Earth-Science Reviews 164 (2017) 193–207

Contents lists available at ScienceDirect

Earth-Science Reviews

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

Invited review

Salt-marsh testate amoebae as precise and widespread indicators of sea-level change

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ARTICLE INFO

Article history:
Received 10 June 2016
Received in revised form 4 November 2016
Accepted 10 November 2016
Available online 24 November 2016

Keywords:
Sea level
Testate amoebae
Salt marsh
North Atlantic
Transfer function

ABSTRACT

Salt-marsh sediments are routinely used to reconstruct sea-level changes over past millennia. These reconstructions bridge an important gap between geological and instrumental sea-level records, and provide insights into the role of atmospheric, oceanic, climatic and anthropogenic sea-level drivers, thereby improving understanding of contemporary and future sea-level changes. Salt-marsh foraminifera, diatoms and testate amoebae are three of the proxies capable of accurately reconstructing former sea level over decadal to millennial timescales. Datasets of surface assemblages are collated along elevational gradients to provide modern analogues that can be used to infer former marsh-surface elevations from fossil assemblages. Testate amoebae are the most recently developed proxy and existing studies suggest that they are at least as precise as the two other proxies. This study provides a synthesis of sea-level research using testate amoebae and collates and analyses existing surface datasets of intertidal salt-marsh testate amoebae from sites throughout the North Atlantic. We test the hypothesis that intertidal testate amoebae demonstrate cosmopolitan intertidal zonation across wide geographical areas in a way that is unique to this proxy. Testate amoebae assemblages are harmonised under a unified taxonomy and standardised into a single basin-wide training set suitable for reconstructing sea-level changes from salt-marsh sediments across the North Atlantic. Transfer functions are developed using regression modelling and show comparable performance values to published local training sets of foraminifera, diatoms and testate amoebae. When used to develop recent (last 100 years) sea-level reconstructions for sites in Norway and Quebec, Canada, the testate amoebae-based transfer function demonstrated prediction uncertainties of ±0.26 m and ±0.10 m respectively. These uncertainties equate to 10% and 11% of the tidal ranges at each site, which is of comparable precision to other published sea-level reconstructions based on foraminifera or diatoms. There is great scope for further developing intertidal testate amoebae as precise sea-level indicators and their application should be tested at sites beyond the North Atlantic.

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http://dx.doi.org/10.1016/j.earscirev.2016.11.002
0012-8252/

1. Introduction

Testate amoebae are a group of unicellular test producing organisms (protists) that inhabit a range of freshwater and brackish environments (Medioli and Scott, 1983) with a wide applicability to palaeoenvironmental research (Tolonen, 1986; Medioli et al., 1999; Charman, 2001). Testate amoebae belong to the kingdom of Protozoa (Cavalier-Smith, 1981) and earlier works have referred to them as 'rhizopods' (e.g., Tolonen, 1986), arcellaceans (e.g., Patterson et al., 1985), 'testaceans' (e.g., Tolonen et al., 1992) and 'thecamoebians' (e.g., Riveiros et al., 2007). The systematic classification of testate amoebae has evolved over past decades (c.f., Charman et al., 2000) and is still subject to revision in light of recent advancements applying multigene molecular phylogeny. Currently, the group has been classified within two dominant clades. Taxa with filiform pseudopodia are in the class Imbricatea, subphylum Filosa, and phylum Cercozoa (Cavalier-Smith, 1998; Cavalier-Smith and Chao, 2003). Taxa with lobed pseudopodia are found predominantly within the order Arcellinida (Kent, 1880; Nikolaev et al., 2005), class Tubulinea (Smirnov et al., 2005), subphylum Lobosea (Carpenter, 1861; Cavalier-Smith, 2009) and phylum Amoebozoa (Lühe, 1913; Smirnov et al., 2011; Cavalier-Smith, 2013).

