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Review

Evolutionary patterns in Antarctic marine invertebrates: An update on molecular studies

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ABSTRACT

The present distribution of Antarctic marine invertebrates has been driven by their phylogeographic history, their dispersal capabilities, and the ability of resident species and new colonizers to adapt to the changing extreme environmental conditions. The processes behind the structuring and distribution of marine Antarctic fauna have been approached using a wide array of methodologies, but it is only recently that the advent of molecular sequencing technologies has provided an enormous potential to shed light on such driving forces. In this review we aim to provide a comprehensive view of the most common molecular techniques applied to assess the genetic diversity and connectivity in the Antarctic marine realm, and how they have advanced our understanding of the evolutionary patterns of marine invertebrates in the Southern Ocean. The different results obtained for the most commonly studied Antarctic invertebrates (arthropods, molluscs, and echinoderms) have often revealed contrasting stories explained by both the dispersive capabilities of the species involved and/or sheltering processes in refuges during glacial cycles, which highlight the need for further studies. In addition, we suggest that the sampling of neglected taxa and collecting in understudied areas should help to understand wider distribution and gene flow patterns among Antarctic marine invertebrates.

Contents

1. Introduction

Reports on the age of marine Antarctic fauna dated it prior to Antarctic cooling (more than 55 mya), and revealed strong affinities with the fauna inhabiting the Sub-Antarctic regions, including South America (reviewed in Allcock and Strugnell, 2012; Thatje, 2012). The factors driving the evolutionary history of Antarctic marine invertebrates are related to their phylogenetic and phylogeographic history, their dispersal capabilities and the ability of resident species and new colonizers

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to adapt to the changing extreme environmental conditions (Allcock and Strugnell, 2012; Thatje, 2012). Many investigations have focused on unraveling the processes behind the structuring and distribution of marine Antarctic fauna, using a wide array of methodologies (Thatje et al., 2005; Allcock and Strugnell, 2012; Thatje, 2012). However, in relatively recent years, the advent of molecular sequencing technologies has provided an enormous potential to shed light on the driving forces shaping the Antarctic marine fauna (e.g., Grant and Linse, 2009; Wilson et al., 2009; Allcock et al., 2011; Grant et al., 2011). In this review we aim to provide a comprehensive overview of the most widely used molecular sequencing techniques used to assess the genetic diversity and connectivity in the Antarctic marine realm, and how they have helped us to understand the evolutionary patterns of marine invertebrates in the Southern Ocean.

2. Why study genetic diversity and connectivity in marine benthic invertebrates of Antarctica?

The Southern Ocean provides a unique framework for the assessment of the factors affecting the genetic diversity and connectivity of marine benthic invertebrates. The Antarctic waters contain a huge number of endemic species (Kaiser et al., 2013), most of them believed to have a circumpolar eurybathic distribution (e.g., Dayton, 1990), impacted by the environmental, oceanographic, and tectonic changes over time. Historically, the main factors that might have contributed to shape the fauna inhabiting the Southern Ocean are the glacial cycles, which were caused by periodic changes in the Earth's orbit (known as Milankovitch oscillations) and were followed by stable periods of some thousand years (Berger, 1988). During the Pliocene–Pleistocene, periods of large shelf ice extent and low sea water level (glacial periods) alternated with periods of small shelf ice extent and high sea water level (interglacial periods). The alternation of these cycles, which presumably destroyed many of the available habitats, might have had a dramatic impact on the marine benthic fauna from the continental shelf, more vulnerable to the glacial maxima (Thatje et al., 2005). However, it now appears that the continental shelf was not ice-covered equally across the Antarctic coastline, allowing some ice-free refuges for fauna during the glacial maxima (Thatje et al., 2005; Convey et al., 2009; Strugnell et al., 2012).

The glacial–interglacial events resulted in an acute divergence between the fauna in the shallow areas and the fauna inhabiting deep waters as a result of bottleneck and cryptic speciation events (Barnes and Kuklinski, 2010; Post et al., 2010), which may have also acted as a diversity pump promoting allopatric speciation (Clarke and Crame, 1989; Clarke et al., 1992). The deeper and ice-free shallow areas may have also provided refuge habitats; these organisms could have evened the loss in diversity of shallow water areas by facilitating recolonization when environmental conditions allowed it (Thatje et al., 2005; Allcock and Strugnell, 2012). Repeated glaciation events have left characteristic signatures of bottlenecks, expansion events or limited gene flow. These signatures can be accessed by investigating genetic markers in populations of the target species, which provide essential information for explaining speciation processes and the current faunal distribution in these waters (Allcock and Strugnell, 2012).

