

1 **Title**

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

3

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21

22 **Abstract**

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

47 as precise sea-level indicators and their application should be tested at sites beyond the North
48 Atlantic.

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50

51 **Keywords**

52 Sea level, testate amoebae, salt marsh, North Atlantic, transfer function

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75 **1. Introduction**

76 Testate amoebae are a group of unicellular test producing organisms (protists) that inhabit a
77 range of freshwater and brackish environments (Medioli and Scott, 1983) with a wide
78 applicability to palaeoenvironmental research (Tolonen, 1986; Medioli et al., 1999; Charman,
79 2001). Testate amoebae belong to the kingdom of Protozoa (Cavalier-Smith, 1981) and
80 earlier works have referred to them as ‘rhizopods’ (e.g., Tolonen, 1986), arcellaceans (e.g.,
81 Patterson et al., 1985), ‘testaceans’ (e.g., Tolonen et al., 1992) and ‘thecamoebians’ (e.g.,
82 Riveiros et al., 2007). The systematic classification of testate amoebae has evolved over past
83 decades (c.f., Charman et al., 2000) and is still subject to revision in light of recent
84 advancements applying multigene molecular phylogeny. Currently, the group has been
85 classified within two dominant clades. Taxa with filiform pseudopodia are in the class
86 Imbricatea, subphylum Filosa, and phylum Cercozoa (Cavalier-Smith, 1998; Cavalier-Smith
87 and Chao, 2003). Taxa with lobed pseudopodia are found predominantly within the order
88 Arcellinida (Kent, 1880; Nikolaev et al., 2005), class Tubulinea (Smirnov et al., 2005),
89 subphylum Lobosea (Carpenter, 1861; Cavalier-Smith, 2009) and phylum Amoebozoa (Lühe,
90 1913; Smirnov et al., 2011; Cavalier-Smith, 2013).

91 From a palaeoecological perspective, early studies most commonly documented testate
92 amoebae in peatland (Tolonen, 1966; Warner, 1987, 1989) and lacustrine (Patterson et al.,
93 1985; Medioli and Scott, 1988) environments. However, studies have also described
94 assemblages from coastal sediments subjected to brackish conditions (Medioli et al., 1990),
95 including coastal lakes (e.g., Nicholls and MacIsaac, 2004) and beaches (e.g., Golemansky,
96 1998a,b), intertidal salt marshes (Scott et al., 1977; Charman et al., 1998, 2002) and
97 mangroves (Duleba and Debenay, 2003). Palaeoenvironmental studies have used testate
98 amoebae as bioindicators of hydrological balance (e.g., Woodland et al., 1998; McGlone and
99 Wilmshurst, 1999), pH (e.g., Mitchell et al., 2013), pollution (e.g., Kandeler et al., 1992),

100 temperature (Royles et al., 2013) and sea-level changes (e.g., Charman et al., 1998). The
101 recent development of geographically expansive testate amoebae-based hydrological transfer
102 functions ranging from tropical (Swindles et al., 2014), temperate (Li et al., 2015; Amesbury
103 et al., 2016) and high-latitude southern (van Bellen et al., 2014) and northern (Swindles et al.,
104 2015) hemisphere peatland environments demonstrate the wide applicability of testate
105 amoebae as a proxy tool. The application of testate amoebae as precise sea-level indicators in
106 salt-marsh environments commenced during the late 1970s (Scott et al., 1977) but, until
107 recently, has lagged behind alternative proxy counterparts such as salt-marsh macrophytes,
108 foraminifera and diatoms (Shennan et al., 2015).

109 This review has two main purposes. First, we present an account of existing literature on
110 coastal wetland testate amoebae and their use as proxies of sea-level change. Second, we
111 develop a basin-wide dataset (or ‘training set’) of modern salt-marsh testate amoebae suitable
112 for reconstructing recent relative sea-level changes in the North Atlantic region. Alternative
113 proxies rely on training sets from single sites, or multiple sites in close proximity, to develop
114 transfer functions suitable for local sea-level reconstructions (e.g., Horton and Edwards,
115 2005). In this paper we demonstrate that assemblages of testate amoebae are broadly similar
116 in many coastal settings around the North Atlantic and, for the first time, we provide a means
117 to reconstruct relative sea-level changes at salt-marsh sites in the entire North Atlantic region
118 using a single training set under a unified taxonomy.

119

120

121 **2. Salt-marsh testate amoebae**

122 Surface testate amoebae from salt-marsh environments were first described in Atlantic
123 Canada (Scott et al., 1977; Medioli and Scott, 1983) in the greater than 63 μm sediment

124 fraction, alongside foraminifera, from estuarine and coastal environments (Scott and Martini,
125 1982; Scott et al., 1991, 1995, 2001; Barbosa et al., 2006). Whereas foraminifera are found
126 throughout marine and brackish environments, only a small number of testate amoebae taxa
127 are able to tolerate the saline conditions experienced in tidal marshes (c.f., Patterson and
128 Kumar, 2002). Specific testate amoebae assemblages related to tidal influence occupy high
129 salt-marsh environments transitioning into the supratidal zone (Patterson et al., 1985;
130 Charman et al., 1998). Salt-marsh testate amoebae have been sampled along transects across
131 marsh surfaces with the aim of identifying vertical assemblage zones attributable to
132 environmental variables (Charman et al., 1998, 2002; Gehrels et al., 2001, 2006; Riveiros et
133 al., 2007; Ooms et al., 2011, 2012; Barnett et al., 2013, 2016). This practise has been applied
134 regularly using salt-marsh foraminifera (Edwards and Wright, 2015) and diatoms (Zong and
135 Sawai, 2015). However, work based on testate amoebae is comparably limited despite the
136 significant potential of this proxy (Charman, 2015).

137

138 ***2.1 Contemporary surface assemblages***

139 Systematic studies of salt-marsh testate amoebae typically include samples along surface
140 transects which traverse the elevation gradient from the high marsh into the low marsh (Scott
141 and Medioli, 1980). The two marsh zones are commonly characterised by their surface
142 vegetation (e.g., Charman et al., 1998; Gehrels et al., 2006; Barnett et al., 2013). Sampling
143 along such transects must extend beyond highest astronomical tide (HAT) levels and into the
144 supratidal setting in order to recognise assemblage populations that are not affected by tidal
145 inundation (Gehrels et al., 2001, 2006; Ooms et al., 2012). At the other end of the gradient,
146 the lowest testate amoebae are usually encountered near mean high water spring (MHWS)
147 levels (Gehrels et al., 2001, 2006). However, in northern Norway (Barnett et al., 2013),

148 testate amoebae populations were found down to near mean high water neap (MHWN) levels
149 while in the Magdalen Islands, in the Gulf of St Lawrence, Canada, where micro-tidal
150 conditions prevail, assemblages were described down to near mean sea level (Barnett et al.,
151 2016). This implies that, in order to capture the full turnover of species data (c.f., Wright et
152 al., 2011), it may be necessary to sample well below the level of MHWS.

153 Surface data from different locations record site-specific assemblage trends. However, intra-
154 site comparisons regularly reveal common testate amoebae zonation (Charman et al., 2002).
155 For example, an early study of salt-marsh testate amoebae from three sites in the UK
156 identified high-marsh biozones that typically included taxa such as *Tracheleuglypha dentata*
157 and *Trinema* spp. (Charman et al., 2002). The taxon *T. dentata* was subsequently identified in
158 numerous later studies as a ubiquitous high-marsh species that commonly dominated
159 biozones near HAT (Gehrels et al., 2006; Ooms et al., 2011, 2012; Barnett et al., 2013, 2016).
160 Various taxa within the genus *Centropyxis*, perhaps most commonly *Centropyxis cassis* type,
161 are described in most (if not all) salt-marsh studies, frequently demonstrating broad
162 environmental ranges (e.g., Riveiros et al., 2006). Commonly described taxa from lower in
163 the intertidal realm include *Cyphoderia ampulla* (e.g., Charman et al., 2002; Ooms et al.,
164 2011) and *Diffflugia pristis* type (e.g., Gehrels et al., 2006; Ooms et al., 2012; Barnett et al.,
165 2013). In contrast to other salt-marsh organisms, such as foraminifera, which display greater
166 site specific differences (Horton et al., 1999), regular occurrences of common taxa could
167 suggest a regionally-robust testate amoebae ecology across the North Atlantic (Charman et
168 al., 2010). In this paper we test, therefore, the hypothesis that intertidal zonation of testate
169 amoebae is similar across the North Atlantic region.

170

171 ***2.2 Environmental controls and elevation***

172 The relative influences of environmental controls on salt-marsh testate amoebae assemblages
173 have been investigated by a number of studies since the early 2000s. A range of variables
174 have been considered, including the pH, salinity, organic content and grain size of the sample
175 sediments whence the assemblages originated (Charman et al., 2002; Riveiros et al., 2007;
176 Ooms et al., 2011, 2012; Barnett et al., 2016). Camacho et al. (2015) went further and
177 analysed nutrient characteristics (total (in-)organic carbon and carbon: nitrogen ratios) as well
178 as dissolved oxygen at sample locations. In all the studies cited above, sample elevation
179 exerted the most significant control on assemblage compositions. Although elevation is not
180 an ecological variable itself (Kemp and Telford, 2015), it is used as a linear approximation of
181 tidal inundation (Gehrels, 2000; Gehrels et al., 2001; Wright et al., 2011; Barlow et al., 2013)
182 due to the close relationship it shares with inundation frequency (e.g., Scott and Medioli,
183 1980; Horton et al., 1999). Observed correlation between secondary variables and tidal level
184 supports the use of elevation as a surrogate variable capable of capturing the effect that
185 changes in marine influence has on assemblage compositions (Charman et al., 2002).

