

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

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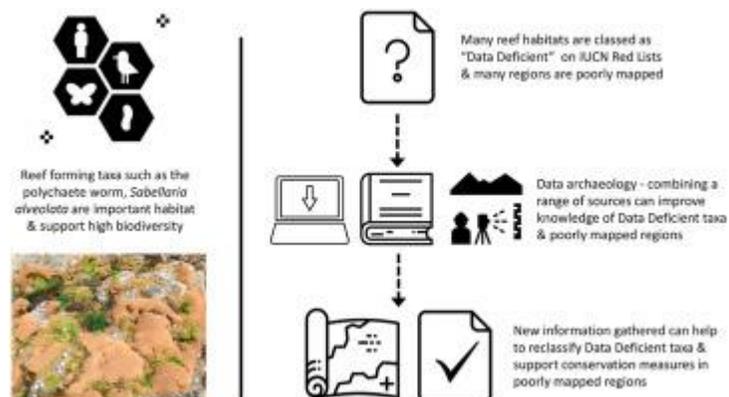
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### Abstract :

Data that can be used to monitor biodiversity through time are essential for conservation and management. The reef-forming worm, *Sabellaria alveolata* (L. 1767) is currently classed as 'Data deficient' due to an imbalance in the spread of data on its distribution. Little is known about the distribution of this species around Ireland. Using data archaeology, we collated past and present distribution records and discovered that *S. alveolata* has a discontinuous distribution with large gaps in distribution. Many regions lack data and should be targeted for sampling. Biodiversity surveys revealed that *S. alveolata* supported diverse epibiotic algal communities. Retrograding (declining) reefs supported greater infaunal

diversity than prograding (growing) reefs or sand, suggesting that *S. alveolata* is a dynamic ecosystem engineer that has a lasting legacy effect. Similar research should be carried out for other data deficient species, habitats and regions. Such data are invaluable resources for management and conservation.

### Graphical abstract



### Highlights

► Improving the knowledge base of data deficient species will enable greater protection. ► We identified knowledge gaps for the distribution of a data deficient species in a poorly mapped region. ► *S. alveolata* reefs supported diverse epibiotic algal assemblages. ► Retrograding (declining) reefs supported greater infaunal diversity than prograding (growing) reefs. ► Such research should be done for other data deficient species and habitats.

**Keywords** : Baseline data, Biodiversity, Biogenic habitat, Marine Protected Area, Reef, Sustained observations

58 **1. INTRODUCTION:**

59 Biodiversity loss in the face of global environmental change is one of the greatest challenges  
60 of our time. Increasingly, extinctions are being documented coupled with predictions of the  
61 sixth mass extinction, primarily as a result of anthropogenic activities (Wake and  
62 Vredenburg, 2008). In 2021, the Convention on Biological Diversity (CBD) will adopt a  
63 post-2020 global biodiversity framework as a stepping stone towards the 2050 Vision of  
64 'Living in harmony with nature'. Understanding the level of extinction risk faced by poorly-  
65 mapped species and why interspecific differences in risk arise remains one of the greatest  
66 challenges facing conservation biology. Assessment frameworks for threatened species are  
67 crucial to identifying risk and monitoring progress toward CBD targets (Jones et al., 2011).  
68 One of the most well-known is the International Union for Conservation of Nature (IUCN)  
69 Red List (Bland et al., 2017; IUCN, 2020). Despite recent improvement in the taxonomic  
70 coverage of the IUCN Red List (Bland et al., 2015), ~15% of the >65,000 species assessed  
71 are still classified as data deficient due to a lack of information on taxonomy, geographic  
72 distribution, population status, or threats (IUCN, 2020). A taxon in this category may be well  
73 studied, and its biology well known, but appropriate data on abundance and/or distribution  
74 may be lacking resulting in this 'data deficient' classification.