Traditionally, the Antarctic Circumpolar Current (ACC) was thought to be responsible for the connectivity between marine Antarctic populations, having a homogenizing effect in the populations by transporting larvae and/or adults along the Antarctic region (Arntz et al., 1994; Waters, 2008). As a consequence, the species would present a high degree of population homogeneity (lack of structure) (Allcock and Strugnell, 2012). However, other currents, such as the Antarctic Coastal Current (ACoC), may also have the same effect but in the opposite direction of the ACC. Recent studies screening molecular markers to analyze circumpolarity in Antarctica have indeed found strong genetic structuring between populations of species with an assumed circumpolar distribution (e.g., Hemery et al., 2012; Gäbler-Schwarz et al., 2015). In fact, several cryptic species complexes have been detected in Antarctic invertebrates like annelid polychaetes, nemerteans, molluscs, arthropods, and echinoderms (e.g., Wilson et al., 2007, 2009; Janosik and Halanych, 2010; Schueller et al., 2013). These results challenge the theory about the stable, endemic, and largely connected fauna due to the ACC, which has only been tested for a few benthic taxa (Nikula et al., 2010; Raupach et al., 2010; Allcock et al., 2011; Arango et al., 2011; Dömel et al., 2015). Many oceanographic barriers between relatively close areas have been described hampering the genetic flow for species with large dispersal abilities, like the ACoC, the Weddell Gyre, and the area where the Weddell Sea and the Scotia Arc meet (e.g., Bargelloni et al., 2000; Gäbler-Schwarz et al., 2015).

Locally, the reproductive strategy and its effect on the dispersal abilities of the organisms have a crucial influence on the degree of connectivity between populations (Palumbi, 1994; Thatje, 2012), the species with planktotrophic larvae usually being the ones showing less genetic structure (“more mixing”) in their populations (Kinlan and Gaines, 2003; Allcock and Strugnell, 2012; Thatje, 2012). Therefore, besides the oceanic barriers and the past glacial periods, the biological features of the organisms could be responsible for the degree of connectivity between Antarctic benthic invertebrate populations. However, the scarce information about the phylogeography and genetic connectivity of the Antarctic marine invertebrates hinders our understanding of their distribution patterns. In addition, the accelerated rate in the warming of the Antarctic Peninsula (Vaughan et al., 2003) leaves biodiversity under a serious threat, that could result in higher extinction rates (Spielman et al., 2004); this is particularly true for shallow-water species that will be facing the major effects of climate change. Thus, if the species considered to be widely distributed along the Antarctic region are in fact cryptic species with reduced distribution ranges, data about Antarctic marine biodiversity might be remarkably underestimated, and many species could disappear before even being identified.

3. Molecular markers for genetic diversity and connectivity

Mitochondrial genes are relatively fast evolving (Avise, 2009) and have traditionally been used to assess genetic connectivity and gene flow in marine organisms, not without caveats (Song et al., 2008; Avise, 2009). Among the most used mitochondrial markers are *cytochrome oxidase I* (*COI*) and *16S rDNA* (*16S*), although some others, like *cytochrome B* (*CytB*), have also been used in studies dealing with Antarctic species (Baird et al., 2011; see Table 1). Mitochondrial genes are mainly useful because of their maternal inheritance, which allows for null recombination and therefore ensures that the mutations alone account for the exclusive genetic variety observed in animal populations (Avise, 2009). In addition, the universality of the *COI* marker, also known as the genetic Barcode, which is relatively easy to amplify thanks to the Folmer primers (Folmer et al., 1994), has provided a powerful tool for the assessment of genetic diversity, gene flow and, therefore, speciation patterns.

The Marine Barcode of Life (MarBOL) project is an international collaboration with the main goal of developing marine barcoding as a research tool in taxonomy. The bases of the barcode approach are settled upon the use of a fragment of 658 base pairs of the *COI* gene (Hebert et al., 2003; Savolainen et al., 2005), and no other gene is currently accepted to be held in the Barcode of Life Database (BOLD: http://www.boldsystems.org/). This fragment of the *COI* gene is universally used as a proxy for species identification and also to set the genomic boundaries between cryptic species and even genera (Hebert et al., 2003; Savolainen et al., 2005). For Antarctic organisms, the efforts to provide barcoding databases have been particularly fuelled by the Census of Antarctic Marine Life (CAML; http://www.caml.aq), and researchers have provided approximately 23,000 sequences so far, 11,026 barcodes in BOLD and the rest in non-BOLD databases (Grant and Linse, 2009; Grant et al., 2011), for more than 500 marine Antarctic species (or 2300 morphospecies). Among them, barcodes of invertebrates are

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