186 Gradient analysis is used to statistically describe the relationships between multiple
187 environmental variables and assemblage compositions (Juggins and Birks, 2012). Whether
188 datasets of intertidal testate amoebae exhibit linear responses (e.g., Ooms et al., 2011, 2012;
189 Camacho et al., 2015) or unimodal responses (Charman et al., 2002; Riveiros et al., 2006;
190 Barnett et al., 2016) along environmental gradients, variables associated with tidal inundation
191 (i.e., flooding and elevation) consistently explain a significant proportion of assemblage
192 variation. When quantified, these variables alone may typically account for between 20 and
193 50 % of total species variation within assemblages (Charman et al., 2002; Barnett et al.,
194 2016). Although secondary variables such as pH (e.g., Camacho et al., 2015) and salinity
195 (e.g., Charman et al., 2002; Riveiros et al., 2006) have been documented, the dominance of

196 elevation in defining assemblage characteristics means that collecting environmental data of
197 alternative variables is not strictly necessary in all cases (e.g., Gehrels et al., 2006).

198

199 **2.3 Fossil assemblages**

200 When the relationship between sea-level indicators, such as intertidal testate amoebae, and
201 tidal levels is well established in the modern environment, this understanding can be applied
202 to fossil assemblages in order to infer changes in past sea level (van de Plassche, 1986;
203 Shennan, 2007, 2015). As an example, in Scotland (Lloyd, 2000) and eastern Canada
204 (Patterson et al., 1985), fossil testate amoebae from sediment cores were used to describe
205 marine to freshwater transitions in coastal basins which became isolated from tidal conditions
206 as a result of land uplift. A study of different coastal deposits around Britain (isolation basins,
207 coastal back barriers, brackish fens and intertidal marshes) by Roe et al. (2002) revealed that
208 fossil assemblages evolved as local tidal conditions changed at the sites. However, in certain
209 sediment types, notably those from salt marshes, taxa diversity and abundance was found to
210 be low, possibly as a result of test degradation with preferential preservation of certain taxa,
211 or because the depositional environment exceeded the lower limit of testate amoebae
212 occurrence (Roe et al., 2002). An analysis of salt-marsh cores from Wells, Maine, and
213 Chezzetcook, Nova Scotia, found testate amoebae present in good concentrations (*c.* 5000 to
214 30,000 tests g⁻¹) throughout the core tops (Charman et al., 2010). Below depths
215 approximately equivalent to pre-20th century, test concentrations reduced significantly. As the
216 cores originated from the lower limits of testate amoebae occurrence (i.e., close to MHWS),
217 the lack of test abundance and diversity, as found by Roe et al. (2002), may have been due
218 either to a lower depositional environment or post-burial diagenesis. In addition, these
219 studies, alongside others (e.g., Barnett et al., 2015), repeatedly report the absence of

220 Euglyphids (siliceous, plate-forming taxa) in fossil assemblages, whilst noting their
221 abundance in contemporary assemblages. Continuous fossil sequences of intertidal testate
222 amoebae spanning the past *c.* 500 years from Quebec, Canada (Barnett et al., *in review*), and
223 preserved salt-marsh assemblages from Viðarhólmi, Iceland, dating from *c.* 1200 to 1600 AD
224 (Haynes, 2011), suggest that, under favourable conditions, testate amoebae can be preserved
225 in older coastal sediments.

226 The preferential loss of idiosomic taxa (those formed of siliceous plates) versus that of
227 xenosomes (taxa formed from agglutinated particles) in down-core sediment profiles from
228 terrestrial environments was first recorded several decades ago (Lousier and Parkinson,
229 1981). The ready deterioration of certain idiosomic taxa, such as *Euglypha* spp. (Patterson
230 and Kumar, 2002), in peatland settings is possibly a result of acidic pore-water conditions
231 (Swindles and Roe, 2007), which may apply to high salt-marsh environments that
232 characteristically have a pH of around 6.0 (e.g., Charman et al., 2002; Barnett et al., 2016).
233 Despite this, Mitchell et al. (2008) demonstrate that, for *Sphagnum*-dominated peatlands,
234 post-burial changes in fossilised assemblage compositions do not necessarily equate to loss in
235 palaeoecological reconstruction performance. This notion is yet to be tested empirically for
236 salt-marsh testate amoebae based sea-level reconstructions and represents an important facet
237 related to the efficacy of future work.

238

239

240 **3. Sea-level research**

241 Sea-level reconstructions using salt-marsh organisms rely on sampling contemporary
242 assemblages and measuring their elevation (Scott and Medioli, 1978, 1980). These
243 measurements can be used to define precise indicative meanings, or ranges (c.f., Shennan,

244 2007, 2015), for surface assemblages based on either a visual assessment or statistical
245 calibration of the data or ‘training set’ (Imbrie and Kipp, 1971; Guilbault et al., 1995). By
246 applying the relationship to down-core assemblages via a transfer function, the
247 contemporaneous elevational range that the fossilised assemblages occupied can be estimated
248 (see Barlow et al. (2013) for a review) and the height of former sea level can be derived with
249 necessary consideration given to correction factors (e.g., palaeo-tidal changes, sediment
250 compaction, local sedimentation regime).

251

252 ***3.1 Training sets and transfer functions***

253 Charman et al. (1998) presented the first training set of salt-marsh testate amoebae designed
254 to derive indicative meanings related to sea level based on surface assemblage zonation.
255 Cluster analysis was used to identify four groups of assemblages which defined marsh zones
256 between HAT and MHWS levels. Following this pioneering study, training sets of surface
257 data were developed in the United Kingdom (Gehrels et al., 2001; Charman et al., 2002) and
258 North America (Gehrels et al., 2006). In these cases, indicative meanings were calculated
259 using a ‘transfer function’ based on regression modelling (ter Braak and Juggins, 1993; Birks,
260 1995) rather than the previously used cluster analysis or visual assessment methods. The
261 transfer function approach models the contemporary species-elevation relationship producing
262 an equation which can be calibrated on species assemblage data to estimate the elevation
263 from which the assemblage data derives (see Kemp and Telford (2015) for a review). Using
264 the transfer function method, local training sets of testate amoebae were capable of predicting
265 salt-marsh surface elevations with sub-decimetre vertical uncertainties (Gehrels et al., 2001,
266 2006).

267 The success of using testate amoebae as precise marsh-surface elevation indicators has since
268 been repeated in Belgium (Ooms et al., 2011, 2012), Norway (Barnett et al., 2013) and
269 Canada (Barnett et al., 2016). These studies report transfer functions with 1σ uncertainties
270 ranging from ± 0.08 to ± 0.24 m (Table 1). Numerous factors contribute to the magnitude of
271 these model uncertainties. The largest reported uncertainties originate from the Scheldt
272 Estuary, Belgium, where the intertidal marsh is located over 50 km up river and experiences a
273 spring tidal range of over 5 m (Ooms et al., 2012). Salt-marsh based sea-level studies using
274 foraminifera and diatoms also report greater-than-average uncertainties at macro-tidal (4 to 6
275 m range) sites (Horton and Edwards, 2005; Massey et al., 2006; Hill et al., 2007). Comparing
276 reconstruction uncertainties against tidal range sizes (Table 1, and Table 3 in Barlow et al.
277 (2013)) reveals that transfer function RMSEP values for foraminifera, diatoms and testate
278 amoebae training sets are typically lower than $\sim 10\%$ of the tidal range.

279 The length of the sampled environmental gradient is also vital for establishing robust and
280 realistic model uncertainties. Wright et al. (2011) show the importance of capturing the full
281 length of species turnover along the gradient of interest. In the case of testate amoebae, this
282 translates to sampling below the lowest limit of test occurrence and beyond the level of tidal
283 influence so that non-intertidal taxa dominate assemblage compositions. Earlier studies, such
284 as Gehrels et al. (2006), postulated that low model uncertainties may be a factor of an under-
285 sampled environmental gradient and insufficient training set size (e.g., Table 1). Assimilating
286 local datasets of intertidal testate amoebae into a regional training set, thereby extending the
287 sampled gradient length, provides an opportunity for developing more robust and accurate
288 sea-level reconstructions.

289

290 ***3.2 Sea-level reconstructions***

291 Charman et al. (2010) demonstrated the robustness of salt-marsh testate amoebae by applying
292 a transfer function built from training sets of contemporary assemblages from the United
293 Kingdom (Gehrels et al., 2001; Charman et al., 2002) to reconstruct recent (past *c.* 100 years)
294 sea-level changes in Maine and Nova Scotia. The two reconstructions based on the UK
295 training set had comparable uncertainties (± 0.07 to ± 0.10 m) to similar reconstructions
296 which were developed using a North American (Gehrels et al., 2006) training set (± 0.05 to \pm
297 0.06 m), thereby demonstrating that regional training sets of surface assemblage data may be
298 applicable across wide geographical areas.

