda, Polychaeta, Gastropoda and Amphipoda (Wolff, 1970, Beliaev, 1989).

The restricted distribution of key taxa within these groups to specific trenches underpins the conventional view that hadal trenches are hotspots of species endemism driven by a combination of geographic isolation and potent selection pressures (Wolff, 1960; Wolff, 1970). For example, within the amphipod genus *Hirondellea*, *H. dubia* is restricted to the Kermadec, Tonga and New Hebrides trenches in the southwest Pacific (Lacey et al., 2016), *H. gigas* is located in trenches in the northwest Pacific trenches studied thus far (France, 1993), and newly described *Hirondellea* species have been identified in the Peru-Chile Trench in the southeast Pacific (Fujii et al., 2013; Kilgallen, 2015). However, this assertion that hadal trenches are hotspots of species endemism is difficult to reconcile with the seemingly cosmopolitan distribution of other amphipod species. Chiefly, *Eurythenes gryllus* which has been described as having a pan-oceanic distribution from bathyal to hadal depths, and has been located in every hadal trench investigated to date in addition to the intervening abyssal plains (Barnard, 1961; Thurston et al., 2002; Havermans et al., 2013; Eustace et al., 2016). This cosmopolitan distribution of a supposedly single *E. gryllus* species is complicated by morphological and phylogeographic differences between different global populations (Havermans et al., 2013) and even within a single trench population (Eustace et al., 2016). This suggests *E. gryllus* actually represents multiple species each defined by geographic and bathymetric isolation and associated drift and selection (Havermans, 2016).

A capacity for hadal trenches to promote genetic divergence within and between species appears counter to the depth-differentiation

* Corresponding author.
E-mail address: heather.ritchie.07@aberdeen.ac.uk (H. Ritchie).
[1] Present Address: School of Marine Science and Technology, Ridley Building, Newcastle University, Newcastle Upon Tyne NE1 7RU, UK.

http://dx.doi.org/10.1016/j.dsr.2016.11.006
Received 2 June 2016; Received in revised form 17 November 2016; Accepted 21 November 2016
0967-0637/ © 2016 Elsevier Ltd. All rights reserved.

hypothesis (Rex and Etter, 2010). This states there should be a reduction in barriers to gene flow with increasing depth from the continental shelf due to the increase in environmental homogeneity with bathymetric depth. A growing body of data from across deep-sea environments in the bathyal and abyssal zones supports the depth-differentiation hypothesis, largely showing connectivity between populations (e.g. Cowart et al., 2014; Quattrini et al., 2015; Ritchie et al., 2013). It is unclear how disjunct topographical features such as seamounts, spreading centres (ridges), fracture zones and canyons disrupt the depth differentiation paradigm, but it appears patterns of genetic structure are variable across taxa, life history strategies and geographic locations (Baco et al., 2016; Clark et al., 2010). To date there has been no indication of how the hadal zone fits into the depth-differentiation hypothesis paradigm. Primarily because of the dearth of information on population genetic structure based upon the distribution of neutral genetic variation. A demonstration that hadal trenches have equivalent frequencies of neutral polymorphisms would indicate a high degree of connectivity, and conversely significant genetic structure would highlight that each trench represents a demographically independent unit with minimal gene flow. Examining the patterns of gene flow in the context of trench location, geological ages of trenches, topographical features of the abyssal plains and contemporary bottom currents will allow speculation on possible routes of historical colonisation of the hadal trenches and identify the major drivers influencing patterns of dispersal at an oceanic scale.

Here we examine the patterns of genetic structure between populations of two Lysianassoid amphipods, *Paralicella tenuipes* and *P. caperesca,* across five trenches around the Pacific Rim. The two sister species from the *Paralicella* genus provide an excellent model for testing patterns of gene flow as they are characteristic of the abyssal fauna with an abyssal-hadal distribution (Barnard and Schulenberger, 1969; De Broyer et al., 2004) allowing us to examine differences between trenches in the context of dispersal patterns across the intervening abyssal plains. *P. tenuipes* and *P. caperesca* also have overlapping pan-oceanic geographical distributions (Barnard and Shulenberger, 1969; Thurston, 1979) that will facilitate examination of parallel patterns of connectivity across trench populations across the species.

This study represents the first investigation elucidating patterns of gene flow and connectivity between hadal trenches. We exploit a suite of microsatellite DNA markers that were previously mined from an Illumina MiSeq library of *P. tenuipes* (Ritchie et al., 2016) to test the null hypothesis that there is extensive gene flow between trench populations, in both species, leading to a lack of significant population genetic structure.

