

1 **TITLE:**

2 **On the diversity and distribution of a data deficient habitat in a poorly mapped region:**  
3 **the case of *Sabellaria alveolata* L. in Ireland**

4

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39

#### 40 **Highlights**

41 • Improving the knowledge base of data deficient species will enable greater protection.

42 • We identified knowledge gaps for the distribution a data deficient species in a poorly  
43 mapped region.

44 • *S. alveolata* reefs supported diverse epibiotic algal assemblages.

45 • Retrograding (declining) reefs supported greater infaunal diversity than prograding  
46 (growing) reefs.

47 • Such research should be done for other data deficient species and habitats.

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49

50

51 **Abstract**

52 Data that can be used to monitor biodiversity through time are essential for conservation and  
53 management. The reef-forming worm, *Sabellaria alveolata* (L. 1767) is currently classed as  
54 ‘Data deficient’ due to an imbalance in the spread of data on its distribution. Little is known  
55 about the distribution of this species around Ireland. Using data archaeology, we collated past  
56 and present distribution records and discovered that *S. alveolata* has a discontinuous  
57 distribution with large gaps in distribution. Many regions lack data and should be targeted for  
58 sampling. Biodiversity surveys revealed that *S. alveolata* supported diverse epibiotic algal  
59 communities. Retrograding (declining) reefs supported greater infaunal diversity than  
60 prograding (growing) reefs or sand, suggesting that *S. alveolata* is a dynamic ecosystem  
61 engineer that has a lasting legacy effect. Similar research should be carried out for other data  
62 deficient species, habitats and regions. Such data are invaluable resources for management  
63 and conservation.

64

65 **Keywords**

66 Baseline data, Biodiversity, Biogenic habitat, Marine Protected Area, Reef, Sustained  
67 observations

68

69 **1. INTRODUCTION:**

70 Biodiversity loss in the face of global environmental change is one of the greatest challenges  
71 of our time. Increasingly, extinctions are being documented coupled with predictions of the  
72 sixth mass extinction, primarily as a result of anthropogenic activities (Wake and  
73 Vredenburg, 2008). In 2021, the Convention on Biological Diversity (CBD) will adopt a  
74 post-2020 global biodiversity framework as a stepping stone towards the 2050 Vision of  
75 ‘Living in harmony with nature’. Understanding the level of extinction risk faced by poorly-

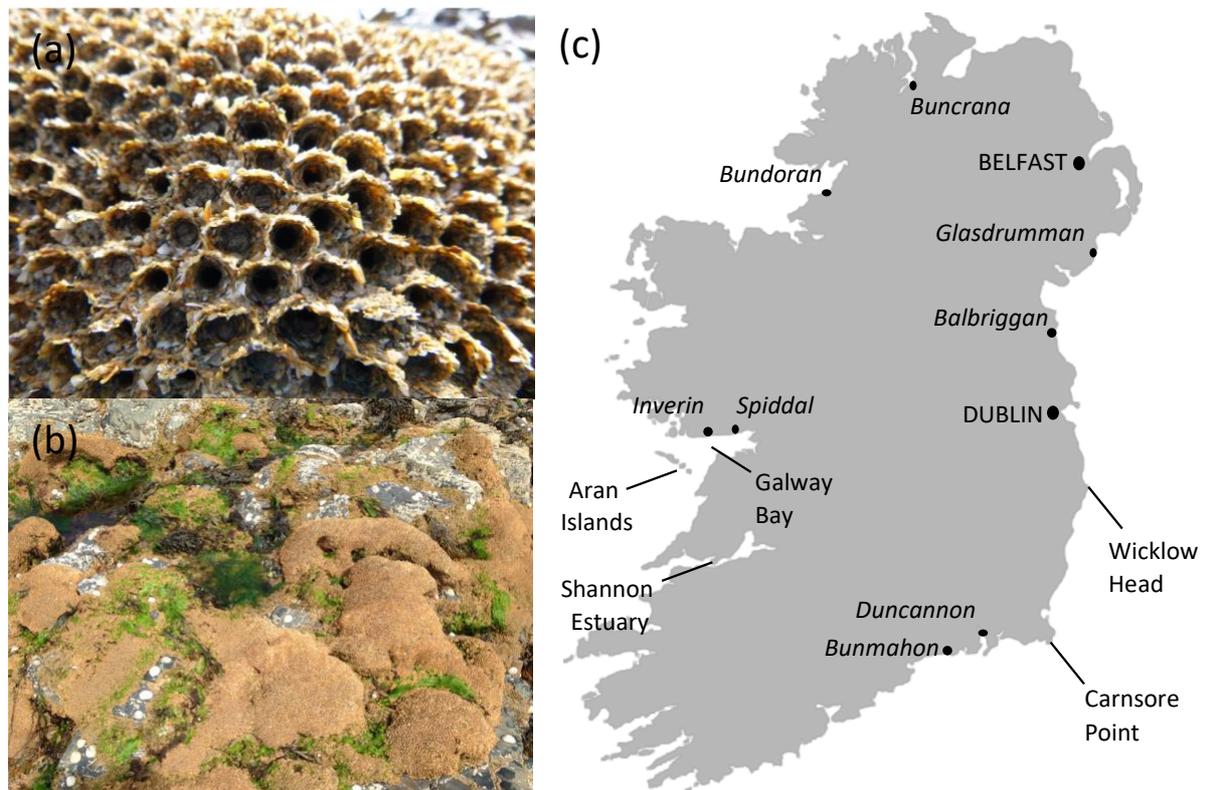
76 mapped species and why interspecific differences in risk arise remains one of the greatest  
77 challenges facing conservation biology. Assessment frameworks for threatened species are  
78 crucial to identifying risk and monitoring progress toward CBD targets (Jones et al., 2011).  
79 One of the most well-known is the International Union for Conservation of Nature (IUCN)  
80 Red List (Bland et al., 2017; IUCN, 2020). Despite recent improvement in the taxonomic  
81 coverage of the IUCN Red List (Bland et al., 2015), ~15% of the >65,000 species assessed  
82 are still classified as data deficient due to a lack of information on taxonomy, geographic  
83 distribution, population status, or threats (IUCN, 2020). A taxon in this category may be well  
84 studied, and its biology well known, but appropriate data on abundance and/or distribution  
85 may be lacking resulting in this 'data deficient' classification.

86

87 In the marine environment, biogenic reefs formed by corals, bivalves and polychaetes have  
88 long been recognised for their role in ecosystem functioning and the consequent services that  
89 they provide (Beck et al., 2011; Lemasson et al., 2017). The concept that biogenic reefs  
90 promote biodiversity is also well known (e.g. corals: Cornell and Karlson, 2000; Buhl-  
91 Mortenson et al., 2010; mussels: D'Anna et al., 1985; oysters: Lenihan, 1999). Diversity  
92 patterns can vary with reef development phases (Grigg, 1983), especially in dynamic reef  
93 building species such as sand or honeycomb worms such as *Phragmatopoma*, *Gunnarea* and  
94 *Sabellaria* (Gruet, 1986; Dubois et al., 2002; Curd et al., 2019). Temperate biogenic reefs are  
95 probably among the most threatened habitats globally (Beck et al., 2011). For example, in  
96 Europe, biogenic reefs are listed under Annex 1 of the Habitats Directive, which records the  
97 habitat types that are considered to be the most in need of conservation at a European level  
98 (Holt et al., 1998). The European Red List of Habitats (Gubbay et al., 2017) identified that  
99 60% of biogenic reef habitats in Europe were data deficient. Of those for which there were  
100 sufficient data, 50% were considered to be either critically endangered or endangered.

101

102 The honeycomb worm *Sabellaria alveolata* L. (Figure 1) is a warm-water reef-forming  
103 species that is distributed from Morocco/Western Sahara to southwest Scotland (Gruet, 1986;  
104 Curd et al., 2020; Lourenço et al., 2020). *Sabellaria alveolata* is a broadcast spawner that  
105 produces planktotrophic larvae, which settle and metamorphose preferentially on the  
106 cemented sand tubes of conspecific adults (Wilson, 1968), typically in areas where rocky  
107 reefs abut sandy beaches supplying coarse sand for tube-building (Gruet, 1984). Colonies of  
108 individuals can form biogenic structures ranging from small patches, hummocks, and veneers  
109 to the largest biogenic reefs in Europe (5.52 and 6.76 ha, Bajjouk et al., 2020) in Mont-Saint-  
110 Michel Bay, France (Holt et al., 1998; Lecornu et al., 2016). The worms, their biogenic  
111 structures (hereafter ‘reefs’) and the associated biological communities play an important role  
112 in ecosystem functioning, delivering services such as nutrient cycling, biofiltration and wave  
113 attenuation (Dubois et al., 2009; Lefebvre et al., 2009; Cugier et al., 2010; Jones et al., 2018).  
114 On rock, *S. alveolata* can be ecologically dominant, overgrowing and displacing other  
115 common rocky-reef assemblages developing at similar tidal levels such as mussels or brown  
116 macroalgae (Wilson, 1971). Reefs undergo natural cycles of growth (progradation) and  
117 decline (retrogradation) (*sensu* Curd et al., 2019 after Gruet, 1986) that are reflected in their  
118 appearance and associated biodiversity. Prograding reefs are typically dominated by occupied  
119 tubes and have few epibionts, whereas retrograding reefs are characterised by mosaics of  
120 occupied and unoccupied tubes that show signs of reef erosion and extensive coverage of  
121 epibionts and biofilms (Wilson, 1976; Curd et al., 2019).