299 Salt-marsh testate amoebae have also been used to reconstruct falling late Holocene relative
300 sea-level trends in northern Norway (Barnett et al., 2015). However, beyond these few
301 published studies, no other sequences of fossil intertidal assemblages have been used to
302 generate continuous and precise records of former sea level. Ongoing works in the Gulf of St
303 Lawrence (Pascal Bernatchez, *pers. comm.*) and Newfoundland, Canada, (Andy Kemp, *pers.*
304 *comm.*) have begun to incorporate this proxy into sea-level reconstructions where alternative
305 options (such as foraminifera) prove less viable. In parts of eastern Canada, where relative
306 sea level is rising by up to 4 mm.yr^{-1} and intertidal marshes are being submerged (Bernatchez
307 et al., 2008, 2010, 2012), salt-marsh testate amoebae will be capable of capturing
308 environmental transitions from fully terrestrial coastal peatland to intertidal marine
309 conditions. This useful tool will be valuable for quantifying recent rapid relative sea-level rise
310 in locations that lack tide gauges or where tide-gauge records are very short.

311

312

313 **4. Analytical procedures**

314 Since early reports of salt-marsh testate amoebae described in samples prepared for
315 foraminifera (Scott et al., 1977; Scott and Martini, 1982), preparation techniques have been
316 honed to maximise the recovery of tests from sediment samples. Importantly, Charman et al.
317 (1998) identified significant testate amoebae diversity in size fractions (in particular, less than
318 63 μm) which were not included within foraminifera preparations. The latest preparation
319 protocols are detailed by Charman (2015) based on developments of a method developed for
320 peatland testate amoebae (Hendon and Charman, 1998; Charman et al., 2000) and adapted for
321 salt-marsh sediments (Charman et al., 2010; Barnett et al., 2013). In summary, a known
322 volume of sediment is warmed, soaked and disaggregated in water prior to being sieved
323 through 15 and 300 μm meshes. The addition of a chemical pre-treatment (e.g., KOH) stage
324 is optional and can be used to concentrate tests if abundance is low (Hendon and Charman,
325 1998; Barnett et al., 2013).

326 A count total of 100 tests per sample is widely cited as a sufficient figure for palaeoecological
327 studies (Woodland et al., 1998; Mitchell et al., 2000; Payne and Mitchell, 2009; Barnett et al.,
328 2015). Where testate amoebae are found in low numbers, such as in the low marsh or in
329 certain sections of sediment cores, researchers have occasionally compiled assemblages
330 based on count totals of fewer than 100 specimens (e.g., Charman et al., 2010). In peatland
331 studies it has been demonstrated that transfer function standard errors may remain consistent
332 for count totals greater than 60 specimens (Payne and Mitchell, 2009). Providing statistically
333 significant counts are reached for each taxon (defined by fractional abundance detection
334 limits; Fatela and Taborda, 2002), these low abundance samples retain significant
335 palaeoecological value. For count totals that are analogous to the sample sizes found in this
336 study, (typically 50 to 200 tests ; Supplementary Material I), taxa which make up fewer than
337 5 % of the assemblages are capable of distinguishing environments that differ by 4 % at the
338 95 % confidence interval (Patterson and Fishbein, 1989). If greater precision is required, then

339 count totals of several hundred to several thousand become necessary to identify small
340 environmental changes in the presence of low abundance taxa. By identifying minimum
341 count size totals for individual taxa following Fatela and Taborda (2002), those that have
342 been insufficiently detected to be deemed representative of a particular environment can be
343 highlighted and, if necessary, removed from the dataset based on their relative abundance
344 proportion (p) value (c.f., Fatela and Taborda (2002); Supplementary Material I).

345

346

347 **5. A North Atlantic regional transfer function**

348 The second purpose of this study was to develop and test a basin-wide training set of salt-
349 marsh testate amoebae capable of reconstructing sea-level changes in the North Atlantic. To
350 this end, assemblages from studies throughout the North Atlantic were collated and screened
351 to ensure that only samples containing consistent test sizes (15 to 300 μm) and suitable count
352 totals (>50 tests) were incorporated into the dataset. Following the screening process, a total
353 of 14 sites provided modern assemblage data of testate amoebae with associated
354 environmental (elevation) information (Fig. 1). There are three sites from Canada (two from
355 the Magdalen Islands in Quebec (Barnett et al., 2016) and one from New Brunswick (Gehrels
356 et al., 2006)), three from the USA (Maine, Delaware (Gehrels et al., 2006) and Connecticut
357 (this study)), one from Iceland (Haynes, 2011), two from Norway (Barnett et al., 2013) and
358 one from Belgium (Ooms et al., 2012). The remaining four sites are from Wales, Devon,
359 Norfolk (Charman et al., 2002) and Cornwall (this study) in the UK.

360

361 ***5.1 Data acquisition and standardisation***

362 The original studies provided 275 samples of salt-marsh testate amoebae following removal
363 of assemblages containing count sizes of fewer than 50 tests (Supplementary Material I). As
364 count totals varied from ~50 tests to over 1000 in some cases, proportional uncertainties (*p*-
365 values) were calculated for each sample following Fatela and Taborda (2002)
366 (Supplementary Material I). The *p*-value is a function of sample size (*n*) and represents the
367 minimum proportional abundance required for a given species to have been sufficiently
368 detected at the 95 % confidence limit (equation 1). This value significantly decreases (thereby
369 increasing confidence in the assemblage counts) with increasing count totals.

370
$$p = 1 - f(0.05)^{1/n} \quad (1) \text{ Fatela and Taborda (2002)}$$

371 Each sample contained a corresponding elevation constraint cited relative to a local water
372 level or datum. All elevation constraints were converted to height above local mean water
373 level (MWL) based on information from the original studies and recent Admiralty Tide
374 Tables (2015). Absolute sampled ranges varied between sites (Fig. 1). Supratidal sampling
375 (i.e., elevations above HAT) occurred at 8 of the total 14 sites. The lowest extent of testate
376 amoebae generally occurs at, or close to, MHWS tidal elevations (n.b., the height of MHWS
377 tides is unavailable for Viðarhólmi in Iceland and Leipsic River in Delaware, USA). Where
378 studies have used two local sites to compile a training set of surface data (see Magdalen
379 Islands, Canada, and Vesterålen Islands, Norway; Fig. 1), only a single estimation of the
380 lowest extent of testate occurrence is included.

381 A standardised water level index (SWLI) was developed in order to account for the difference
382 in tidal ranges between the individual sites and to normalise elevation constraints within the
383 wider dataset (c.f., Gehrels, 1999; Gehrels, 2000; Horton et al., 1999). Using such an index,
384 sample elevations can be expressed relative to common low elevation and high elevation tidal
385 markers (e.g., Wright et al., 2011). Here, sample elevations are normalised by using the

386 lowest extent of testate amoebae as a consistent low marker and standardising the distance
387 between this and HAT at all the sites (equation 2):

$$388 \quad \text{SWLI} = ((S - L) / (HAT - L)) \times 100 \quad (2)$$

389 where S is sample elevation and L is lowest occurrence of testate amoebae.

390

391 *5.2 Unifying the taxonomy*

392 There is a wide literature available for identifying testate amoebae. Early compilations of
393 descriptions and monographs began in the late 19th (Leidy, 1879; Penard, 1890) and early 20th
394 centuries (Penard, 1902; Cash and Hopkinson, 1905, 1909; Cash et al., 1915). Subsequent
395 taxonomic works have contributed to the reclassification of species and genera, commonly
396 resulting in the renaming and/or splitting of species and morphospecies into distinct clades.
397 Charman et al. (2000) provide a useful insight into some issues associated with the evolving
398 taxonomy of testate amoebae with particular reference to the problems of applying
399 descriptions based on modern specimens to fossil assemblages used in palaeoecological
400 studies. Morphological characteristics used to distinguish living taxa may be unapparent in
401 fossilised specimens. For this reason we advocate the use of ‘type’ groups when developing a
402 consistent and coherent taxonomy for certain salt-marsh specimens. These may include suites
403 of morphospecies which represent a continuum of change rather than distinct morphological
404 features (Medioli and Scott, 1983), or groups of similar taxa which are difficult to distinguish
405 under light microscopy yet share common ecological niches. These methods augment the
406 fundamental systematic classification developed for peatland testate amoebae (Charman et
407 al., 2000) with the increasingly comprehensive taxonomic literature accounting for taxa
408 found in salt-marsh and littoral environments (Golemansky, 1974, 1998a,b; Nicholls, 2003,

409 2005, 2007, 2009; Golemansky and Todorov, 2004, 2005, 2007; Nicholls and MacIsaac,
410 2004; Todorov et al., 2009; Heger et al. 2010).

411 Existing published assemblages of intertidal marsh testate amoebae have been catalogued
412 using a range of the available literature (e.g., Charman et al., 1998; Gehrels et al., 2006;
413 Riveiros et al., 2007; Ooms et al., 2011), resulting in some inconsistencies between individual
414 datasets. We applied a single unified taxonomy to harmonise the data. Type groups were used
415 to collate taxa where: i) morphologically indistinguishable species have been reported under
416 different names, ii) specimens show morphological variation along a continuum of change,
417 yet lack clear and discernible distinguishing features, iii) similar taxa (often belonging to the
418 same genus) occupy comparable ecological niches, therefore separation yields no additional
419 palaeoenvironmental information, and, iv) distinguishing features of similar species (or
420 morphospecies) are unable to be identified using light microscopy, particularly for fossil
421 specimens. Of the original 156 taxa reported from the studies mentioned above, 57 taxa or
422 type groups have been used to classify the full dataset under a unified taxonomy
423 (Supplementary Material II). Surface assemblages were then re-classified using the new
424 taxonomy so that a coherent regional training set could be developed. Whilst this has resulted
425 in greater grouping of taxa than is applied in individual studies, it avoids spurious inferences
426 as a consequence of differences between observers.

