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Limited phylogeographic structure for five bathyal ophiuroids at continental scales

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ABSTRACT

There have been comparatively few large-scale studies on spatial genetic structure of bathyal seafloor fauna, despite the importance of these data to the successful management of the world's oceans. We use a comparative analysis of mitochondrial DNA from five bathyal (200–3500 m) species of brittle-stars (Ophiuroidea) to assess phylogeographic structure along an extensive (8000 km) longitudinal gradient at temperate latitudes (28–56°S) from south-west Australia (113°E) to seamounts east of New Zealand (175°W). We found no evidence of a genetic discontinuity between Australia and New Zealand, either across the temperate Tasman Sea or across the Southern Ocean between the South Tasman Rise and the Macquarie Ridge. However, there were latitudinal phylogeographical breaks between tropical, temperate and polar regions; longitudinal breaks across the eastern Indian Ocean; and a bathymetric break at approximately 1700 m. Although there was limited regional structure in the frequency of haplotype distributions within the major clades, and no clade appeared to be strictly panmictic, the regional structure in general was not concordant with a simple isolation-by-distance model. Demographic structure varied with three clades having a simplified haplotype network, low effective population sizes and no evidence of significant population expansion, and two clades having a high diversity of haplotypes, relatively high effective population sizes and signs of recent population expansion. These results are discussed with respect to putative dispersal strategies. We hypothesise that the 'brooding' species produce both brooded young and pelagic larvae, allowing for both the maintenance of local populations and long-distance dispersal.

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1. Introduction

Our knowledge of deep-sea macro-ecological patterns and processes is deficient. Investigating large-scale patterns of biodiversity remains a logistical challenge. Data are difficult and expensive to collect and many studies are limited in temporal and spatial scope. Nevertheless, an understanding of the spatial extent of interconnected populations is fundamental to our successful management of the world's oceans, including the mitigation of the effects of fisheries and mining, and the design of successful marine protected areas systems (UNESCO, 2009).

Assessing the spatial extent of deep-sea benthic organisms has been problematic. Although many morphologically similar forms appear to have widespread distributions, cryptic species are common (e.g., Jörger et al., 2012), and recent ecological research has shown that deep-sea habitats can be patchily distributed at various spatial scales (McClain and Hardy, 2010).

There have been relatively few large-scale phylogeographical studies in the deep sea due to the degraded state of specimen DNA in historical collections, the high cost of collecting new material from remote locations and the difficulty of working across a seascape fragmented into separate national jurisdictions. Many of the studies that have been performed are from specialised chemosynthetic habitats on mid-ocean ridges (e.g., Plouviez et al., 2009) or from seamounts (e.g., Cho and Shank, 2010; Miller et al., 2010) and may not be representative of the deep sea in general.

The South-western Pacific has emerged as a key region for bathyal (200–3500 m) macro-ecological research because of recent concurrent programs of marine biodiversity discovery around Australia, New Zealand, New Caledonia and surrounding seafloor (O'Hara et al., 2011). Large collections of marine invertebrates are available from continental slope and seamount habitats. Biogeographic analyses of marine species (defined by morphology) across this region show differing patterns for continental shelf (0–200 m) compared to continental slope (200–3500 m) biomes. Southern Australia and New Zealand shallow-water marine assemblages form distinct subregions, including south-western and south-eastern Australia and northern and southern New

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Zealand (Spalding et al., 2007). However, analyses of bathyal assemblages at most distinguish south-western Australia (Schnabel et al., 2011) or combine the entire region in an extensive latitudinal band bordered by a tropical region to the north and polar region to the south (O'Hara et al., 2011). With limited exceptions (Miller et al., 2010), these extensive bathyal ranges have not been tested with genetic data. It is unclear whether bathyal animals (particularly brooding megafauna) can disperse across the wide abyssal plain of the Tasman Basin between southern Australia and New Zealand.

Among benthic invertebrates, brittle-stars (Ophiuroidea) have become useful model organisms for phylogeographic and biogeographic studies. They are abundant and frequently occur across a range of habitats, from intertidal to hadal depths, from equatorial to polar regions, and from rocky to muddy substrata (Cho and Shank, 2010; O'Hara et al., 2011, 2013). Moreover, ophiuroids display a variety of dispersal strategies that affect population connectivity, including planktotrophic (feeding) larvae, lecithotrophic (non-feeding) larvae, viviparity (brooding) and asexual fissiparous reproduction (Byrne and Selvakumaraswamy, 2002).

In this study we use a comparative analysis of mitochondrial DNA from five bathyal (200–3500 m) species of ophiuroids to assess phylogeographic structure along an extensive (8000 km) longitudinal gradient at temperate latitudes (28–56°S) from south-west Australia (113°E) to seamounts east of New Zealand (175°W). We compare the phylogenetic relationships of these populations to those in other regions. Specifically, we examine whether the phylogeographic patterns are (1) indicative of longitudinal dispersal across the region via continuous oceanic currents or (2) whether there is evidence of one or more long-term barriers to gene flow. In particular, we investigate the potential dispersal barrier for bathyal species across the abyssal plain (> 3500 m deep) between southern Australia and New Zealand/Macquarie Ridge. We interpret these results in the context of the species' variable dispersal strategies and differences in latitudinal and bathymetric range.