122

123 Figure 1. (a) Photo of the honeycomb structure of the tubes of *Sabellaria alveolata*. (b) Photo

124 of the reef structures attached to rocks – note the mosaic structure with algae growing on the

125 reef structures and limpets and barnacles on the patches of bare rock in between the reef

126 structures. (c) Map of Ireland with locations that are mentioned in this paper. The names in

127 italics are the locations where the biodiversity surveys were carried out.

128

129 Despite being recognised as an ecologically important habitat and designated for protection

130 under international legislation such as the EU Habitats Directive (EEC/92/43), *S. alveolata*

131 reefs are listed in the IUCN European Red List of Habitats as ‘Data deficient’ (Bertocci et al.,

132 2017; Gubbay et al., 2017). Whilst a small number of regions have been subject to

133 experimental research (e.g. northern France (Dubois et al., 2002) and Sicily (Bertocci et al.,

134 2017)), little is known about its distribution or ecology outside of the UK, where there is a

135 strong natural history heritage and a tradition of sustained observations (Wilson, 1971;

136 Hawkins et al., 2013, 2016; Mieszkowska et al., 2014). There was an early interest from

137 conservation agencies (Cunningham et al., 1984) and it is listed as a UK Priority Marine  
138 Habitat (JNCC, 2008). Beyond the UK, whilst *S. alveolata* has been reported to occur on all  
139 coasts of the island of Ireland (hereafter ‘Ireland’ including both the Republic of Ireland and  
140 Northern Ireland), at the time of writing, only 40 records existed in the Oceanographic  
141 Biodiversity Information System (OBIS) database in comparison to 2357 for Britain (OBIS,  
142 2018). In Northern Ireland, *S. alveolata* was described as ‘unknown, not well mapped’ in the  
143 UK National Ecosystem Assessment 2011. Furthermore, a Web of Science search for  
144 ‘*Sabellaria alveolata*’ and ‘Ireland’ produced a single paper (Culloty et al., 2010). Clearly,  
145 there is a lack of information on this important habitat around Ireland.

146

147 Recognising the importance of *S. alveolata* and the paucity of information on its distribution  
148 and ecology in Ireland, our goals were to:

- 149 (1) identify regions with insufficient data that should be targeted for future sampling;
- 150 (2) describe the biodiversity (epibiotic and infaunal) associated with reefs. For epibiota,  
151 we hypothesised that algal richness and abundance would be higher on *S. alveolata*  
152 reef than on rock, and that grazer richness and abundance would be greater on rock  
153 than on *S. alveolata* reef, and for infauna, that richness and abundance would be  
154 higher in retrograding than in prograding reefs; and
- 155 (3) present a potential framework for data gathering that could potentially be applied to  
156 other habitats, species and regions. This information could be used to inform  
157 assessments of the status of data deficient species and habitats, thus providing  
158 potentially invaluable resources for sustained monitoring, management and  
159 conservation.

160

161 **2. METHODS**

162

163 **2.1. Identifying regions with insufficient data on the distribution of *S. alveolata* around**

164 ***Ireland***

165 The distribution of *S. alveolata* around Ireland was recently described by Firth et al. (2020).

166 This paper focused on describing the most important environmental variables (i.e. wave

167 height, tidal amplitude, stratification index, then substrate type) underpinning distribution

168 patterns and abundance changes over time. The dataset used in that paper comprised data

169 from a range of sources including grey literature, museum specimens, published papers and

170 publicly-available databases combined with records from field sampling (including intensive

171 targeted sampling in the 1950s (by Denis Crisp and Alan Southward: Southward and Crisp,

172 1954); 2003-2004 (the MarClim Project: Simkanin et al., 2005; Merder et al., 2018); and by

173 co-authors of this paper between 2013-2018). Using the same dataset, here, we focus in on

174 the six previously-identified discretely bounded regional populations. We examined the

175 spread of both records and SACFOR abundance categories (S=Superabundant, A=Abundant,

176 C=Common, F=Frequent, O=Occasional, R=Rare, and Not Seen). This enabled us to identify

177 any spatial or temporal imbalances in the spread of distributional data. All data were mapped

178 using ArcGIS (ESRI, 2016).

179

180 **2.2. Characterising the epibiotic and infaunal communities associated with *Sabellaria***

181 ***alveolata***

182 To test the hypothesis that *S. alveolata* reefs support higher algal richness and abundance and

183 lower molluscan grazer richness and abundance than adjacent emergent rock (hereafter rock),

184 a minimum of ten (and in most locations twenty) quadrats (25 cm × 25 cm) were randomly

185 placed on both habitat types at eight locations between March and September 2016:

186 Glasdrumman, Balbriggan, Duncannon, Bunmahon, Spiddal, Inverin, Bundoran and

187 Buncrana (Figure 1c). These locations were selected based on their broad geographic

188 coverage of the Irish coastline, and because they had sufficient *S. alveolata* reef cover to  
189 enable a high level of replication. Prograding reefs dominated by progradation phase are not  
190 common in Ireland, and thus only retrograding reefs were sampled for epibiotic communities.  
191 In each quadrat, percentage cover of algae was estimated (points occupied under a  $10 \times 10$   
192 grid), and all mobile grazers were identified and counted.

193

194 To test the hypothesis that infaunal richness and abundance would be higher in retrograding  
195 than prograding reefs, five samples of prograding reefs and five samples from retrograding  
196 reefs were taken at Duncannon, Co. Wexford and Inverin, Co. Galway (Figure 1c) in August  
197 2013 and May 2015 respectively. These locations were selected because they supported large  
198 patches ( $>1 \text{ m}^2$ ) comprising both prograding and retrograding phase types. Prograding  
199 patches were defined as having occupied tubes comprising  $>70\%$  of the area with no visible  
200 damage to the surface. Retrograding patches were defined as having  $>70\%$  of tubes appearing  
201 to be unoccupied by the worms. All samples were collected from the centre of patches ( $\sim 1$   
202  $\text{m}^2$ ) to avoid edge effects. At Inverin, reefs were compared with the adjacent sand ( $>1 \text{ m}$   
203 away from the reef) as an additional habitat comparison. Each sample was taken using a 10  
204 cm diameter circular corer to approximately 15 cm depth, and was preserved in 70%  
205 Industrial Methylated Spirits. In the laboratory, reef samples were carefully picked apart and  
206 washed through  $500\mu\text{m}$  mesh. All individuals retained were identified to the lowest  
207 taxonomic level. Due to problems transporting samples from Inverin, only three were  
208 processed from each habitat type

209

### 210 **2.3. Statistical analyses**

211 Epifauna: Comparison of algal abundance and richness, and molluscan grazer abundance and  
212 richness were made between reef types (prograding; retrograding) and locations (8) were

213 compared using linear-mixed effects (lme) models including reef type and location as fixed  
214 and random factors respectively, and estimated using restricted maximum likelihood  
215 (REML). Optimal model selection for each metric was based on Akaike Information  
216 Criterion (AIC)(Zuur et al., 2009) and models were validated to check for normality and  
217 homogeneity of the residuals. Tukey post-hoc contrasts were used to compare differences  
218 between reef types within locations.

219

220 Infauna: Multiple one-factor analysis of variance (ANOVA) tests were used to compare  
221 richness and abundance among habitat types (prograding reef; retrograding reef; sand  
222 (Inverin only)) at Duncannon and Inverin locations, which were considered separately.

223 Richness and abundance measures were calculated for 5 taxonomic classifications: (1) All  
224 taxa; (2) Annelida; (3) Arthropoda; (4) Mollusca; and (5) Other. Prior to ANOVA, tests for  
225 homogeneity of variance were performed using Levene's test (*car* package). Tukey post-hoc  
226 contrasts used to compare habitat types at Inverin.