427

428 ***5.3 The training set***

429 The 275 samples comprising the North Atlantic regional training set were subjected to an
430 unconstrained cluster analysis (Oksanen et al., 2015) which identified five distinguishable
431 biozones (Fig. 2). Although the cluster analysis does not use the elevation data in determining
432 clusters, there was a strong relationship between the clusters defined by assemblage

433 composition and their elevation, and the biozonation was therefore orientated along an
434 elevation gradient, as defined by sample SWLI scores (Fig. 2). Low elevation samples are
435 represented by biozone 1. Here, assemblages derive from near or below MHWS tidal levels
436 with typical SWLI values of between 3 and 34 (mean \pm 1 standard deviation).

437 Taxonomically, the zone is characterised by a low diversity of halophytic taxa, commonly
438 dominated by *Arcella catinus-discoides* type and *Centropyxis platystoma* type. Biozone 2 is
439 typically characterised by different dominating taxa (e.g., *Centropyxiella* type, *Corythionella*
440 type, *Diffflugia pristis* type) and a greater diversity of low abundance taxa (e.g.,
441 *Pseudocorythion* type, *Pseudohyalosphenia* spp., *Cyphoderia ampulla* type). This zone
442 represents upper intertidal environments with typical SWLI values between 11 and 84.

443 Biozone 3 also represents intertidal assemblages from below HAT levels (SWLI 34 to 95)
444 which predominantly comprise of taxa belonging to the genus *Centropyxis*. Biozone 4
445 represents transitional assemblages between intertidal and ‘supratidal’ (defined here as
446 elevations above HAT, although some degree of marine influence remains as a result of, e.g.,
447 storm events) environments whereas biozone 5 is predominantly comprised of supratidal
448 samples with SWLI scores of 64 to 175. Both of these zones contain significantly different
449 assemblages from the lower intertidal biozones and are largely comprised of taxa from the
450 *Euglypha*, *Tracheleuglypha* and *Trinema* genera (Fig. 2). A small number of samples from
451 the top of biozone 5 derive from intertidal, rather than supratidal, environments as
452 demonstrated by their low SWLI scores. These samples come from the Scheldt Estuary in
453 Belgium which experiences greater freshwater influence than comparative sites (Ooms et al.,
454 2011, 2012). This may account for why high marsh taxa such as *Euglypha* spp.,
455 *Tracheleuglypha* sp. and *Trinema* spp. are found lower in the intertidal realm at this location
456 (Fig. 2).

457 Canonical correspondence analysis (CCA; ter Braak, 1986, 1987) was used to test the
458 strength of the relationship between the testate amoebae assemblages and elevation. CCA
459 axis 1 is constrained by sample SWLI scores which exert the primary control on assemblage
460 distributions (Fig. 3). The effects of inconsistently sampled gradients between the 14 sites can
461 be seen in the ordination plots. Certain sites, such as those from Delaware and Belgium, make
462 up disproportionate percentages of certain biozones, such as zones 1 and 5 respectively,
463 which raises the potential issue of spatial autocorrelation in transfer function development
464 (Telford and Birks, 2005, 2011). Despite this, the different biozones and taxa remain clearly
465 distributed along CCA axis 1 with elevation (as a surrogate for tidal inundation) explaining a
466 significant proportion (30 %) of the variance, which is comparable to single-site training sets
467 for which elevation typically explains 20 to 30 % of total species variance (e.g., Charman et
468 al., 2002; Barnett et al., 2016). The distribution of samples and taxa along the second axis
469 (CA axis 1) is controlled by unmeasured variables and there is the suggestion of an arch-
470 effect (Gauch et al., 1977) deriving from this constrained ordination. We apply a simple
471 unconstrained non-metric multidimensional scaling (NMDS; Minchin, 1987) ordination to
472 determine whether the distribution seen in the CCA analyses may contain such an effect (Fig.
473 3). The lack of an arch in the NMDS ordination space suggests that the second axes in the
474 canonical ordination (and possibly subsequent axes) is not fully independent from the
475 canonical axis (elevation). This may not be surprising as additional environmental variables
476 (e.g., pH, salinity, surface wetness, nutrient and dissolved oxygen content, and vegetation
477 cover) are likely to demonstrate proportional relationships with our surrogate variable of
478 elevation.

479

480 *5.4 Transfer functions*

481 Using Detrended Canonical Correspondence Analysis (DCCA; ter Braak and Prentice, 1988),
482 it was possible to estimate overall species response to changes in elevation (Šmilauer and
483 Lepš, 2014). A DCCA score for the North Atlantic training set (3.5 standard deviations units)
484 demonstrates that taxa collectively respond unimodally along the environmental gradient
485 (Birks, 1995). With this in mind, a suite of suitable regression models was applied to develop
486 transfer functions and test the predictive capabilities of the regional training set (Juggins,
487 2015). Weighted-averaging partial least squares (WAPLS; ter Braak and Juggins 1993)
488 models with between 1 and 5 components were selected as WAPLS regression displays
489 greater performance over alternatives when used alongside training sets with long
490 compositional gradients (ter Braak et al., 1993). As WAPLS with 1 component reduces to a
491 weighted-averaging (WA; ter Braak and Looman, 1986) model with inverse deshrinking
492 (Juggins and Birks, 2012), and combined with the improved performance of WAPLS (ter
493 Braak and Juggins, 1993; ter Braak et al., 1986), it was not necessary to include additional
494 WA models in the analyses. Each WAPLS model was run using bootstrapping (Stine, 1990)
495 and leave-one-site-out (LOSO; Manly, 1997) cross-validation techniques and then re-run
496 following a square root data transformation of the species data to expand the influence of less
497 abundant taxa on transfer function performance. Cross-validated root mean squared errors of
498 prediction (RMSEP) and coefficient of determination (r^2) are used as measures of model
499 performance whilst model residuals are critically appraised using average and maximum
500 biases (Juggins and Birks, 2012). The significance of the cross-validated models were
501 assessed using randomisation t-tests (van der Voet, 1994) and illustrated using p -values.

502 Model results (Table 2) show that, due to the negative percentage change in RMSEP scores
503 from incorporating additional components, a simple weighted averaging regression model
504 may be most suitable for the training set. Likewise, the p -value results from the significance
505 testing imply that only WAPLS(1), and occasionally WAPLS(2), models are suitable for

506 predicting marsh-surface elevations. Correlation between observed and predicted SWLI
507 values are highest in the transfer function with bootstrap cross-validation following a square
508 root transformation of the data suggesting that some low abundance taxa are useful
509 indicators of changing marsh elevation. The increased performance when using bootstrapping
510 versus LOSO cross-validation further implies the presence of auto-correlation in the training
511 set. This suggests that transfer functions based on this training set may be suitable for sites
512 with accompanying surface data, yet may lack precision when used to predict marsh-surface
513 elevations at new study sites where surface assemblages remain unexplored.

514 In an attempt to improve model performance further, outlier removal was carried out on the
515 training set following Edwards et al. (2004). Samples demonstrating residual scores greater
516 than ± 1 standard deviation of the environmental gradient (in SWLI units) were identified and
517 removed from the dataset. Outliers typically originated from the gradient ends where the
518 transfer function models under-predicted (at high elevations) or over-predicted (at low
519 elevations) SWLI values (Fig. 4). New regression models were run with the truncated
520 training set based on the best performing models from the original runs (i.e., WAPLS with
521 bootstrapping cross-validation and square root data transformation). All measures of transfer
522 function performance are improved upon by using outlier removal and there is justification
523 for using WAPLS models with 1 component (Fig. 4) for predicting marsh-surface elevation
524 from assemblage data (Table 2).

525

526 *5.5 Applying the North Atlantic Testate amoebae Transfer function (NATT)*

527 The potential for application of a basin-wide training set to reconstruct local marsh surface
528 elevation changes was explored by Charman et al. (2010) by using a training set from the UK
529 to reconstruct former sea-level height on the east coast of North America. Here, we explore

530 this prospect further by using the North Atlantic testate amoebae transfer function (hereafter
531 referred to as *NATT*) to produce two RSL reconstructions using fossil testate amoebae from
532 either side of the Atlantic basin. The purpose of this exercise was to determine if *NATT* was
533 capable of estimating local RSL changes from recently buried fossil testate amoebae
534 assemblages. The accuracy of the two reconstructions was assessed using nearby tide-gauge
535 data which extend back to the mid-1900s.

536 Fossil testate amoebae counts used in the reconstructions derive from salt-marsh sediment
537 cores taken in Svinøyosen, Norway (Barnett et al., 2015) and the Magdalen Islands, Canada
538 (Barnett et al. *in review*). These two sites offer the longest continuous sequences of published
539 fossil salt-marsh testate amoebae for which accompanying surface data are available.