From a palaeoecological perspective, early studies most commonly documented testate amoebae in peatland (Tolonen, 1966; Warner, 1987, 1989) and lacustrine (Patterson et al., 1985; Medioli and Scott, 1988) environments. However, studies have also described assemblages from coastal sediments subjected to brackish conditions (Medioli et al., 1990), including coastal lakes (e.g., Nicholls and MacIsaac, 2004) and beaches (e.g., Golemansky, 1998a, 1998b), intertidal salt marshes (Scott et al., 1977; Charman et al., 1998, 2002) and mangroves (Duleba and Debenay, 2003). Palaeoenvironmental studies have used testate amoebae as bioindicators of hydrological balance (e.g., Woodland et al., 1998; McGlone and Wilmshurst, 1999), pH (e.g., Mitchell et al., 2013), pollution (e.g., Kandeler et al., 1992), temperature (Royles et al., 2013) and sea-level changes (e.g., Charman et al., 1998). The recent development of geographically expansive testate amoebae-based hydrological transfer functions ranging from tropical (Swindles et al., 2014), temperate (Li et al., 2015; Amesbury et al., 2016) and high-latitude southern (van Bellen et al., 2014) and northern (Swindles et al., 2015) hemisphere peatland environments demonstrate the wide applicability of testate amoebae as a proxy tool. The application of testate amoebae as precise sea-level indicators in salt-marsh environments commenced during the late 1970s (Scott et al., 1977) but, until recently, has lagged behind alternative proxy counterparts such as salt-marsh macrophytes, foraminifera and diatoms (Shennan et al., 2015).

This review has two main purposes. First, we present an account of existing literature on coastal wetland testate amoebae and their use as proxies of sea-level change. Second, we develop a basin-wide dataset (or 'training set') of modern salt-marsh testate amoebae suitable for reconstructing recent relative sea-level changes in the North Atlantic region. Alternative proxies rely on training sets from single sites, or multiple sites in close proximity, to develop transfer functions suitable for local sea-level reconstructions (e.g., Horton and Edwards, 2005). In this paper we demonstrate that assemblages of testate amoebae are broadly similar in many coastal settings around the North Atlantic and, for the first time, we provide a means to reconstruct relative sea-level changes at salt-marsh sites in the entire North Atlantic region using a single training set under a unified taxonomy.

2. Salt-marsh testate amoebae

Surface testate amoebae from salt-marsh environments were first described in Atlantic Canada (Scott et al., 1977; Medioli and Scott, 1983) in the >63 μm sediment fraction, alongside foraminifera, from estuarine and coastal environments (Scott and Martini, 1982; Scott et al., 1991, 1995, 2001; Barbosa et al., 2005). Whereas foraminifera are found throughout marine and brackish environments, only a small number of testate amoebae taxa are able to tolerate the saline conditions experienced in tidal marshes (c.f., Patterson and Kumar, 2002). Specific testate amoebae assemblages related to tidal influence occupy high salt-marsh environments transitioning into the supratidal zone (Patterson et al., 1985; Charman et al., 1998). Salt-marsh testate amoebae have been sampled along transects across marsh surfaces with the aim of identifying vertical assemblage zones attributable to environmental variables (Charman et al., 1998, 2002; Gehrels et al., 2001, 2006; Riveiros et al., 2007; Ooms et al., 2011, 2012; Barnett et al., 2013, 2016). This practise has been applied regularly using salt-marsh foraminifera (Edwards and Wright, 2015) and diatoms (Zong and Sawai, 2015). However, work based on testate amoebae is comparably limited despite the significant potential of this proxy (Charman, 2015).

2.1. Contemporary surface assemblages

Systematic studies of salt-marsh testate amoebae typically include samples along surface transects which traverse the elevation gradient from the high marsh into the low marsh (Scott and Medioli, 1980). The two marsh zones are commonly characterised by their surface vegetation (e.g., Charman et al., 1998; Gehrels et al., 2006; Barnett et al., 2013). Sampling along such transects must extend beyond highest astronomical tide (HAT) levels and into the supratidal setting in order to recognise assemblage populations that are not affected by tidal inundation (Gehrels et al., 2001, 2006; Ooms et al., 2012). At the other end of the gradient, the lowest testate amoebae are usually encountered near mean high water spring (MHWS) levels (Gehrels et al., 2001, 2006). However, in northern Norway (Barnett et al., 2013), testate amoebae populations were found down to near mean high water neap (MHWN) levels while in the Magdalen Islands, in the Gulf of St Lawrence, Canada, where micro-tidal conditions prevail, assemblages were described down to near mean sea level (Barnett et al., 2016). This implies that, in order to capture the full turnover of species data (c.f., Wright et al., 2011), it may be necessary to sample well below the level of MHWS.

Surface data from different locations record site-specific assemblage trends. However, intra-site comparisons regularly reveal common testate amoebae zonations (Charman et al., 2002). For example, an early