227

228 All statistical analyses were performed in R (R Core Team, 2020).

229

### 230 **3. RESULTS**

231

#### 232 ***3.1. Identifying regions with insufficient data on the distribution of *S. alveolata* around***

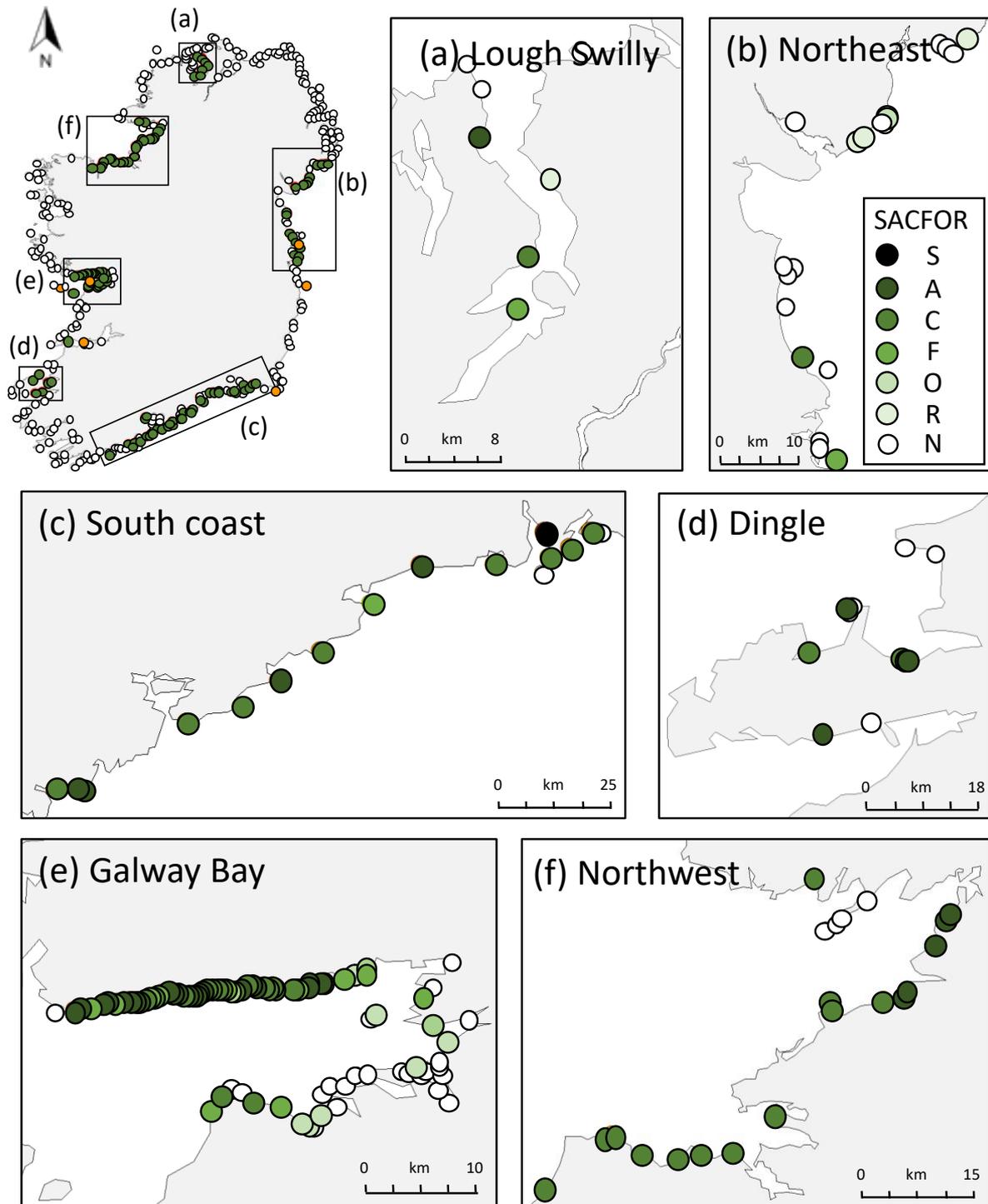
##### 233 ***Ireland***

234 A total of 981 records were collated between 1836 and 2018: 319 (33%) of these were  
235 'positive' observations (i.e. present) and 662 (67%) were 'negative' observations (i.e.  
236 absent/not seen). The vast majority of the records (954) were from intertidal habitats with  
237 very few records from subtidal habitats (27). Unsurprisingly, sampling effort varied spatially  
238 and temporally, resulting in an imbalance of records among regions and sampling periods.

239

240 3.1.1. Subtidal populations

241 Of the 27 subtidal records available (orange dots in Figure 2), only a single record from Clare  
242 Island (Southern, 1912) reported a negative observation (not seen); the rest were all positive  
243 observations, largely from grab sampling. Due to the discovery of a subtidal reef-forming  
244 population off Wicklow Head in 1997 (De Grave and Whitaker, 1997), the Wicklow Reef  
245 Special Area of Conservation (SAC) was designated (*inter alia*) specifically for the presence  
246 of a subtidal *S. alveolata* reef based on the fact that it is “an extremely unusual feature and  
247 may be the first record for Britain and Ireland” (NPWS, 2014). Subsequent sampling of the  
248 region off Wicklow Head confirmed the presence of subtidal *S. alveolata* in the local area,  
249 but not necessarily at the exact location of the SAC. Furthermore, it is not known if it forms  
250 reefs. Other positive subtidal records exist from grab samples for outer Galway Bay, the Aran  
251 Islands, Carnsore Point and the Shannon Estuary.



252

253 Figure 2. Map illustrating the presence (full circles) and absence (empty circles) of *Sabellaria*

254 *alveolata* around Ireland. All records for intertidal (green circles) and subtidal (orange

255 circles) observations between 1836 and 2018 are shown. (a-f) Maps of the six discretely-

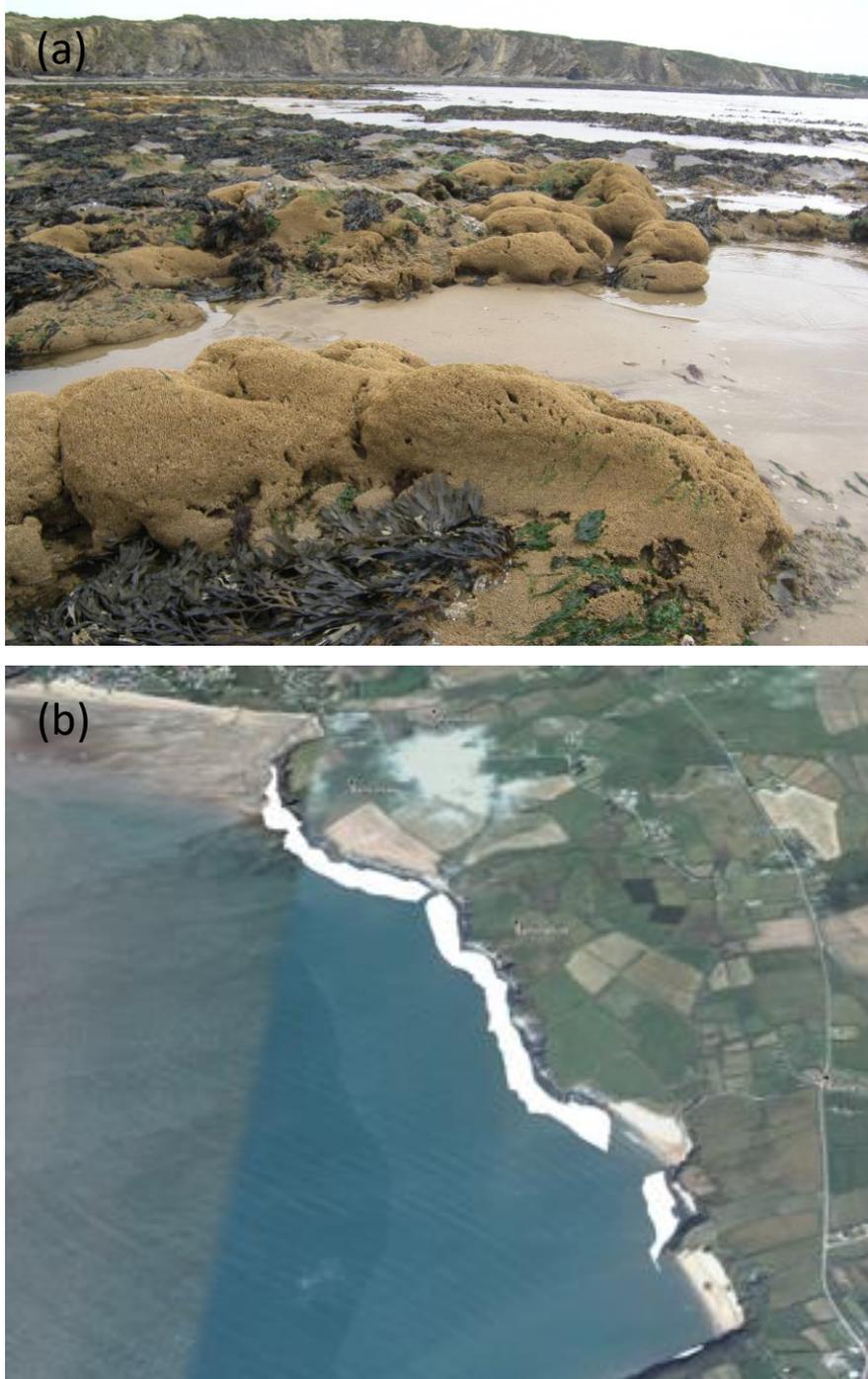
256 bounded populations in Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway

257 Bay and the northwest. For zoomed-in maps, only data from 2013-2018 are shown.

258

259 3.1.2. Intertidal populations

260 Of the 954 intertidal records collated, 293 (31%) were positive observations and 661 (69%)  
261 were negative observations. *S. alveolata* has a discontinuous distribution around the Irish  
262 coastline, with six discretely-bounded populations found in the northeast (Coney Island, Co.  
263 Down to Howth, Co. Dublin), south coast (Cullenstown, Co. Wexford to Galley Head, Co.  
264 Cork), Dingle Peninsula, Galway Bay (Black Head, Co. Clare to Cloghmore, Co. Galway),  
265 northwest (Killala Bay, Co. Mayo to Fintra Beach, Co. Donegal) and Lough Swilly (Figure  
266 2). The northernmost population was found at Portsalon, Co. Donegal (55.21°N), and two  
267 coincident leading range edges were identified on the north coast (Dunree, Lough Swilly, Co.  
268 Donegal) and the east coast (Greencastle Rocks, Carlingford Lough, Co. Down). The reefs  
269 located at Duncannon, Co. Wexford represent the largest (~14ha in 2015, compared to  
270 previous estimate of 20ha (NPWS, 2011)) and best example of intertidal reefs (in terms of  
271 both condition and extent) in Ireland (Figure 3); and one of the only locations dominated by  
272 prograding reefs. It is also the only location surveyed that was assigned the Superabundant  
273 SACFOR category.