540 Taxonomies used in the original studies were standardised to accord with the salt-marsh
541 based taxonomy developed in this study. A WAPLS transfer function with 1 component
542 following a square root transformation of the species data and outlier removal (see section
543 5.4) was used to establish palaeommarsh-surface elevation predictions in SWLI units for the
544 fossil assemblages (Table 3). Indicative ranges relative to local MWL were calculated based
545 on SWLI values (equation 2) and converted to estimations of former sea level by subtracting
546 the indicative range from the elevation of the fossil assemblage relative to MWL (Gehrels,
547 1999). Chronological constraints for the sediment cores were available in the form of ^{210}Pb
548 derived age-depth profiles from the original studies that allowed the reconstructions to extend
549 back *c.* 100 years, which coincided with available tide-gauge data (Table 3).

550 The Vesterålen Islands in northwest Norway currently experience gradual RSL fall (Fig. 5),
551 largely as a result of residual land uplift since deglaciation of the Fennoscandian Ice Sheet
552 (Marthinussen, 1960, 1962). The tide-gauge data from Kabelvåg records this trend,
553 displaying an average linear rate of -1.1 mm yr^{-1} for the period 1948-2015. Our testate
554 amoebae-based RSL reconstruction conforms to the available tide-gauge record and the sea-

555 level envelope displayed by the proxy data captures a similar trend to the instrumental data
556 (Fig. 5a). Once converted from SWLI units, the transfer function vertical error terms at the
557 Vesterålen Islands are ± 0.26 m (Table 3). This equates to 10 % of the spring tidal range at
558 the salt-marsh site, which is 2.6 m (Barnett et al., 2013) and encompasses the inter-annual
559 RSL periodicity seen in the tide-gauge record at Kabelvåg (Fig. 5a).

560 In contrast to northwest Norway, the Magdalen Islands in eastern Canada experience RSL
561 rise as a result of land subsidence (Peltier et al., 2015) and different oceanographic processes
562 which contribute to rising local sea levels (Dubois and Grenier, 1993). Tide-gauge data from
563 Cap-aux-Meules are only available for intermittent periods over the past few decades but
564 show approximately 0.2 m of RSL rise since the 1960s (Fig. 5b). The testate amoebae-based
565 reconstruction captures this rising trend and demonstrates the value of this method in
566 providing sea-level constraints where instrumental data are not available. The proxy data
567 display acceleration in the rate of RSL rise during the mid-20th century but direct
568 comparisons with the tide-gauge record are restricted by the record length. A wider look at
569 tide gauge RSL trends along the east coast of North America reveals that many locations
570 experienced a peak in rising RSL trends during the 1930s and 1940s, including the more
571 northerly gauges at Boston, Halifax, Nova Scotia, and Charlottetown, Prince Edward Island
572 (Boon, 2012; Holgate et al., 2013; PSMSL, 2016). The local reconstruction from the
573 Magdalen Islands may reflect these regional sea-level trends suggesting that *NATT* is capable
574 of accurately predicting local RSL changes from fossil testate amoebae preserved in salt-
575 marsh sediments.

576 The transfer function error terms at the Magdalen Islands are ± 0.10 m (Table 3) following
577 conversion from SWLI units, which represents 11 % of the spring tidal range (0.9 m) at the
578 reconstruction site (Barnett et al., 2016). As SWLI is a function of tidal range, sites with a
579 larger tidal range are assigned greater vertical uncertainty terms following application of

580 *NATT* to a local reconstruction. This suggests that the universal transfer function may be
581 valid at a range of sites with varying tidal range sizes as it may help prevent overly optimistic
582 prediction errors. The two reconstructions shown here suggest that, over the recent past
583 where comparable tide-gauge data are available for validation, a basin-wide training set of
584 salt-marsh testate amoebae may be used to reconstruct local RSL changes from fossil
585 assemblages using a universally applicable transfer function.

586

587

588 **6. Discussion**

589 Our review of testate amoebae occurrences in salt marshes around the North Atlantic shows
590 that these organisms are excellent indicators of sea level. When applied to short cores, the
591 transfer functions derived from the modern distribution of testate amoebae produce sea-level
592 reconstructions that are in good agreement with tide-gauge records. The two example
593 reconstructions contain prediction uncertainties of ± 0.10 and 0.26 m. These RMSEP values
594 are comparable to transfer function uncertainties derived from foraminifera and diatom
595 training sets from across the globe (Table 3 in Barlow et al., 2013). The most precise
596 regression models available using these other proxies have RMSEP values of ± 0.04 to 0.06
597 m (Gehrels et al., 2005; Southall et al., 2006; Kemp et al., 2009), which are similar to best
598 performing models using local testate amoebae data (± 0.07 m; Table 1). Although
599 reconstruction uncertainties for the Magdalen Islands and Norway using *NATT* (± 0.10 and
600 0.26 m) are greater than locally derived RMSEP values (± 0.08 and 0.09 m; Table 1), the
601 regional training set encompasses greater ecological diversity across a longer gradient length.
602 This contributes to a more robust transfer function as it is more likely that fossil assemblages
603 are represented by modern counterparts (e.g., Horton and Edwards, 2005; Watcham et al.,

604 2013). RMSEP values from locally derived training sets commonly demonstrate decimetre
605 uncertainty precisions (Table 1). Local transfer functions from sites that experience macro-
606 tidal conditions tend to have greater uncertainty ranges. In the case of reconstructing former
607 sea level at the Magdalen Islands (a micro-tidal region), decimetre level precision remains
608 achievable when using the basin wide training set of *NATT*.

609 As *NATT* is a regional transfer function based on multiple sites it avoids over-optimistic
610 RMSEP values arising from possible autocorrelation within training sets from individual
611 sites. The suite of transfer functions that use LOSO cross-validation (Table 2) suggests that
612 the training set suffers from some spatial autocorrelation as the transfer functions demonstrate
613 weaker performance when used to predict surface elevations at a given site after local data
614 are omitted from the training set (Telford and Birks, 2005). However, over-optimistic
615 performance values, which are often present in auto-correlated datasets (Telford and Birks,
616 2009), are avoided due to the more robust prediction uncertainties that *NATT* offers.

617 An additional uncertainty which is introduced by building a regional training set of surface
618 data is the imposed presence of uneven sampling along the environmental gradient (Telford
619 and Birks, 2011). Local training sets are sampled along surface transects at regular vertical
620 intervals which ensures even sampling of the local environmental gradient (elevation).
621 However, due to a lack of standardised practice, and many surface samples being collected
622 originally for studies on foraminifera (e.g., Gehrels et al., 2001, 2006), there is significant
623 disparity in the concentration and range of samples at different elevations when the local
624 datasets are combined (Fig. 1). A segment-wise RMSEP procedure (Telford and Birks, 2011)
625 was used to investigate the effect of an unevenly sampled gradient within *NATT*. The full
626 training set was divided into bins of 25.5 SWLI units which represented the standardised
627 sampled range (207 SWLI) divided by the mean standardised sampling resolution (8.1 SWLI)

628 of all the sites, and RMSEP values calculated for each segment using the best performing
629 transfer function (Fig. 6).

630 The concentration of samples between 0 and 100 SWLI represents the intertidal proportion of
631 the training set (Fig. 6). Above HAT (100 SWLI) the number of samples per bin decreases as
632 different local datasets terminate near or slightly above this tidal level. Transfer function
633 performance remains robust (i.e., comparable or lower RMSEP values to overall
634 performance) for the bins that represent intertidal and transitional environments. Bins beyond
635 150 SWLI all contain segment-wise RMSEP values that exceed overall model uncertainty.
636 This suggests (rather unsurprisingly) that supratidal testate amoebae assemblages above 150
637 SWLI are poor at predicting marsh surface elevations, because of the diminished influence of
638 tidal inundation relative to alternative environmental controls. Despite the unevenly sampled
639 gradient (i.e., variable sample numbers per bin), transfer function performance for intertidal
640 and transitional assemblages appears reliable. It is likely that vertical zonation of testate
641 amoebae remains apparent beyond HAT as some degree of marine influence remains.
642 However, if fossil assemblages indicate an elevation that exceeds 150 SWLI, and the
643 provenance of the assemblages cannot be clearly ascertained, then they should be used as
644 limiting sea-level index points in sea-level reconstructions (Shennan et al., 2015) rather than
645 being assigned a precise (but possibly inaccurate) indicative meaning.

646 As transfer function uncertainties approach the sampling resolution of this reconstruction
647 method (classically *c.* 0.05 m), improvements in precision become hard to find. One
648 technique applied recently has been to use stable carbon isotope geochemistry (Lamb et al.,
649 2006; Khan et al., 2015) to identify whether fossil salt-marsh samples originate from above or
650 below the level of mean higher high water (Kemp et al., 2010). These additional data can
651 then be used to ‘trim’ sea-level index points which have vertical uncertainties based on
652 alternative proxies, such as foraminifera (Kemp et al., 2013), in order to shrink reconstruction

653 uncertainty boxes. The development of multi-proxy sea level reconstructions from salt marsh
654 sediments has been investigated in the past by pairing diatom and foraminifera data (Kemp et
655 al., 2009), foraminifera and testate amoebae data (Barnett et al., 2016), and even data of all
656 three proxies (Gehrels et al., 2001), and comparing transfer function performance against that
657 of single-proxy models. In general, multi-proxy transfer functions usually improve on the
658 standalone performance of the weaker proxy, but fail to increase precision in comparison to
659 the stronger proxy (Barnett et al., 2016). Different proxy datasets might be conjoined to
660 improve transfer function robustness, or additional proxies may be developed into
661 independent reconstructions that can assist in validation, both of which have positive
662 contributions to sea-level studies. The approach of trimming sea-level index point vertical
663 uncertainties by developing independent reconstructions from multiple proxies and limiting
664 the size of index points to common indicative ranges is yet to be tested empirically and is not
665 widely encouraged. Recent advancements in modelling sea-level envelopes which
666 incorporate full horizontal (temporal) and vertical (spatial) uncertainties (Cahill et al., 2015a;
667 Parnell and Gehrels, 2015; Lawrence et al., 2016) likely represent a more holistic and robust
668 approach. The continued development of transfer function models that are capable of
669 incorporating multiple proxies with differing uncertainties (Cahill et al., 2015b) are also
670 likely to aid reconstruction attempts in the future.

