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Species diversity in the cryptic abyssal holothurian *Psychropotes longicauda* (Echinodermata)

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ABSTRACT

Despite the plethora of studies on swallow-water invertebrates, almost nothing is known about the evolution and population structure of deep-sea species at the global scale. The aim of this study was to assess phylogeographic patterns of a common and cosmopolitan, predominantly abyssal sea cucumber, *Psychropotes longicauda*, based on samples from the Atlantic, Southern, Indian and Pacific oceans. Sequences of the mitochondrial *COI* and *16S* genes were analysed for 128 specimens of *P. longicauda*. In addition, temporal genetic variation was investigated at one site, the Porcupine Abyssal Plain, NE Atlantic Ocean over a period of 34 years. Two distinct lineages within the global distribution were identified. The sister clades probably could be classified as separate species based on the observed genetic divergence (> 5.0%) and phylogenetic reconstruction with indications of a Southern Hemisphere origin. Moreover, significant population differentiation was detected between the North Atlantic and localities in both the Pacific and Indian oceans. No bathymetric structuring was detected among lineages. Temporal genetic shifts were detected in a time series of samples from 1977 to 2011. Our data confirm the previously suspected cryptic species diversity throughout the wide distributional range previously attributed to the single species *P. longicauda*. The presence of sympatric species in the North Pacific and Indian Oceans has been underestimated by previous morphological analyses. The differentiation at the population level detected in the main lineages among the four oceans could suggest restricted gene flow despite wide-scale dispersal potential of the species.

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1. Introduction

Genetic investigations on organisms inhabiting the deep sea have been hindered because of the paucity of fresh specimens. As a result, basic information of spatial and temporal population differentiation is limited and the evolutionary forces leading to population divergence and speciation are not fully understood (Zardus et al., 2006). On continental slopes, bathymetric and

geomorphological barriers may provide ecological and physiological isolating mechanisms that shape populations at bathyal depths (Zardus et al., 2006; Etter et al., 2011; Brown and Thatje, 2014). However, it is likely that the horizontal and vertical scales on which benthic genetic structuring occurs, are different in bathyal and abyssal environments (Etter et al., 2005; Raupach et al., 2007). Strong barriers to gene flow in taxa on abyssal plains have yet to be identified, even across great geographic distances (Pawlowski et al., 2007; Lecroq et al., 2009). Additionally, patterns of primary productivity have been found to drive bathymetric and latitudinal links between spatial variations in the flux of food to the deep-sea floor and trends of faunal biomass and abundance (Thurston et al., 1998; Wolff et al., 2011).

The majority of molecular studies on holothurians have focused on coastal and commercially valuable species. As in other marine invertebrates, results suggest that larval ecology is likely to play an

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important role in determining patterns of gene flow and thus, the evolutionary biology of many species (Uthicke and Benzie, 2003). Traditional models of dispersal suggest some species with long-lived planktotrophic larvae lack significant population structure (Uthicke et al., 2001). However, paradoxically, other species with the potential for wide dispersal have limited gene flow resulting in higher than expected genetic structuring contradicting the previous general trend (Uthicke and Benzie, 2003; Hunter and Halanynch, 2008, 2010). In the first study of deep-sea holothurians using genetic techniques, cryptic speciation and high levels of population differentiation were discovered in a number of species inhabiting bathyal depths in the Antarctic (O'Loughlin et al., 2011). A variety of mechanisms were thought to be driving differences, with evidence for allopatric and sympatric genetic differentiation, and speciation over relatively small geographic and bathymetric scales. However, to date little evidence exists regarding genetic population structure among cosmopolitan predominantly abyssal species with the potential for wide-scale dispersal (Havermans et al., 2013). Therefore, the potential ecological or historical mechanisms affecting patterns of such spatial and temporal differentiation remain largely unexplored.

Studies have focused mainly on population structure in shallow-water echinoderms, reporting the lack of genetic homogeneity and the existence of cryptic speciation for a wide range of marine taxa, including species with both poor and excellent potential dispersal abilities (Waters and Roy, 2003; Neigel et al., 2007). Potential divergence drivers have been equally diverse, including altered current patterns during the Pleistocene, the presence of modern day land barriers and ocean currents, vicariance events, upwelling areas, topography and the isolation of populations in refugia (Lessios et al., 1999; Uthicke et al., 2004; Boissin et al., 2008; Hunter and Halanynch, 2008; O'Loughlin et al., 2011). Whilst temporal changes in genetic population structure have received much less attention, differences between cohorts of echinoderms in the Mediterranean have been linked to changes in prevailing circulation conditions (Calderón et al., 2012).