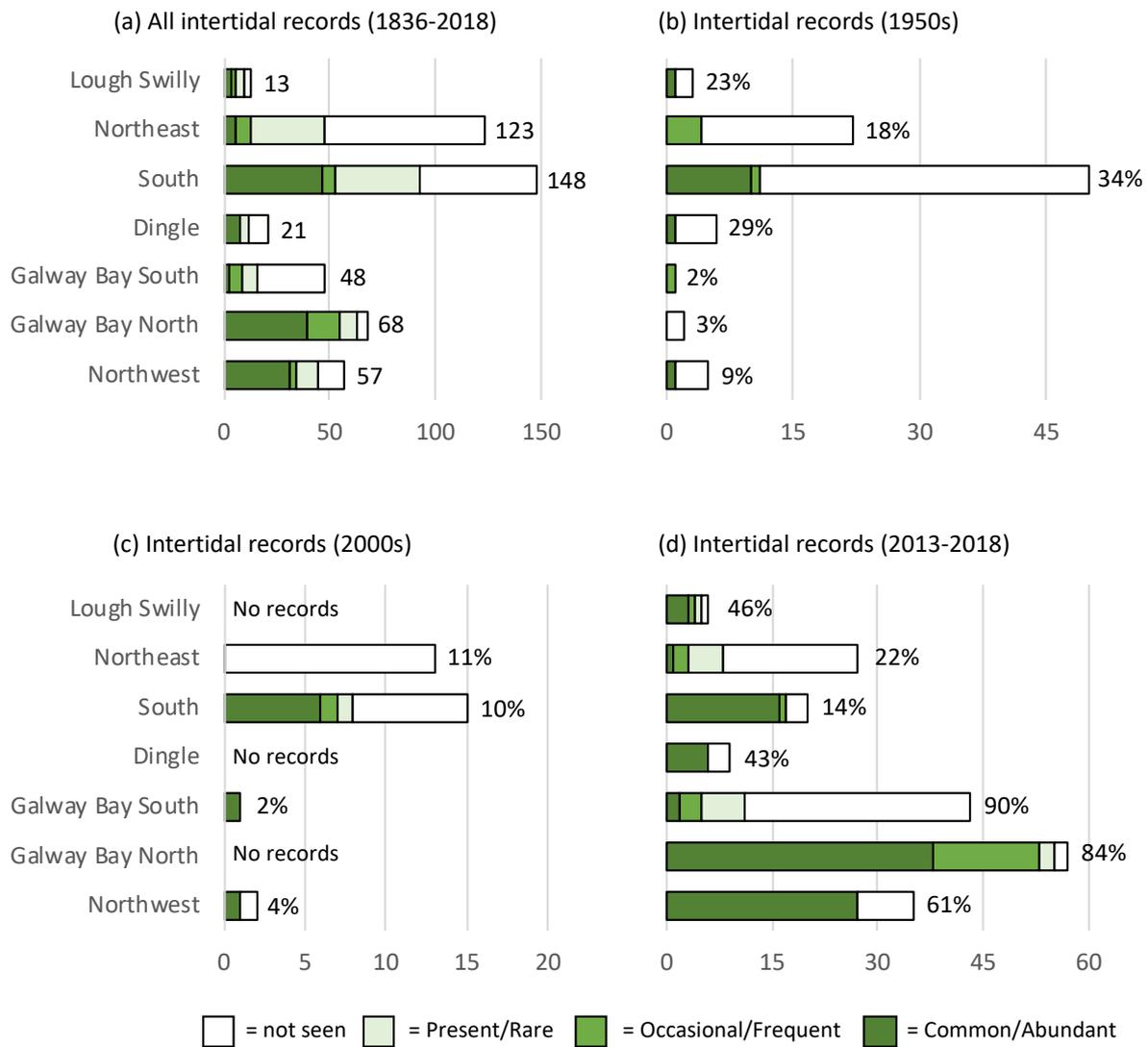


274

275 Figure 3. (a) Photo of the *Sabellaria alveolata* reefs at Duncannon, Co. Wexford. (b) Image  
276 showing extent (~14ha in 2015) of the reefs at Duncannon. The conservation of *S. alveolata*  
277 reefs at Duncannon was specifically mentioned as a target in the River Barrow and River  
278 Nore Special Area of Conservation (site code: 2162) Conservation Objectives (NPWS, 2011).

279

280 Sampling effort varied spatially and temporally (Figure 4). Over the longer term, the  
281 northeast and the south coasts appeared to subjected to intensive sampling (123 and 148  
282 records respectively, Figure 4a). In both regions, however, the majority of the records were  
283 collected prior to 2013. Data collected between 2013-2018 for the northeast and south coasts  
284 only represented 22% and 14% of records respectively for each region across the entire study  
285 period. This suggests that these regions were under-sampled in the most recent intensive  
286 sampling. Due to the availability of sufficient historical data at the same locations over time,  
287 long-term comparisons were possible for both regions. Locations in the northeast had few  
288 records in the higher SACFOR categories (figures 2, 4), and populations were very ‘dynamic’  
289 through time with evidence of population increases, declines, extirpations and recolonisations  
290 throughout the region (discussed in detail in Firth et al., 2020). In contrast, the south coast  
291 exhibited greater stability over time, with many locations exhibiting persistently higher  
292 SACFOR abundance categories through time (Figure 4). The remaining regions were  
293 generally poorly sampled (<70 records in total), with most regions either having very few  
294 records in total (i.e. Lough Swilly (13) and Dingle (21)) or very few older records (all except  
295 northeast and south). This limited any meaningful temporal comparison.



296

297 Figure 4. Summary of the relative frequency of occurrence of the various SACFOR scores for

298 each of the six discretely-bounded populations: Lough Swilly, the northeast, south coast,

299 Dingle Peninsula, Galway Bay (separated into north and south), and the northwest. (a) All

300 intertidal records collated from all sources spanning the entire sampling period 1836-2018.

301 The numbers on the right represent the total number of all records spanning the entire study

302 period for each regional population. (b) All intertidal records collected by Crisp and

303 Southward in the 1950s; (c) all intertidal records collected during the MarClim project 2003-

304 2004; (d) all intertidal records collected by co-authors of this paper 2013-2018. Note the scale

305 on the X-axis changes in each panel. These three temporal sub-sets of data were selected

306 because they had sufficient geographic coverage and reported SACFOR estimates. The

307 numbers on the right in b-c represent the % of all records for each region represented by that  
308 temporal subset. Note that other records for each region exist outside these temporal subsets.  
309  
310 The recent sampling that was carried out between 2013-2018 (Figures 2, 4d) provides the  
311 most up-to-date assessment of the distribution and abundance of *S. alveolata* around the Irish  
312 coastline. Sampling in the previously-identified distribution gaps confirmed that large  
313 swathes of coastline were devoid of *S. alveolata* (discussed in detail in Firth et al., 2020).  
314 Despite intensive sampling during this period and the filling in of important data gaps (i.e.  
315 Galway Bay, northwest and to a lesser degree Lough Swilly and the Dingle Peninsula), most  
316 regions remain relatively poorly sampled with <50 records each. Galway Bay was the most  
317 intensively sampled region, and was split based on relative differences in SACFOR  
318 abundance categories. Galway Bay North exhibited high prevalence (67%) of the higher  
319 SACFOR categories (i.e. Abundant/Common) and low prevalence of negative observations  
320 (4%) (Figure 4d). Conversely, Galway Bay South exhibited low prevalence (5%) of the  
321 higher SACFOR categories and high prevalence of negative observations (74%) (Figure 4d).  
322 Of the 35 records from the northwest, 77% exhibited the higher SACFOR categories. Whilst  
323 few records (<10 each) were available for the Dingle and Lough Swilly, both regions  
324 supported populations exhibiting the higher SACFOR categories.