671 To date, intertidal testate amoebae have been used to identify the isolation of coastal marine
672 basins from oceans (Patterson et al., 1985; Lloyd, 2000; Roe et al., 2002) and define precise
673 estimations of past sea level in regions that have experienced RSL fall during the late
674 Holocene (Barnett et al., 2015). They are also proven precise sea-level indicators in regions
675 experiencing RSL rise (e.g., Charman et al., 2010), and it is here where they might be most
676 valuably applied in sea-level studies. Surface datasets of intertidal testate amoebae show
677 narrow vertical zonation across marsh environments that encompass MHWs tide levels,

678 HAT, and the supratidal zone (Gehrels et al., 2006; Ooms et al., 2012; Barnett et al., 2016;
679 this study). The indicative ranges of these assemblages are consistently narrow and can be
680 used to predict salt-marsh surface elevations with relatively high precision. In addition,
681 assemblages originating from near, or slightly above, HAT can be readily identified by the
682 high abundance of *Trinema* spp. and occasional presence of e.g., *Heleopera* spp. and *Nebela*
683 spp. Testate amoebae from fossil sediments that record transitions from coastal terrestrial to
684 marine intertidal environments can, therefore, provide a unique opportunity to investigate
685 coastline submergence rates related to recent rapid RSL rise (e.g., Kopp et al., 2016).

686

687

688 **7. Conclusions**

689 This study has provided a summary of the use of testate amoebae in sea-level research since
690 the late 1970s. Having been originally identified in studies targeting foraminifera (e.g., Scott
691 et al., 1977), they have since been developed into a unique and valuable proxy of their own.
692 Their early use as precise sea-level indicators (Charman et al., 1998, 2002) demonstrated
693 capabilities equal to, or better than, alternative proxies such as foraminifera or diatoms
694 (Gehrels et al., 2001). More recently, developments in applying salt-marsh testate amoebae in
695 sea-level reconstructions supported the notion that surface assemblages were cosmopolitan
696 across wide geographical areas and that training sets from the UK were applicable to
697 reconstructions from North America (Charman et al., 2010).

698 To explore this notion further, this study has collated the available surface datasets of
699 intertidal salt-marsh testate amoebae from the North Atlantic (Supplementary Material I) and
700 harmonised them under a single unified taxonomy. This taxonomy comprises 57 different
701 taxa or type groups (Supplementary Material II) and accounts for each specimen identified in

702 the original datasets and used in this study. The further development of type groups (c.f.,
703 Charman et al., 2000) has been used to reduce ambiguity between studies by grouping
704 morphologically similar taxa that occupy similar ecological niches. The taxonomy is valuable
705 for future studies on salt-marsh testate amoebae and is able to evolve in order to
706 accommodate additional intertidal taxa that are likely to arise as research progresses beyond
707 the North Atlantic.

708 The training set, comprising of 275 samples from 14 different sites, encompasses an
709 environmental gradient extending from below MHWS tide level and up into the supratidal
710 zone. The assemblages were portioned into five broad groups, which zoned in relation to
711 elevation, using unconstrained cluster analysis. Three biozone groups represented intertidal
712 environments between the lowest extent of testate amoebae and HAT, a single biozone
713 represented a transitional group occurring across the boundary of HAT and the remaining
714 biozone represented a predominantly supratidal group.

715 Following standardisation of the datasets to account for differences in the tidal range between
716 sites (expressed as a standardised water level index - SWLI), a comparison of several transfer
717 functions revealed that a WAPLS regression model with 1 or 2 components following square
718 root species data transformation and outlier removal was suitable for predicting marsh-
719 surface elevations using the composite training set. These transfer functions had RMSEP
720 values of ± 27 SWLI units, which represented 13 % of the sampled environmental gradient
721 (207 SWLI units), a precision comparable with transfer function performances based on local
722 training sets (Table 1). When used to reconstruct recent sea-level histories from Norway and
723 Quebec, Canada, the precision of the transfer function yielded site specific RMSEP values of
724 ± 0.26 m and ± 0.10 m respectively, which equated to 10 % and 11 % of the tidal ranges at
725 each site, again comparable to precisions based on alternative salt-marsh proxies and more
726 localised training sets.

727 The North Atlantic testate amoebae-based transfer function developed in this study provides
728 evidence for the cosmopolitan nature of salt-marsh testate amoebae and confirms that the
729 relationship between sea level and assemblage composition is similar across the whole of the
730 region. Such a wide-scale regional training set captures greater ecological diversity in
731 comparison to local datasets. This contributes to more robust reconstructions when used to
732 estimate former sea-level positions. Testate amoebae can also be valuable in sea-level studies
733 when other proxies are missing. In the case of foraminifera, testate amoebae can be used to
734 extend the sampled environmental gradient beyond the highest limit of foraminifera
735 occurrence and potentially into the supratidal realm. This expands the elevational range of
736 environments that a transfer function can be used to reconstruct, allowing the reconstruction
737 of larger amplitude sea-level changes or possibly allowing the extension of reconstructions
738 further back in time. To date, the exploratory use of testate amoebae as precise sea-level
739 indicators has been predominantly focussed in the North Atlantic. There is significant scope
740 for the expansion and development of this proxy, which may represent one of the most
741 precise indicators available for reconstructing pre-industrial sea-level changes.

742

743

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754

755

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- 1180
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1182

1183 **Table and Figure Captions**

1184

1185 **Table 1**

1186 Published transfer function performance criteria of salt-marsh testate amoebae based training
1187 sets from the North Atlantic. Model prediction uncertainties (RMSEP values) are also given
1188 as a percentage of local tidal range size and sampled environmental gradient.

1189

1190 **Table 2**

1191 Transfer function performance statistics for the regional North Atlantic testate amoebae based
1192 training set. Weighted averaging partial least squares (WAPLS) models were used with
1193 between 1 and 5 components. Both bootstrapping and leave-one-site-out cross validation
1194 methods were used on the full dataset following a square root transformation of the species
1195 data. The training set was also subjected to outlier removal before re-running of the best
1196 performing transfer function models (bootstrapping with square root species data
1197 transformation). The model used to apply the North Atlantic testate amoebae training set is
1198 shown in bold print.

1199

1200 **Table 3**

1201 Sea-level reconstruction criteria for sediment cores from the Vesterålen Islands, Norway
1202 (Barnett et al., 2015), and the Magdalen Islands, Canada (Barnett et al., in prep). Given are
1203 palaeo-marsh surface elevation predictions from the regional North Atlantic transfer function
1204 (*'NATT'*) in SWLI units and local elevations following a conversion to account for

1205 differences in tidal range. Also given are corresponding chronological data based on ^{210}Pb
1206 based age-depth profiles from the original studies.

1207

1208 **Figure 1**

1209 Map showing locations of the original datasets used in this study (a). Also shown are the
1210 distributions of surface samples taken from each location in relation to standardised tidal
1211 regimes (b). The purple circle indicates the lowest extent of salt-marsh testate amoebae, the
1212 red circle at 100 SWLI units represents the level of highest astronomical tides and the blue
1213 projections mark elevations below mean high water tides for each location.

1214

1215 **Figure 2**

1216 Composite assemblage data for the North Atlantic training set of salt-marsh testate amoebae.
1217 SWLI units represent standardised sample elevations where 0 = the lowest extent of testate
1218 amoebae and 100 = highest astronomical tide level. Also shown are biozone clusters which
1219 result from unconstrained cluster analysis of the entire dataset. Taxa abbreviations correspond
1220 with taxonomic descriptions provided in Appendix I.

1221

1222 **Figure 3**

1223 Canonical correspondence analysis of the North Atlantic testate amoebae based training set
1224 showing individual sample scores by location (top left), sample scores grouped according to
1225 unconstrained cluster analysis (bottom left) and individual species scores (top right). Also
1226 shown is the unconstrained NMDS ordination of the dataset (bottom right) which
1227 demonstrates the potential arch effect displayed by the CCA ordinations.

1228

1229 **Figure 4**

1230 Model predicted versus measured SWLI elevation values and model residuals following
1231 weighted averaging partial least squares (WAPLS) regression with 1 component using
1232 bootstrapping cross-validation following square root transformation of the species data and
1233 outlier removal. A loess smoothing is shown in red (top plot) for comparison against the
1234 identity line (1:1) and samples omitted following outlier removal are highlighted in the
1235 bottom plot.