75

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

90

91 The honeycomb worm *Sabellaria alveolata* L. (Figure 1) is a warm-water reef-forming  
92 species that is distributed from Morocco/Western Sahara to southwest Scotland (Gruet, 1986;  
93 Curd et al., 2020; Lourenço et al., 2020). *Sabellaria alveolata* is a broadcast spawner that  
94 produces planktotrophic larvae, which settle and metamorphose preferentially on the  
95 cemented sand tubes of conspecific adults (Wilson, 1968), typically in areas where rocky  
96 reefs abut sandy beaches supplying coarse sand for tube-building (Gruet, 1984). Colonies of  
97 individuals can form biogenic structures ranging from small patches, hummocks, and veneers  
98 to the largest biogenic reefs in Europe (5.52 and 6.76 ha, Bajjouk et al., 2020) in Mont-Saint-  
99 Michel Bay, France (Holt et al., 1998; Lecornu et al., 2016). The worms, their biogenic  
100 structures (hereafter 'reefs') and the associated biological communities play an important role

101 in ecosystem functioning, delivering services such as nutrient cycling, biofiltration and wave  
102 attenuation (Dubois et al., 2009; Lefebvre et al., 2009; Cugier et al., 2010; Jones et al., 2018).  
103 On rock, *S. alveolata* can be ecologically dominant, overgrowing and displacing other  
104 common rocky-reef assemblages developing at similar tidal levels such as mussels or brown  
105 macroalgae (Wilson, 1971). Reefs undergo natural cycles of growth (progradation) and  
106 decline (retrogradation) (*sensu* Curd et al., 2019 after Gruet, 1986) that are reflected in their  
107 appearance and associated biodiversity. Prograding reefs are typically dominated by occupied  
108 tubes and have few epibionts, whereas retrograding reefs are characterised by mosaics of  
109 occupied and unoccupied tubes that show signs of reef erosion and extensive coverage of  
110 epibionts and biofilms (Wilson, 1976; Curd et al., 2019).

111

112 Despite being recognised as an ecologically important habitat and designated for protection  
113 under international legislation such as the EU Habitats Directive (EEC/92/43), *S. alveolata*  
114 reefs are listed in the IUCN European Red List of Habitats as ‘Data deficient’ (Bertocci et al.,  
115 2017; Gubbay et al., 2017). Whilst a small number of regions have been subject to  
116 experimental research (e.g. northern France (Dubois et al., 2002) and Sicily (Bertocci et al.,  
117 2017)), little is known about its distribution or ecology outside of the UK, where there is a  
118 strong natural history heritage and a tradition of sustained observations (Wilson, 1971;  
119 Hawkins et al., 2013, 2016; Mieszkowska et al., 2014). There was an early interest from  
120 conservation agencies (Cunningham et al., 1984) and it is listed as a UK Priority Marine  
121 Habitat (JNCC, 2008). Beyond the UK, whilst *S. alveolata* has been reported to occur on all  
122 coasts of the island of Ireland (hereafter ‘Ireland’ including both the Republic of Ireland and  
123 Northern Ireland), at the time of writing, only 40 records existed in the Oceanographic  
124 Biodiversity Information System (OBIS) database in comparison to 2357 for Britain (OBIS,  
125 2018). In Northern Ireland, *S. alveolata* was described as ‘unknown, not well mapped’ in the

126 UK National Ecosystem Assessment 2011. Furthermore, a Web of Science search for  
127 ‘*Sabellaria alveolata*’ and ‘Ireland’ produced a single paper (Culloty et al., 2010). Clearly,  
128 there is a lack of information on this important habitat around Ireland.

129

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

132 (1) identify regions with insufficient data that should be targeted for future sampling;

133 (2) describe the biodiversity (epibiotic and infaunal) associated with reefs. For epibiota,  
134 we hypothesised that algal richness and abundance would be higher on *S. alveolata*  
135 reef than on rock, and that grazer richness and abundance would be greater on rock  
136 than on *S. alveolata* reef, and for infauna, that richness and abundance would be  
137 higher in retrograding than in prograding reefs; and

138 (3) present a potential framework for data gathering that could potentially be applied to  
139 other habitats, species and regions. This information could be used to inform  
140 assessments of the status of data deficient species and habitats, thus providing  
141 potentially invaluable resources for sustained monitoring, management and  
142 conservation.

143

## 144 2. METHODS

145

### 146 2.1. *Identifying regions with insufficient data on the distribution of S. alveolata around* 147 *Ireland*

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

149 This paper focused on describing the most important environmental variables (i.e. wave  
150 height, tidal amplitude, stratification index, then substrate type) underpinning distribution  
151 patterns and abundance changes over time. The dataset used in that paper comprised data

152 from a range of sources including grey literature, museum specimens, published papers and  
153 publicly-available databases combined with records from field sampling (including intensive  
154 targeted sampling in the 1950s (by Denis Crisp and Alan Southward: Southward and Crisp,  
155 1954); 2003-2004 (the MarClim Project: Simkanin et al., 2005; Merder et al., 2018); and by  
156 co-authors of this paper between 2013-2018). Using the same dataset, here, we focus in on  
157 the six previously-identified discretely bounded regional populations. We examined the  
158 spread of both records and SACFOR abundance categories (S=Superabundant, A=Abundant,  
159 C=Common, F=Frequent, O=Occasional, R=Rare, and Not Seen). This enabled us to identify  
160 any spatial or temporal imbalances in the spread of distributional data. All data were mapped  
161 using ArcGIS (ESRI, 2016).