2. Materials and methods

2.1. Sample collection

A total of 109 amphipods were collected from across five hadal trenches over the course of six sampling campaigns between 2007 and 2013 using an autonomous deep-ocean lander vehicle (Jamieson et al., 2009a, 2009b) incorporating small baited funnel traps (see Table 1 and Ritchie et al., 2015). Upon recovery of the lander, amphipods were transferred immediately to 99% ethanol prior to morphological identification to genus level in a shore-based laboratory (National Institute for Water and Atmospheric Research, New Zealand or latterly the Australian Museum) using morphological characteristics outlined in Barnard and Karaman (1991). Total genomic DNA was extracted from the whole body of individual specimens using a standard phenol-chloroform approach.

2.2. Species identification

The *Paralicella* genus has traditionally been considered to contain two predominant species, *P. tenuipes* and *caperesca* (Barnard and Schulenberger, 1969). However, identification of these *Paralicella* species has been problematic given the morphological characters used to differentiate between them may be confused by ontogenetic variation or phenotypic plasticity (Barnard and Shulenberger, 1969). Recent molecular phylogenetic analysis based upon mitochondrial 16S and COI markers (Ritchie et al., 2015) identified two distinct phylogenetic clades within the *Paralicella* genus consistent with the presence of two species, but these were not congruent with the morphological characteristics conventionally used to distinguish *P. caperesca* and *P. tenuipes*. As such, here we define taxonomic groups within the *Paralicella* genus from genetic differences that can readily be discerned using a PCR-RFLP assay based on sequence variation at the mitochondrial COI locus. A 710 bp fragment of the mitochondrial COI gene was PCR amplified using the COI primers and conditions outlined in Ritchie et al., (2015). PCR amplicons were then double-digested for 2 h at 37 °C with 1.5 units of each of the restriction enzymes *Mbo*II and *Nla*III. Restriction profiles were visualised using agarose electrophoresis with individuals producing a two-band profile (135 bp and 575 bp) being classified as RFLP species 1 (Group 1 in Ritchie et al., 2015) and individuals with a three-band profile (135 bp, 220 bp and 355 bp) being classified as RFLP species 2 (Groups 2, 3 and 4 in Ritchie et al., 2015).

In total, the 109 individuals were separated into seven *a priori* populations of *Paralicella* spp. RFLP species 1 individuals were found in the Kermadec (n=4), Japan (n=24), Mariana (n=24) and Peru-Chile trenches (n=15), and RFLP species 2 individuals were found in the Kermadec (n=26), Peru-Chile (n=2) and New Hebrides trenches (n=14).

2.3. Microsatellite genotyping

All individuals were genotyped at 16 microsatellite loci designed specifically for *Paralicella* (Ritchie et al., 2016). PCR reaction conditions followed Ritchie et al. (2016) and amplicons were resolved using an ABI 3730 DNA Capillary DNA Sequencer (Dundee, DNA Sequencing Services Ltd). Genotypes were scored eye with Genemarker v 1.4 (SoftGenetics, 2010) against a GD-500 (LIZ) size standard.

2.4. Population genetic analyses

Micro-Checker 2.2.3 (van Oosterhout et al., 2004) was used to establish whether any heterozygote deficiencies were attributable to null alleles and/or scoring errors. Linkage disequilibrium between all combinations of loci for each sampling location was tested using Genepop 4.0.10 (Raymond and Rousset, 1995; Rousset, 2008) and significance was evaluated using Fisher's exact test with Bonferroni correction (Ryman et al., 2006). Genetic diversity was described using observed heterozygosity (H_O), number of effect alleles (n_e) and allelic richness (a_r) in the diveRsity package in R (Keenan et al., 2013).

Pairwise genetic differentiation among the seven putative populations was estimated using F_{ST} (Cockerham and Weir, 1984). Global and pairwise F_{ST} values were calculated using diveRsity and significance was evaluated using Fisher's exact test where Bonferroni correction was applied. To estimate the proportion of genetic differentiation attributable to differences between the RFLP identified species and between the *a priori* populations a hierarchical analysis of molecular variance (AMOVA) was implemented using GenAlEx 6.5 (Peakall and Smouse, 2006).

Structure 2.3.3 (Pritchard et al., 2000) was used to implement Bayesian MCMC inference of *a posteriori* genetic clusters. The number of assumed genetic clusters (K) was set from one to seven, with 10 independent runs performed for each value of K. A total of 10,000,000 MCMC iterations were ran using the admixture ancestry model with correlated allele frequencies where the first 100,000 iterations were

Download English Version:

https://daneshyari.com/en/article/5764741

Download Persian Version:

https://daneshyari.com/article/5764741

Daneshyari.com