1236

1237 **Figure 5**

1238 Sea-level reconstructions based on criteria given in Table 3 for two locations using the
1239 regional North Atlantic testate amoebae based transfer function (*'NATT'*). Grey boxes bound
1240 vertical uncertainties based on model RMSEP values and horizontal chronological
1241 uncertainties (see text and Table 3 for details). Also shown are available tide-gauge data from
1242 nearby stations in blue.

1243

1244 **Figure 6**

1245 Segment-wise cross-validation of the best performing transfer function (WAPLS1 with
1246 bootstrapping cross-validation following square root species data transformation and outlier
1247 removal) showing RMSEP values for consecutive 25.5 SWLI unit bins (green). Also shown
1248 is a sample frequency distribution based on SWLI scores (blue). The overall RMSEP value
1249 for the transfer function is given in red.

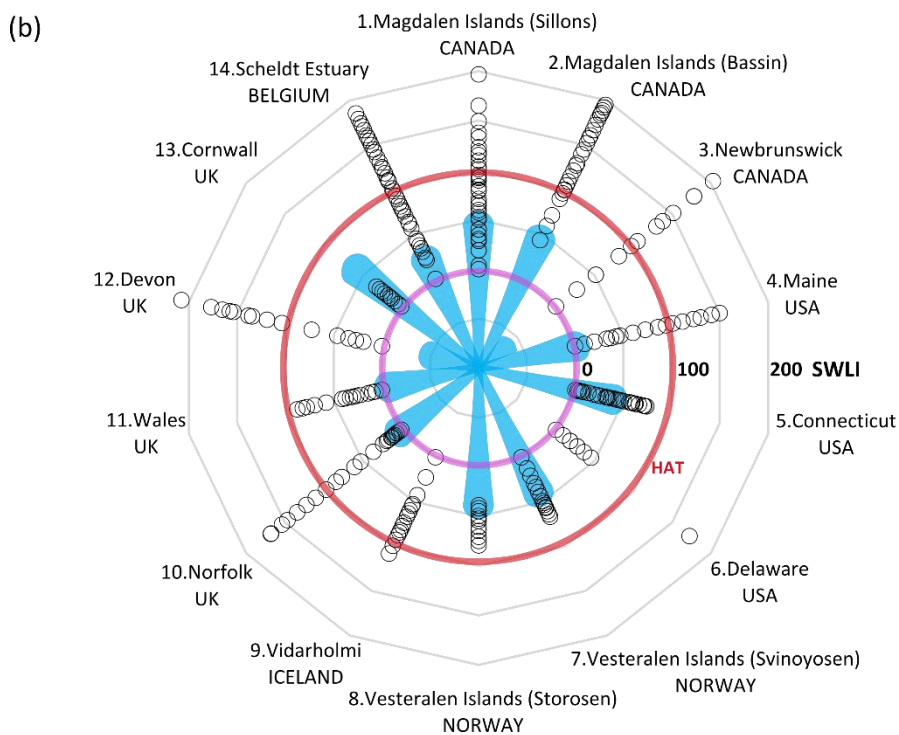
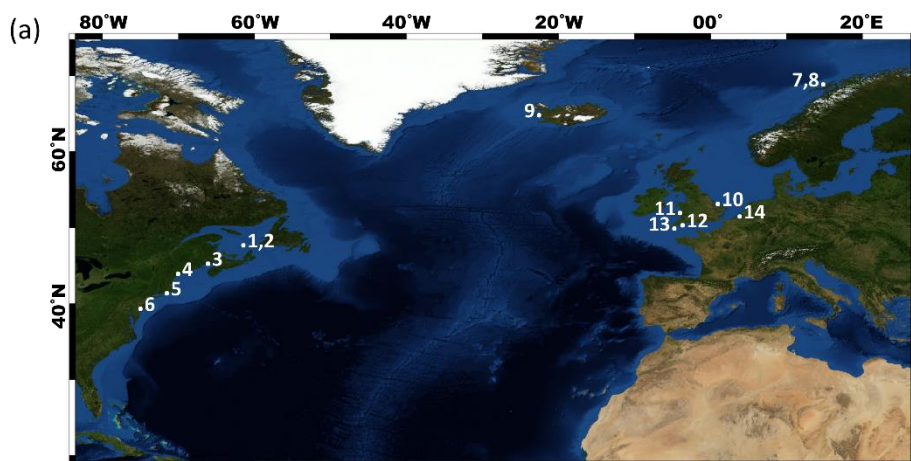
1250 **Tables and Figures**1251 **Table 1**

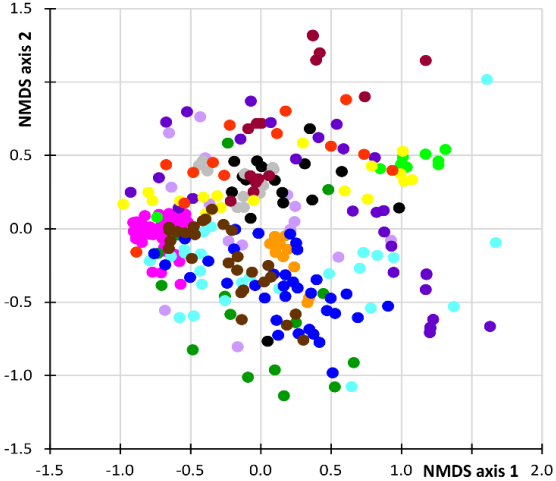
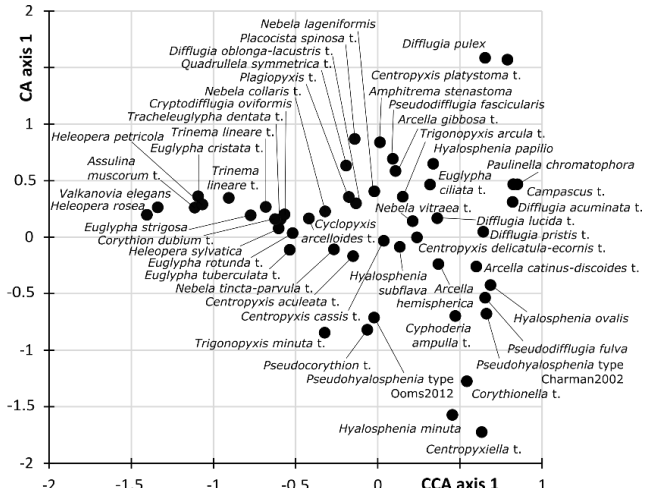
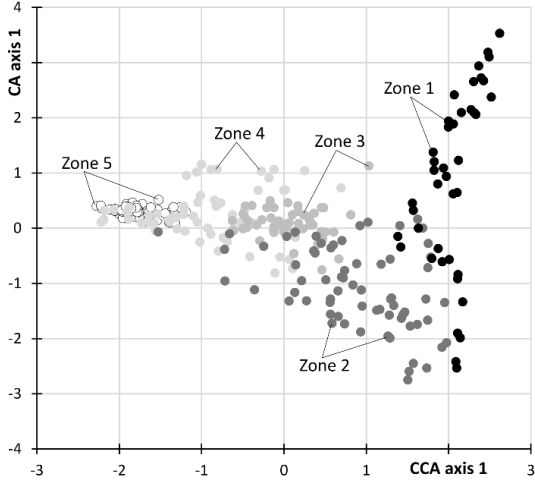
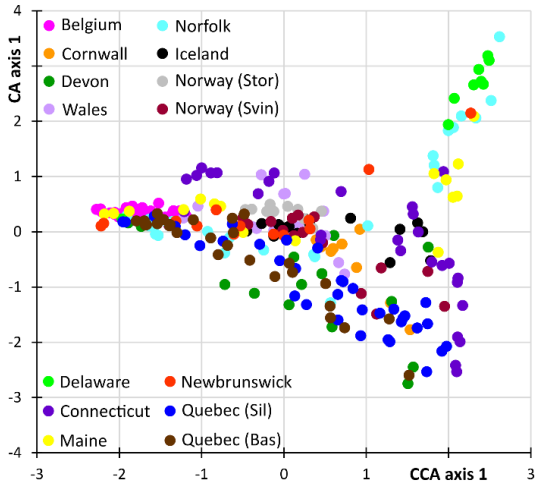
Training set	Reference	Spring tidal range (m)	Number of samples	Model type	Reported RMSEP (m)	Elevation range of samples (m)	RMSEP/tidal range (%)	RMSEP/elevation range of samples (%)
UK (regional)	Gehrels et al. (2001)	-	52	WA	0.08 (<i>norm</i>)	0.35 (<i>norm</i>)	-	15.2
Brancaster, UK	"	6.0	-	"	0.25 (<i>local</i>)	-	4.2	-
Erme, UK	"	4.7	-	"	0.17 (<i>local</i>)	-	3.6	-
Taf, UK	"	6.6	-	"	0.28 (<i>local</i>)	-	4.2	-
New Brunswick, Canada	Gehrels et al. (2006)	5.8	12	WA	0.08	0.75	1.3	10.7
Maine, USA	Gehrels et al. (2006)	2.6	17	WA	0.07	1.05	2.7	6.7
Delaware, USA	Gehrels et al. (2006)	1.8	9	WA	0.07	0.14	3.9	50
Scheldt estuary, Belgium	Ooms et al. (2012)	5.5	37	WAPLS	0.24	1.88	4.4	12.8
Vesterålen Islands, Norway	Barnett et al. (2013)	2.6	29	WA	0.09	0.76	3.5	11.8
Magdalen Islands, Canada	Barnett et al. (2016)	0.6	62	WA	0.08	0.69	13.3	11.6