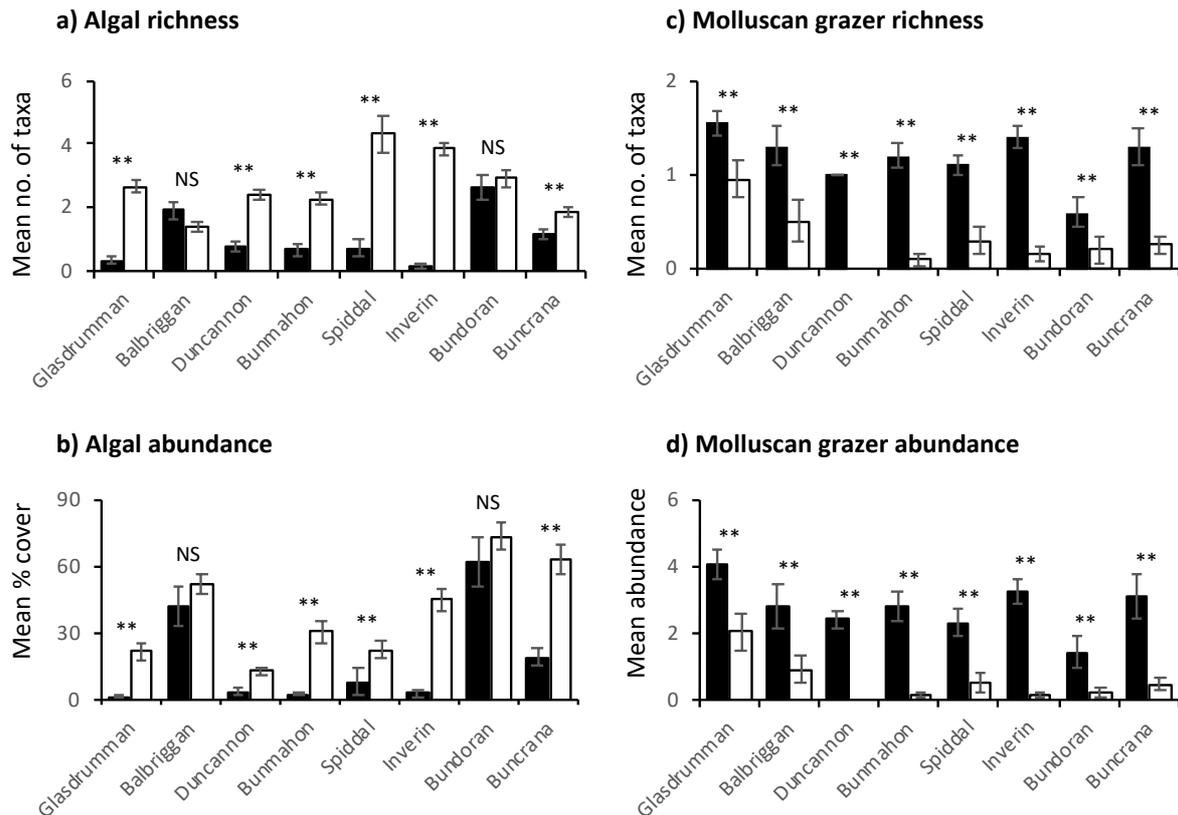
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326

### 327 **3.2. Characterising the epibiotic and infaunal communities associated with *Sabellaria*** 328 ***alveolata***

329 A total of 40 taxa were recorded across all seven locations comprising 22 algae, eight  
330 molluscs, four annelids, three arthropods and one taxon each of lichen, cnidarian and  
331 bryozoan. Of these, 36 taxa (90%) were recorded on *S. alveolata* reefs (13 unique, including  
332 11 algae) and 25 taxa (63%) were recorded on rock (four unique) (Table S1). *Sabellaria*

333 *alveolata* reef supported significantly greater algal richness ( $F_{1,251} = 191.1$ ,  $P < 0.0001$ ) and  
334 algal abundance ( $F_{1,251} = 112.1$ ,  $P < 0.0001$ ) than rock at the majority of locations (Figure  
335 5a,b). Conversely, rock supported significantly greater molluscan grazer richness ( $F_{1,251} =$   
336  $215.7$ ,  $P < 0.0001$ ) and abundance ( $F_{1,251} = 179.8$ ,  $P < 0.0001$ ) than *S. alveolata* reef at all  
337 locations (Figure 5c,d).



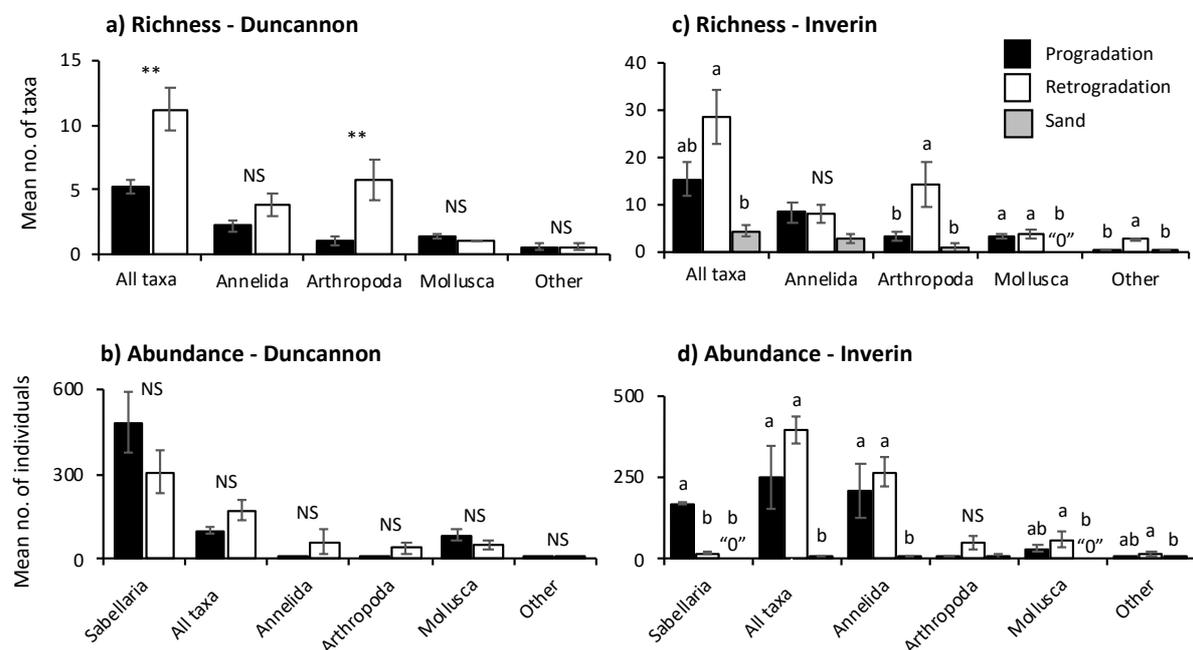
338  
339 Figure 5. Mean (a) algal richness, (b) algal % cover, (c) molluscan grazer richness, (d)  
340 molluscan grazer abundance per quadrat (0.25 x 0.25cm) on emergent rock and *Sabellaria*  
341 *alveolata* reefs at eight locations around Ireland (n = 10 or 20 ± SE). NS = Not significant; \*\*  
342 P < 0.01.

343

344

345 *Comparison of infaunal communities among S. alveolata reef phases and sand*

346 Excluding *S. alveolata*, 77 infaunal taxa were recorded across both locations comprising 36  
 347 arthropods, 26 annelids, 10 molluscs and five ‘other phyla’ (comprising Cnidaria, Sipuncula,  
 348 Nemertea and Nematoda). Of these, 75 taxa (97%) were recorded on *S. alveolata* reefs (67  
 349 unique) and 10 were recorded in sand (two unique) (Table S2). The results varied among  
 350 response variables and locations. At Duncannon, overall mean richness was statistically  
 351 higher in retrograding compared with prograding reef patches (Figure 6a). There were no  
 352 significant differences in abundances between prograding and retrograding reef patches at  
 353 Duncannon (Figure 6b). At Inverin, mean richness was similar between retrograding and  
 354 prograding reef patches for the majority of groups compared; except arthropoda and other  
 355 taxa, which were significantly higher in retrograding than prograding reef patches (Figure  
 356 6c). In general, sand supported significantly lower richness and abundance than retrograding  
 357 reef patches (Figure 6c,d).



358  
 359 Figure 6. Mean (a) infaunal richness and (b) infaunal abundance among progradation (black  
 360 bars) and retrogradation phases (white bars) of *Sabellaria alveolata* reefs at Duncannon (n=5  
 361 ± SE). Mean (c) infaunal richness and (d) infaunal abundance among progradation and  
 362 retrogradation phases of *S. alveolata* reefs and adjacent sand (grey bars) at Inverin (n=3 ±

363 SE). *Sabellaria alveolata* was not included in calculations of either richness or abundance of  
364 all species or annelids. NS = Not significant; \*\*  $P < 0.01$ . For Inverin, letters above bars  
365 denote significant differences between treatments.