2. Materials and methods

2.1. Tissue sampling

We obtained specimens from numerous deep-sea expeditions (1999–2012) that have been deposited in museums in Australia and New Zealand (Table S1). We selected five ophiuroid species for molecular analysis on the basis of their widespread occurrence in Indo-Pacific temperate bathyal waters and diversity of habitat requirements or life history strategies. Because ophiuroid morpho-species have been shown to frequently contain cryptic species (Boissin et al., 2011; O'Hara et al., 2013; Hoareau et al., 2013), we investigated species boundaries by including some similar specimens from other regions as putative outgroups in the phylogenetic analyses. Comparative material was sourced from the ICEFISH 2004 (South Atlantic); Poseidon 252, 292, Vital 2002, and Meteor 61/1 (North Atlantic); Akademik Ioffe 29 (South Atlantic Ridge); and James Cook 66 (SW Indian Ocean Ridge) expeditions.

Ophiomyxa vivipara is a dioecious brooding species that has been reported from the Magellanic region of South America, off the island of Tristan da Cunha in the South Atlantic and South Africa (as the subspecies *capensis*) in depths of 75–400 m (Mortensen, 1936). We have found similar specimens on seamounts and continental slopes (300–1100 m) of southern Australia, New Zealand and the Macquarie Ridge (Fig. 1) (O'Hara et al., 2008 as *Ophiomyxa* sp MoV 5486). A similar species, *O. serpentina*, which has large yolky eggs but is apparently non-brooding (Mortensen, 1933), has been described from the North Atlantic

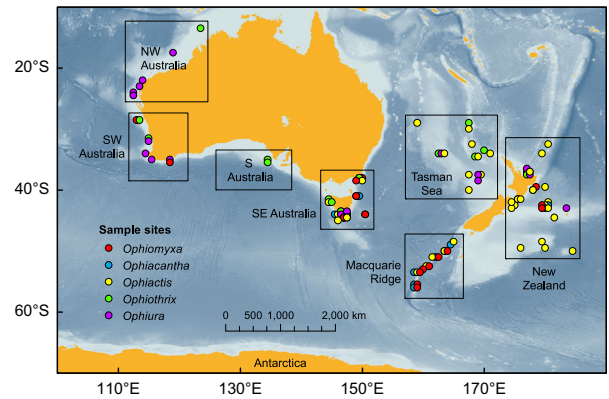


Fig. 1. Map of sample sites and analysis regions for the five species complexes.

Ocean. *Ophiacantha vivipara* is a circum-polar Antarctic species (0–1100 m) that has also been recorded from seamounts off Tasmania, the Graveyard complex on the Chatham Rise, and the Macquarie Ridge (400–1700 m) (O'Hara et al., 2008). It is inferred to be a proterogynic hermaphrodite that broods its young in the bursae (Mortensen, 1936).

Ophiactis abyssicola is known from the North and South Atlantic, including around South Africa in depths of 125–4700 m (Paterson, 1985). It is variable morphologically and currently considered to include several junior synonyms described throughout its extensive range (Paterson, 1985). In the SW Pacific several other similar species or subspecies have been recorded including *Ophiactis abyssicola cuspidata* from the Kermadec Ridge, New Zealand and off Tasmania (800–1772 m), and *Ophiactis amator* from 2340 m off eastern Tasmania (Rowe and Gates, 1995). These species live in cryptic habitats, such as gastropod shells or cavities in corals and sponges, and filter-feed by extending mucus-covered arms into the water column (Pearson and Gage, 1984). *Ophiothrix aristulata* is known from southern Africa to the western Pacific on the upper continental slope (O'Hara, 1998a). It is shallower than the other species across our study area (50–650 m) and does not occur south of 45°S. It is usually associated with sponges and can occur in great abundance. Finally, *Ophiura ooplax* is known from soft sediment habitats on the outer continental shelf and upper slope (100–1100 m) of Japan, Philippines, Southern Australia and New Zealand. A morphologically similar species, *O. trimeni*, has been described from South Africa. Reproduction within these three species complexes has not been previously investigated.

2.2. Examination of gonads

We used a light dissecting microscope to examine gonads from numerous specimens (at least 20 from each species) from the most numerous clade of all five target species, collected at different times of the year (see Table S1), to gain an approximate estimate of maximum egg-size. These resulting measurements are likely to be slight underestimates of actual egg sizes due to shrinkage associated with ethanol preserved tissue.

2.3. Sequencing

The mitochondrial COI gene is considered an effective 'barcoding' gene for echinoderm species diagnosis (Ward et al., 2008) and has been used to demonstrate phylogeographic structure for many ophiuroids (e.g., Cho and Shank, 2010; Hunter and Halanych, 2008; Stöhr et al., 2009). We selected the 'barcode' region of COI in order to include additional ingroup and outgroup sequences generated from several International Barcode of Life (iBOL) projects (O'Hara

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