1252

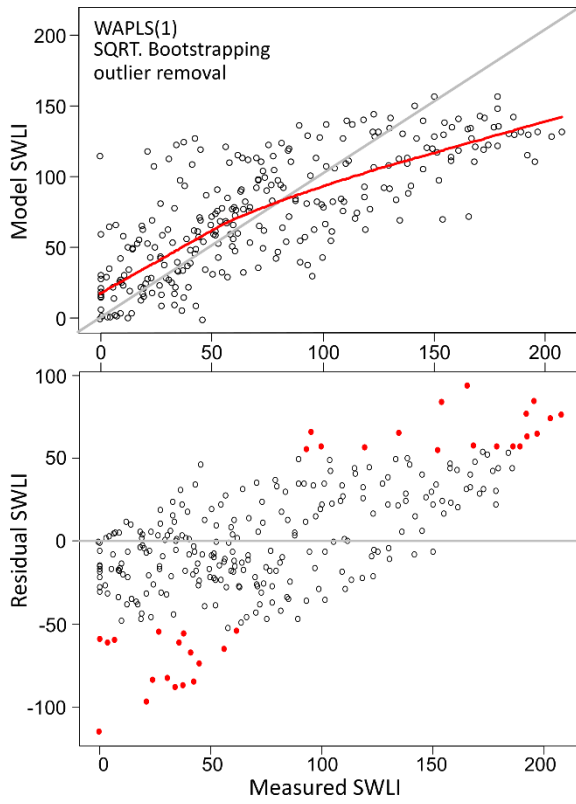
	WAPLS(1)	WAPLS(2)	WAPLS(3)	WAPLS(4)	WAPLS(5)
Bootstrapping					
RMSEP	37.73	37.75	38.64	39.72	40.59
% change	-	-0.05	-2.36	-2.80	-2.19
r ²	0.52	0.55	0.55	0.54	0.54
Ave.Bias	-0.32	-0.34	-0.92	-1.06	-1.26
Max.Bias	75.76	72.55	70.62	67.65	65.50
p-value	0.001	0.116	0.561	0.839	0.843
LOSO					
RMSEP	43.39	49.70	51.69	52.79	53.16
% change	-	-14.54	-4.00	-2.13	-0.70
r ²	0.38	0.30	0.29	0.30	0.30
Ave.Bias	-3.39	-6.65	-9.52	-10.45	-10.85
Max.Bias	83.40	84.90	84.44	81.14	78.81
p-value	0.001	1.000	1.000	0.994	0.808
SQRT.Bootstrapping					
RMSEP	36.72	35.99	36.61	37.74	38.73
% change	-	1.99	-1.72	-3.09	-2.62
r ²	0.55	0.59	0.59	0.59	0.58
Ave.Bias	-0.60	-0.12	-0.51	-0.36	-0.66
Max.Bias	73.40	62.29	56.26	54.52	53.59
p-value	0.001	0.057	0.534	0.869	0.868
SQRT.LOSO					
RMSEP	42.33	48.55	51.95	55.18	58.01
% change	-	-14.69	-7.00	-6.22	-5.13
r ²	0.41	0.35	0.34	0.32	0.30
Ave.Bias	-3.73	-7.51	-10.12	-10.99	-12.12
Max.Bias	82.41	77.63	71.23	69.95	69.07
p-value	0.001	1.000	1.000	1.000	1.000
SQRT.Bootstrapping with outlier removal (Edwards et al., 2004)					
RMSEP	27.26	26.52	26.94	28.01	28.92
% change	-	2.71	-1.58	-3.97	-3.25
r ²	0.7	0.73	0.73	0.72	0.71
Ave.Bias	-0.95	-0.42	-0.64	-0.49	-0.67
Max.Bias	39.04	38.15	41.74	44.59	43.07
p-value	0.001	0.045	0.514	0.977	0.981

Code	Depth in core (m)	<i>h</i> -Elev. to msl (m)	Indicative elev. (SWLI)	RMSEP (SWLI)	RMSEP (local m)	<i>i</i> - Indicative elev. to msl (m)	Sea level (m) ($s = h - i$)	²¹⁰ Pb year (CRS model)	²¹⁰ Pb RMSE (\pm years)
Vest 1	0.003	1.468	72.786	27.181	0.261	1.689	0.261	2007.7	1.0
Vest 2	0.008	1.463	63.912	27.156	0.261	1.604	0.261	2004.2	1.0
Vest 3	0.018	1.453	59.672	27.150	0.261	1.563	0.261	1997.6	1.0
Vest 4	0.028	1.443	53.057	27.190	0.261	1.499	0.261	1989.7	2.0
Vest 5	0.038	1.433	72.235	27.219	0.261	1.683	0.261	1980.7	3.1
Vest 6	0.048	1.423	36.699	27.442	0.263	1.342	0.263	1972.4	4.3
Vest 7	0.058	1.413	62.468	27.203	0.261	1.590	0.261	1961.2	6.3
Vest 8	0.078	1.393	35.637	27.374	0.263	1.332	0.263	1927.9	18.0
Mag 1	0.005	0.225	43.767	27.150	0.096	0.272	0.096	2004.5	1.3
Mag 2	0.015	0.215	45.087	27.354	0.096	0.277	0.096	1995.3	1.8
Mag 3	0.025	0.205	57.714	27.242	0.096	0.321	0.096	1986.6	2.1
Mag 4	0.035	0.195	77.284	27.245	0.096	0.390	0.096	1977.7	2.2
Mag 5	0.045	0.185	79.089	27.140	0.096	0.396	0.096	1968.2	2.5
Mag 6	0.055	0.175	79.541	27.139	0.096	0.398	0.096	1960.5	2.7
Mag 7	0.065	0.165	79.846	27.158	0.096	0.399	0.096	1948.9	3.2
Mag 8	0.075	0.155	77.067	27.265	0.096	0.389	0.096	1931.9	4.2
Mag 9	0.085	0.145	74.505	27.313	0.096	0.380	0.096	1910.1	6.6





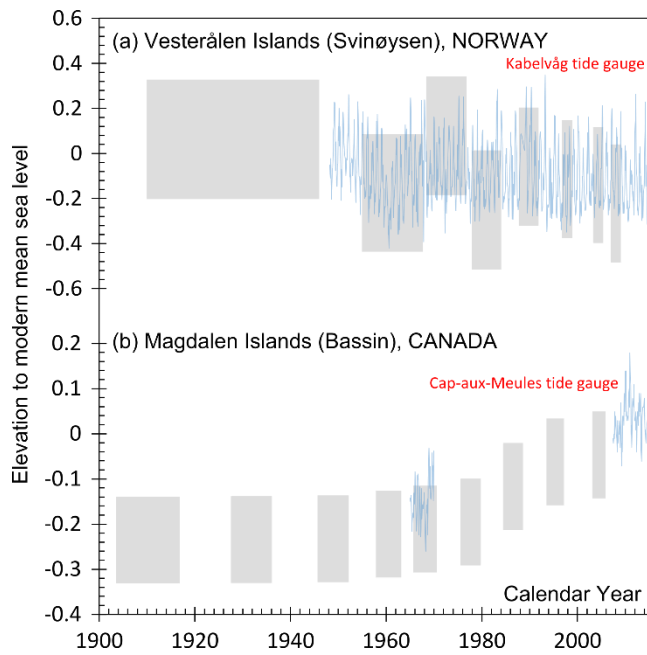
1266 **Figure 4**



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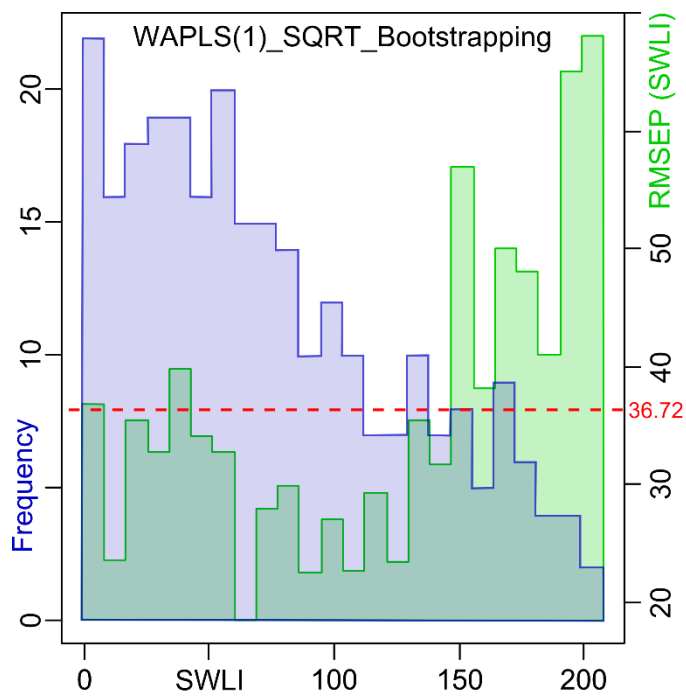
1269 **Figure 5**



1270

1271

1272 **Figure 6**



1273