366  
367

#### 368 4. DISCUSSION

369  
370 Through combining the best available historical and contemporary data, spanning 182 years,  
371 we provide a comprehensive account of broad-scale distribution and abundance of a data  
372 deficient species in a previously data deficient region. We increased the number of records  
373 25-fold from 40 in the OBIS database (OBIS, 2018) to 981; importantly many of these were  
374 absences (67%), enabling us to reliably determine discontinuities in the distribution and  
375 imbalances in the dataset. Despite filling an important knowledge gap for a species of  
376 conservation concern, sampling intensity was imbalanced both spatially and temporally. For  
377 example, 221 records for Northern Ireland make up 23% of our database. The Northern Irish  
378 coastline has received a disproportionate degree of sampling compared with the much longer  
379 coastline of the Republic of Ireland. Similarly, Galway Bay is the only region that has been  
380 sampled with high intensity (and recently), revealing that the north shoreline exhibits a  
381 greater percentage (67%) of higher SACFOR records than the south shoreline (5%). This is  
382 likely to be due to the much-reduced wave energy, and thus greater accumulation of finer  
383 silty sediments on the south shoreline, which in turn is less suitable for tube building than the  
384 larger-grained sandy environment that characterizes the north shoreline (O'Connor et al.,  
385 1993). Without intensive sampling, such observations would not be possible.

386

387 A number of locations have been identified as requiring better protection. Despite Duncannon  
388 exhibiting the most extensive stretches of reef in Ireland that are located within the River  
389 Barrow and River Nore SAC (NPWS, 2011, for which *S. alveolata* reefs are specifically

390 listed as features of interest), this was the only location where a winkle (*Littorina littorea* L.  
391 1758) picker was observed kicking off large chunks of *S. alveolata* reef to access winkles.  
392 Similarly, Preston and Portig (2001) identified winkle collection as a considerable threat to *S.*  
393 *alveolata* at locations in the northeast (Glasdrumman and Ringboy/Minerstown). Further  
394 information on damage caused by harvesting and trampling (Dubois et al., 2002; Plicanti et  
395 al., 2016), or local human activities such as shellfish farming (Dubois et al., 2006) would be  
396 beneficial for identifying locations in need of protection and management, as well as public  
397 awareness efforts (e.g. information boards).

398

399 In the short-term (within 1-2 years), intensive sampling is recommended at all sub-regional  
400 boundary edges to determine the true boundaries. We also recommend that the poorly  
401 sampled Lough Swilly and Dingle Peninsula, and the vulnerable northeast are subjected to  
402 intensive sampling in the short-term. Following this, we recommend that a network of key  
403 locations (spanning all regions) are identified for sustained observations of fixed areas over  
404 medium (5–10 years), and long (20–30 years) timescales. Using a hierarchical sampling  
405 approach (1m, 5m, 10m, and landscape) over fixed areas will yield information about  
406 changes in the nature, extent and ecology of reefs over time. This would be invaluable for  
407 informing managers about any spatio-temporal changes in condition and extent.

408

409 *S. alveolata* reefs in Ireland were typically characterised by a mosaic of development phases  
410 at small spatial scales (<1m), rather than being dominated by either progradation or  
411 retrogradation phase, as can be seen on the larger reefs in Mont-Saint-Michel Bay (Gruet,  
412 1986; Curd et al., 2019). These mosaic reefs were found to support greater algal diversity and  
413 abundance compared with adjacent rock. In addition to algae living as epibionts directly on  
414 the surface of the *S. alveolata* reefs, many macroalgal species can be attached directly to rock

415 and protrude up through cracks in the reef. Despite these algae being attached to the rock,  
416 they are likely to still benefit from a combination of physical habitat amelioration and  
417 associational defence (Bertness et al., 1999) from grazing provided by the reef structure.

418

419 Mosaics of habitat patches, with varying amounts of primary or secondary producers, can  
420 make a major contribution to ecosystem functioning (Giller et al., 2004), with habitat patch  
421 diversity perhaps being more important than species diversity per se in open ecosystems.

422 Biogenic habitats are noted for their structural complexity, facilitating diverse communities  
423 through habitat and refuge provision (Hughes et al., 2014; Walls et al., 2018; Bertolini et al.,

424 2020). Had it been possible to sample large enough patches that were dominated by the  
425 progradation phase, it is unlikely that such patterns would have been observed, and it is  
426 assumed that few algae (or indeed other organisms) would have been attached to the reefs.

427 Prograding reefs comprise tightly-packed tubes containing live individuals and consist almost  
428 entirely of feeding apertures (Wilson, 1968, 1971), which greatly reduce the probability of  
429 successful settlement by larvae of other species and inhibit overgrowth by adjacent organisms  
430 (Jackson, 1977).

431

432 Grazer diversity and abundance was higher on rock compared with *S. alveolata* reefs. A  
433 recent study by Muller et al. (2021) found no grazers represented in the infaunal community  
434 associated with *S. alveolata* reefs. Similar inverse patterns of predator/prey abundance have  
435 been observed in mussel beds due to reduced predation pressure within mussel beds  
436 (Witman, 1985). These processes do not necessarily translate when it comes to grazer/algae  
437 relationships. For example, O'Connor and Crowe (2008) found that algae were more  
438 abundant and diverse within mussel beds than on adjacent rock; but experimental testing of  
439 grazing patterns revealed that grazing intensity was similar between the two habitats

440 suggesting that grazing pressure was not the underlying driver. Crowe et al. (2011) factorially  
441 manipulated limpet grazing and mussel cover, and showed that whilst mussels provided a  
442 refuge (particularly for fucoid germlings) from grazing activity of limpets, other grazing  
443 gastropods were actually found in greater abundance in mussel beds (a pattern also observed  
444 by Wangkulankul et al., 2016), and that there was some evidence of an inverse relationship  
445 between abundance of limpets and other grazers. This highlights that limpets are key grazers  
446 in this system as they are throughout the North-east Atlantic (Hawkins, 1981; Coleman et al.,  
447 2006; Jenkins et al., 2005), and that their grazing activity cannot be matched by other grazers  
448 (O'Connor and Crowe, 2005). Whilst it is probable that *Sabellaria* reefs provides a refuge for  
449 grazing activity from grazers (particularly limpets), experimental manipulation is necessary  
450 before any conclusions can be drawn about the role of grazers in driving epibiotic  
451 biodiversity patterns.

452

453 The 77 infaunal taxa comprised a combination of intertidal, subtidal and terrestrial taxa (i.e.  
454 fly larvae), highlighting that the reefs support a unique combination of taxa from a range of  
455 different environments (Dubois et al., 2002). None of the taxa recorded were of particular  
456 note in terms of rarity or conservation value, although some may be considered important as  
457 either fishing bait (ragworms, *Nereis* and *Nephtys*) or due to their commercial importance  
458 (*Mytilus edulis* L. 1758). *Sabellaria alveolata* reefs and their surrounding sedimentary  
459 habitats are known to support species of commercial importance (Dubois et al., 2006; Plicanti  
460 et al., 2016; Schimmenti et al., 2015), and the worms themselves are also collected as fishing  
461 bait, particularly in the Mediterranean (Gambi et al., 1992). By comparison with continental  
462 Europe, harvesting and bait collection are not currently considered to be especially  
463 detrimental activities in Ireland. The harvesting of winkles (*L. littorea*), purple urchins  
464 (*Paracentrotus lividus* Lamarck, 1816) and mussels (*Mytilus* spp.) are perhaps the most

465 prevalent activities (Cummins et al., 2002; Fahy et al., 2008), and may have detrimental  
466 impacts on *S. alveolata* reefs.  
467  
468 *Sabellaria alveolata* populations fluctuate naturally over time (Gruet, 1986), exhibiting  
469 different life history characteristics, with some colonies growing rapidly while others appear  
470 more senescent, mainly due to very patchy settlements of juveniles onto the reef. Little  
471 experimental work has explored the natural drivers of change, but it has been asserted that  
472 algal blooms and competition for space with competitors such as filter-feeding barnacles and  
473 mussels (Multer and Milliman, 1967) can lead to the weakening of reef structures rendering  
474 them more susceptible to erosion by waves (Wilson, 1971). Extreme climatic events  
475 (extensive colds or intense storms) are known to have long-term effects on reef structures  
476 (Crisp, 1964; Firth et al., 2015, 2020), with long-term and wide-reaching cascading effects.  
477 Furthermore, anthropogenic drivers such as trampling, harvesting of organisms from the reefs  
478 and collection of the worms for bait are all known to expedite the retrogradation process  
479 (Cunningham et al., 1984; Plicanti et al., 2016). Irrespective of morphological type or phase,  
480 all types of reefs (even dead ones) carry out important ecosystem functions and services  
481 (Sheehan et al., 2015; Gribben et al., 2017). Therefore, even the most ‘degraded’ reefs may  
482 provide an important structuring function, providing substrate for colonisation of benthic  
483 organisms (Dubois et al., 2002; Jones et al., 2018). They have an important legacy effect  
484 through potentially serve as catalysts for future large and prograding reefs due to gregarious  
485 settlement of larvae that are attracted to the tube sand and its cement (Wilson, 1968; Pawlik,  
486 1988).  
487  
488 Assessing variability in habitat distribution and abundance is also important at a time when  
489 the implementation of some marine policies (such as the establishment of marine reserves

490 and protected sites such as Special Areas of Conservation (SACs)) assumes a degree of  
491 stability in the features being protected. The Wicklow Reef SAC provides an interesting  
492 example of this. The location was designated for the presence of *S. alveolata*, but a report  
493 from the National Parks and Wildlife Service (NPWS, 2013) pointed out that the occurrence  
494 of *S. alveolata* within this site may be questionable and that the highly dynamic nature of this  
495 area is unlikely to support a stable biogenic reef composed of *S. alveolata* for any length of  
496 time. This highlights the importance of sustained observations, particularly relating to the  
497 designation of sites for the conservation of ephemeral or variable species or habitats.  
498 Incidentally, during the writing of this paper, the Irish government announced plans to  
499 expand Ireland's Marine Protected Area network to 30% by 2030 (currently at 2.13%,  
500 Gov.ie., 2021). The results from this study will feed into this consultation.