Psychropotes longicauda (Psychropotidae) is a predominantly abyssal elasipodid holothurian with a global but discontinuous geographic distribution, inhabiting all major oceans, with the exception of the Arctic (Hansen, 1975). It is often a dominant species of the epibenthic megafauna and has important effects on the rest of the benthic community through its feeding, locomotion and faecal production (Billett, 1991). *Psychropotes longicauda* produces large lecithotrophic eggs up to 4.5 mm diameter (Tyler and Billett, 1988) which appear to lead to the direct development of juveniles greater than 5 cm long within the abyssopelagic zone hundreds to thousands of metres above the seabed (Billett et al., 1985; Gebruk et al., 1997). It is thought that juveniles may be able to drift for long distances before starting their benthic lives (Hansen, 1975), resulting in a very high dispersal potential. *Psychropotes longicauda* exhibits quite variable morphology in body colour, number of dorsal papillae and tubefeet, and shape of dorsal cross-shaped spicules. Most of these characteristics do not seem to exhibit any geographic variation, rendering it difficult to separate *P. longicauda* into geographic subspecies (Hansen, 1975). However, only the number of tubefeet and features of the calcium carbonate spicules in the skin (dorsal crosses) appear to vary geographically. Despite noting these differences, Hansen (1975) believed that the geographic subdivision of the species was inadvisable owing to the high variation seen in morphological characteristics within and between regions. Moreover, Hansen (1975) synonymised a number of previously described species under *P. longicauda*, reaffirming their supposedly cosmopolitan distributions.

The link between elasipodid holothurians, including *Psychropotes longicauda*, and geographic areas with a rich supply of organic matter in the form of Particulate Organic Carbon (POC)

was noted by Hansen (1975). This has been corroborated by a number of authors who have found that *P. longicauda* is absent, or has a greatly reduced abundance, in low productivity sites compared to increased abundance at sites underlying areas of higher productivity (Thurston et al., 1998; Wolff et al., 2011). *Psychropotes longicauda* has been the subject of a long term programme sampling of benthic communities on the Porcupine Abyssal Plain, NE Atlantic, from 1977 to the present day (Billett et al., 2001) and at Station M in the NE Pacific (Ruhl, 2008). During this period, significant fluctuations have occurred in its abundance and population structure, which have been linked to possible changes in the quantity and quality of POC flux to the deep-sea floor (Billett et al., 2001, 2010; Ruhl, 2008).

The current study sought to assess whether (i) molecular approaches could distinguish more species than the one described by Hansen (1975), (ii) separate populations of *P. longicauda* in different oceans could be differentiated genetically, and (iii) the drivers influencing connectivity of abyssal species could be evaluated within and across oceans. To achieve these goals, individuals inhabiting four basins, the Atlantic, Southern, Indian and Pacific Oceans, were collected. Finally, the Porcupine Abyssal Plain time series was used to examine temporal changes over a period of 34 years in the broad genetic structure of the species, and possible interactions with the supply of organic matter to the seafloor.

2. Materials and methods

2.1. Sample collection

Tissue samples of *P. longicauda* were obtained from four main localities in three different oceans over 40 years (total=128 samples, Fig. 1, Appendix A in Supporting Information). Samples from the North East Atlantic (two localities, the Porcupine Abyssal Plain, NEA-PAP=29 samples; and the Whittard Canyon, on the Irish continental margin, NEA-WC=4 samples) were collected during two National Oceanography Centre cruises (RRS *James Cook* cruises JC036 and JC062) using a semi-balloon otter trawl or a Remotely Operated Vehicle (ROV *Isis*). On recovery of the trawl, all samples were taken to a cold room and dissected. Samples were cleaned using 100% ethanol, muscle or gonad tissue was removed avoiding contact with gut contents, and stored. Furthermore, 58 formalin-fixed archived specimens were obtained from the *Discovery Collections* (NEA-DC=58 samples) covering a 34-year period from 1977 to 2011. Samples from the North East Pacific were provided by Scripps Benthic Invertebrate Collection and Monterey Bay Aquarium Research Institute (NEP=13 samples). They were collected by trawl as part of the Station-M long term pulse-chase time series (Smith et al., 2009) and preserved directly in 100% ethanol. Muscle tissue was subsequently dissected from the specimens. Samples were also collected by trawl from two abyssal localities around the Crozet Islands in the Indian sector of the Southern Ocean (SI=9 samples). The samples were obtained as part of the CROZEX study on the effects of natural iron fertilisation on surface production and benthic fauna (Pollard et al., 2009; Wolff et al., 2011). Additionally, four samples collected from the Weddell Sea (Atlantic sector of the Southern Ocean) were processed (SA=4 samples). Finally, muscle tissue from formalin preserved samples from a number of localities in the Pacific, Atlantic and Indian Oceans were provided by the Shirshov Institute of Oceanology (RUS=11 samples), including the Southern and NW Pacific Ocean. All individuals were taken at depths greater than 3700 m apart from 4 individuals from 3592 m in the Whittard Canyon, and one specimen from 2520 m from the Great Australian Bight. The term 'abyssal' used here relates to depths greater than 3000 m, although the actual upper bathymetric limit for species

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