501

502 With such fine-scale mapping of the distribution of this important reef-forming species, it is  
503 anticipated that this will be of significant use to those tasked with the management and  
504 protection of these habitats. This is particularly important as it comes at a time when cross-  
505 border management is very likely to become challenged due to potential changes in  
506 legislation, for example the exit of the UK from the European Union on 1<sup>st</sup> January 2021  
507 (Boyes and Elliott, 2016; Hawkins, 2017). The vast majority of environmental policy and  
508 legislation in the Republic of Ireland, Northern Ireland, and the UK as a whole, is governed  
509 by legal frameworks and regulations set at the European Union level. The island of Ireland is  
510 an excellent example of the need for joint coordinated national responses to achieve effective  
511 resource management between the two jurisdictions (Stokes et al., 2006; Knights et al.,  
512 2015). This highlights the importance of achieving a potential future: a "one island - two  
513 systems" governance framework (Boyes and Elliott, 2016). This is a wider issue that applies  
514 at other national boundaries globally (Hawkins, 2017).

515

516 **Conclusions**

517 Through combining the best available historical and contemporary data, an important  
518 knowledge gap has been filled in the distribution and abundance of a data deficient species in  
519 a data deficient region. Absence of evidence is not evidence of absence: information on both  
520 positive and negative observations collated from a variety of sources can inform estimates of  
521 detectability of species, indicate decline in population or range size, and, ultimately, inform  
522 reassessment to data-sufficient categories (Good et al., 2006). This is particularly true for  
523 biogenic habitat-forming species, for which the mechanisms underpinning reef dynamics are  
524 not fully understood. This type of research could easily be carried out for other data deficient  
525 species and regions. Through doing this, the information gathered could inform future IUCN  
526 assessments. Undoubtedly, species and habitats that are currently classed as ‘Data deficient’  
527 on the IUCN Red Lists would be re-assigned - in many cases to ‘least concern’ (as we  
528 suspect is the case for *S. alveolata*). The data contained in the wide variety of sources that  
529 were used here provide the raw material for data mining and data archaeology. In this current  
530 setting of the global pandemic and cuts in state-funded science, historical and unpublished  
531 data, in addition to data from citizen science projects (Vye et al., 2020) represent potentially  
532 invaluable resources for sustained monitoring, management and conservation (Hawkins et al.,  
533 2013).

534

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548

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931 Table 1. SACFOR scale of abundance used to record *Sabellaria alveolata*. Adapted from  
932 Cunningham et al. (1984).

| Abundance | Description  |
|-----------|--|
| S         | Super-abundant: Massive patches forming hummocks at least 60 cm thick, covering over a total 10 000 m <sup>2</sup> surface within a 30-minute search                                   |
| A         | Abundant: Numerous large patches almost always over 1 m <sup>2</sup> , forming hummocks over 30 cm thick, covering over a total 1000 m <sup>2</sup> surface within a 30-minute search. |

- C Common: Numerous large patches with many over 1 m<sup>2</sup>, forming sheets (veneers) protruding from the substrata less than 30cm, covering over a total 100 m<sup>2</sup> surface within a 30 minutes search
- F Frequent: Many scattered small patches rarely extending over 1 m<sup>2</sup> each, exhibiting at least in some places tubes in a straight or perpendicular orientation to the substrata, covering at least a total 100 m<sup>2</sup> surface within a 30-minute search
- O Occasional: Scattered small patches of tubes, closely adhering to rocks or other hard substrata (veneers), covering less than a total 10 m<sup>2</sup> surface within a 30-minute search
- R Rare: Scattered tubes closely attached to the substrata, covering no more than a couple m<sup>2</sup> surface within a 30-minute search
- N Not seen: Absent

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934

935 Table S1. Inventory of taxa that were found on emergent rock and on *S. alveolata* reefs

936 across all locations surveyed (Glasdrumman, Balbriggan, Duncannon, Bunmahon, Spiddal,

937 Inverin, Bundoran, Buncrana) between March and September 2016.

| Taxonomic group |                                | Presence/Absence |                   |
|-----------------|--------------------------------|------------------|-------------------|
|                 |                                | Rock             | <i>Sabellaria</i> |
| Lichens         | <i>Verrucaria mucosa</i>       | ✓                | X                 |
| Chlorophyta     | <i>Cladophora</i> spp.         | X                | ✓                 |
|                 | <i>Ulva lactuca</i>            | ✓                | ✓                 |
|                 | <i>Ulva</i> spp.               | ✓                | ✓                 |
|                 | <i>Cladostephus spongiosum</i> | X                | ✓                 |
| Phaeophyta      | <i>Fucus serratus</i>          | ✓                | ✓                 |
|                 | <i>Fucus vesiculosus</i>       | ✓                | ✓                 |
|                 | <i>Fucus</i> spp.              | ✓                | ✓                 |
|                 | <i>Elachista fucicola</i>      | ✓                | X                 |
|                 | UnID brown                     | X                | ✓                 |
| Rhodophyta      | <i>Chondrus crispus</i>        | X                | ✓                 |
|                 | <i>Corallina</i> spp.          | ✓                | ✓                 |
|                 | <i>Gastroclonium ovatum</i>    | X                | ✓                 |
|                 | <i>Gracilaria verrucosa</i>    | X                | ✓                 |
|                 | <i>Lithophyllum incrustans</i> | ✓                | ✓                 |
|                 | Lithothamnion                  | ✓                | X                 |

|            |                                  |    |    |
|------------|----------------------------------|----|----|
|            | <i>Lomentaria articulata</i>     | X  | ✓  |
|            | <i>Mastocarpus stellatus</i>     | X  | ✓  |
|            | <i>Osmundea</i> spp.             | ✓  | ✓  |
|            | <i>Palmaria palmata</i>          | ✓  | ✓  |
|            | <i>Polysiphonia</i> spp.         | X  | ✓  |
|            | <i>Porphyra</i> spp.             | ✓  | ✓  |
|            | <i>Rhodothaminella floridula</i> | ✓  | ✓  |
|            | UnID brown                       | X  | ✓  |
| Mollusca   | <i>Steromphala umbilicalis</i>   | ✓  | ✓  |
|            | <i>Littorina littorea</i>        | ✓  | ✓  |
|            | <i>Littorina saxatilis</i> agg.  | ✓  | ✓  |
|            | <i>Littorina obtusata/mariae</i> | ✓  | X  |
|            | <i>Mytilus edulis</i>            | ✓  | ✓  |
|            | <i>Nucella lapillus</i>          | ✓  | ✓  |
|            | <i>Patella vulgata</i>           | ✓  | ✓  |
|            | <i>Phorcus lineatus</i>          | ✓  | ✓  |
| Arthropoda | Barnacles                        | ✓  | ✓  |
|            | <i>Idotea</i> sp.                | X  | ✓  |
|            | Amphipods                        | X  | ✓  |
| Cnidaria   | <i>Actinia equina</i>            | ✓  | ✓  |
| Annelida   | <i>Eulalia viridis</i>           | X  | ✓  |
|            | <i>Lanice conchilega</i>         | ✓  | ✓  |
|            | <i>Spirorbis spirorbis</i>       | ✓  | ✓  |
|            | <i>Spirobranchus triqueter</i>   | ✓  | ✓  |
| Bryozoa    | Bryozoans                        | X  | ✓  |
|            | <b>Total number of taxa</b>      | 27 | 37 |

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949 Table S2. Inventory of taxa that were found in prograding and retrograding *S. alveolata* reefs

950 and sand across the two locations (Duncannon, Co. Wexford (surveyed August 2013) and

951 Inverin, Co. Galway (surveyed May 2015).

|                           |                              | Presence/absence |                |      |
|---------------------------|------------------------------|------------------|----------------|------|
|                           |                              | Progradation     | Retrogradation | Sand |
| Annelida                  | Aphroditidae                 | X                | ✓              | ✓    |
|                           | <i>Aricidea</i> sp.          | ✓                | X              | X    |
|                           | <i>Capitella</i> sp.         | ✓                | ✓              | X    |
|                           | Cirratulidae                 | ✓                | X              | X    |
|                           | <i>Eteone</i> sp.            | ✓                | ✓              | ✓    |
|                           | <i>Eulalia</i> spp.          | ✓                | ✓              | ✓    |
|                           | <i>Eusyllis blomstrandii</i> | X                | ✓              | X    |
|                           | <i>Exogone</i> sp.           | ✓                | X              | X    |
|                           | <i>Fabricia stellaris</i>    | ✓                | ✓              | X    |
|                           | <i>Glycera</i> sp.           | ✓                | ✓              | X    |
|                           | <i>Harmothoe</i> sp.         | ✓                | X              | X    |
|                           | <i>Lepidonotus</i> sp.       | ✓                | X              | X    |
|                           | <i>Lumbrineris latreilli</i> | ✓                | ✓              | X    |
|                           | <i>Nephtys</i> sp.           | ✓                | ✓              | ✓    |
|                           | <i>Nereis</i> sp.            | ✓                | ✓              | X    |
|                           | <i>Odontosyllis</i> spp.     | ✓                | ✓              | ✓    |
|                           | <i>Perinereis cultrifera</i> | ✓                | ✓              | X    |
|                           | <i>Pholoe baltica</i>        | ✓                | X              | X    |
|                           | <i>Phyllodoce</i> sp.        | ✓                | ✓              | X    |
|                           | Polynoinidae                 | ✓                | X              | X    |
| <i>Pseudopolydora</i> sp. | ✓                            | X                | X              |      |
| <i>Pygospio elegans</i>   | ✓                            | ✓                | ✓              |      |
| <i>Spirorbis</i> sp.      | ✓                            | ✓                | X              |      |
| <i>Syllis</i> sp.         | X                            | ✓                | X              |      |

|                                      |                                  |   |   |   |
|--------------------------------------|----------------------------------|---|---|---|
|                                      | <i>Trypanosyllis coeliaca</i>    | X | ✓ | X |
|                                      | <i>Tubificoides pseudogaster</i> | ✓ | ✓ | X |
| Arthropoda                           | Acari                            | ✓ | ✓ | X |
|                                      | <i>Hydrogamasus</i> sp.          | X | ✓ | X |
|                                      | Oribatida                        | X | ✓ | X |
|                                      | <i>Anurida maritima</i>          | X | ✓ | X |
|                                      | Isotomidae                       | X | ✓ | X |
|                                      | Copepoda                         | X | ✓ | ✓ |
|                                      | <i>Coleoptera</i> sp.            | X | ✓ | X |
|                                      | Chironomidae larvae              | ✓ | ✓ | X |
|                                      | <i>Diptera</i> sp.               | X | ✓ | X |
|                                      | Dolichopodidae                   | ✓ | ✓ | X |
|                                      | Aoridae                          | X | ✓ | X |
|                                      | Amphipoda                        | ✓ | ✓ | X |
|                                      | Gammaridae                       | ✓ | ✓ | X |
|                                      | <i>Gammaropsis</i> sp.           | ✓ | ✓ | X |
|                                      | Isaeidae                         | ✓ | ✓ | X |
|                                      | Leucothoidae                     | ✓ | ✓ | X |
|                                      | <i>Bodotria scorpioides</i>      | ✓ | X | ✓ |
|                                      | <i>Atelecyclus rotundatus</i>    | ✓ | ✓ | X |
|                                      | <i>Callianassa subterranea</i>   | ✓ | X | ✓ |
|                                      | <i>Carcinus maenas</i> juvenile  | ✓ | ✓ | X |
|                                      | <i>Pagurus prideauxi</i>         | ✓ | ✓ | X |
|                                      | <i>Xantho pilipes</i>            | ✓ | ✓ | X |
|                                      | <i>Cyathura carinata</i>         | X | ✓ | X |
|                                      | <i>Idotea</i> spp.               | ✓ | ✓ | X |
|                                      | <i>Jaera nordmanni</i>           | X | ✓ | X |
|                                      | Jaeridae                         | ✓ | ✓ | X |
|                                      | <i>Lekanesphaera</i> sp.         | ✓ | ✓ | X |
|                                      | <i>Sphaeroma serratum</i>        | ✓ | ✓ | X |
|                                      | Tanaidacea                       | ✓ | ✓ | X |
|                                      | <i>Tanais dulongii</i>           | ✓ | ✓ | X |
|                                      | <i>Achelia</i> sp.               | ✓ | ✓ | X |
|                                      | <i>Ammothella longipes</i>       | X | ✓ | X |
|                                      | <i>Anoplodactylus petiolatus</i> | ✓ | ✓ | X |
|                                      | <i>Anoplodactylus virescens</i>  | ✓ | ✓ | X |
|                                      | <i>Nymphon</i> sp.               | ✓ | ✓ | X |
|                                      | Ostracoda                        | ✓ | ✓ | X |
| <i>Abra prismatica</i>               | ✓                                | ✓ | X |   |
| <i>Hiatella</i> sp.                  | X                                | ✓ | X |   |
| <i>Modiolula phaseolina</i> juvenile | ✓                                | ✓ | X |   |

|                              |    |    |    |
|------------------------------|----|----|----|
| <i>Mytilus edulis</i>        | ✓  | ✓  | X  |
| <i>Ruditapes decussatus</i>  | ✓  | X  | X  |
| <i>Littorina</i> sp.         | ✓  | ✓  | X  |
| <i>Odostomia</i> sp.         | ✓  | ✓  | X  |
| Omalogyridae                 | X  | ✓  | X  |
| <i>Pyrgiscus crenatus</i>    | ✓  | X  | X  |
| <i>Spiralinella spiralis</i> | ✓  | X  | X  |
| Edwardsiidae                 | X  | ✓  | X  |
| <i>Golfingia elongata</i>    | ✓  | ✓  | X  |
| <i>Nephasoma minutum</i>     | ✓  | ✓  | X  |
| Nemertea                     | ✓  | ✓  | ✓  |
| Nematoda                     | ✓  | ✓  | X  |
| <b>Total number of taxa</b>  | 41 | 63 | 10 |

952 **Figures**

953 Figure 1. (a) Photo of the honeycomb structure of the tubes of *Sabellaria alveolata*. (b) Photo  
 954 of the reef structures attached to rocks – note the mosaic structure with algae growing on the  
 955 reef structures and limpets and barnacles on the patches of bare rock in between the reef  
 956 structures. (c) Map of Ireland with locations that are mentioned in this paper. The names in  
 957 italics are the locations where the biodiversity surveys were carried out.

958

959

960 Figure 2. Map illustrating the presence (full circles) and absence (empty circles) of *Sabellaria*  
 961 *alveolata* around Ireland. All records for intertidal (green circles) and subtidal (orange  
 962 circles) observations between 1836 and 2018 are shown. (a-f) Maps of the six discretely-  
 963 bounded populations in Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway  
 964 Bay and the northwest. For zoomed-in maps, only data from 2013-2018 are shown.

965

966

967 Figure 3. (a) Photo of the *Sabellaria alveolata* reefs at Duncannon, Co. Wexford. (b) Image  
 968 showing extent (~14ha in 2015) of the reefs at Duncannon. The conservation of *S. alveolata*

969 reefs at Duncannon was specifically mentioned as a target in the River Barrow and River  
970 Nore Special Area of Conservation (site code: 2162) Conservation Objectives (NPWS, 2011).

971

972 Figure 4. Summary of the relative frequency of occurrence of the various SACFOR scores for  
973 each of the six discretely-bounded populations: Lough Swilly, the northeast, south coast,

974 Dingle Peninsula, Galway Bay (separated into north and south), and the northwest. (a) All

975 intertidal records collated from all sources spanning the entire sampling period 1836-2018.

976 The numbers on the right represent the total number of all records spanning the entire study

977 period for each regional population. (b) All intertidal records collected by Crisp and

978 Southward in the 1950s; (c) all intertidal records collected during the MarClim project 2003-

979 2004; (d) all intertidal records collected by co-authors of this paper 2013-2018. Note the scale

980 on the X-axis changes in each panel. These three temporal sub-sets of data were selected

981 because they had sufficient geographic coverage and reported SACFOR estimates. The

982 numbers on the right in b-c represent the % of all records for each region represented by that

983 temporal subset. Note that other records for each region exist outside these temporal subsets.

984

985 Figure 5. Mean (a) algal richness, (b) algal % cover, (c) molluscan grazer richness, (d)

986 molluscan grazer abundance per quadrat (0.25 x 0.25cm) on emergent rock and *Sabellaria*

987 *alveolata* reefs at eight locations around Ireland (n = 10 or 20 ± SE). NS = Not significant; \*\*

988 P < 0.01.

989

990 Figure 6. Mean (a) infaunal richness and (b) infaunal abundance among progradation (black

991 bars) and retrogradation phases (white bars) of *Sabellaria alveolata* reefs at Duncannon (n=5

992 ± SE). Mean (c) infaunal richness and (d) infaunal abundance among progradation and

993 retrogradation phases of *S. alveolata* reefs and adjacent sand (grey bars) at Inverin (n=3 ±

994 SE). *Sabellaria alveolata* was not included in calculations of either richness or abundance of

995 all species or annelids. NS = Not significant; \*\*  $P < 0.01$ . For Inverin, letters above bars

996 denote significant differences between treatments.

997

998