162

## 163 **2.2. Characterising the epibiotic and infaunal communities associated with *Sabellaria***

### 164 ***alveolata***

165 To test the hypothesis that *S. alveolata* reefs support higher algal richness and abundance and  
166 lower molluscan grazer richness and abundance than adjacent emergent rock (hereafter rock),  
167 a minimum of ten (and in most locations twenty) quadrats (25 cm × 25 cm) were randomly  
168 placed on both habitat types at eight locations between March and September 2016:

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

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

171 coverage of the Irish coastline, and because they had sufficient *S. alveolata* reef cover to

172 enable a high level of replication. Prograding reefs dominated by progradation phase are not

173 common in Ireland, and thus only retrograding reefs were sampled for epibiotic communities.

174 In each quadrat, percentage cover of algae was estimated (points occupied under a 10 × 10

175 grid), and all mobile grazers were identified and counted.

176

177 To test the hypothesis that infaunal richness and abundance would be higher in retrograding  
178 than prograding reefs, five samples of prograding reefs and five samples from retrograding  
179 reefs were taken at Duncannon, Co. Wexford and Inverin, Co. Galway (Figure 1c) in August  
180 2013 and May 2015 respectively. These locations were selected because they supported large  
181 patches ( $>1 \text{ m}^2$ ) comprising both prograding and retrograding phase types. Prograding  
182 patches were defined as having occupied tubes comprising  $>70\%$  of the area with no visible  
183 damage to the surface. Retrograding patches were defined as having  $>70\%$  of tubes appearing  
184 to be unoccupied by the worms. All samples were collected from the centre of patches ( $\sim 1$   
185  $\text{m}^2$ ) to avoid edge effects. At Inverin, reefs were compared with the adjacent sand ( $>1 \text{ m}$   
186 away from the reef) as an additional habitat comparison. Each sample was taken using a 10  
187 cm diameter circular corer to approximately 15 cm depth, and was preserved in 70%  
188 Industrial Methylated Spirits. In the laboratory, reef samples were carefully picked apart and  
189 washed through 500 $\mu\text{m}$  mesh. All individuals retained were identified to the lowest  
190 taxonomic level. Due to problems transporting samples from Inverin, only three were  
191 processed from each habitat type.

192

### 193 **2.3. Statistical analyses**

194 Epifauna: Comparison of algal abundance and richness, and molluscan grazer abundance and  
195 richness were made between reef types (prograding; retrograding) and locations (8) were  
196 compared using linear-mixed effects (lme) models including reef type and location as fixed  
197 and random factors respectively, and estimated using restricted maximum likelihood  
198 (REML). Optimal model selection for each metric was based on Akaike Information  
199 Criterion (AIC) (Zuur et al., 2009) and models were validated to check for normality and  
200 homogeneity of the residuals. Tukey post-hoc contrasts were used to compare differences  
201 between reef types within locations.

202

203 Infauna: Multiple one-factor analysis of variance (ANOVA) tests were used to compare  
204 richness and abundance among habitat types (prograding reef; retrograding reef; sand  
205 (Inverin only)) at Duncannon and Inverin locations, which were considered separately.  
206 Richness and abundance measures were calculated for 5 taxonomic classifications: (1) All  
207 taxa; (2) Annelida; (3) Arthropoda; (4) Mollusca; and (5) Other. Prior to ANOVA, tests for  
208 homogeneity of variance were performed using Levene's test (*car* package). Tukey post-hoc  
209 contrasts were used to compare habitat types at Inverin.

210

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

212

### 213 3. RESULTS

214

#### 215 *3.1. Identifying regions with insufficient data on the distribution of S. alveolata around* 216 *Ireland*

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

222

##### 223 *3.1.1. Subtidal populations*

224 Of the 27 subtidal records available (orange dots in Figure 2), only a single record from Clare  
225 Island (Southern, 1912) reported a negative observation (not seen); the rest were all positive  
226 observations, largely from grab sampling. Due to the discovery of a subtidal reef-forming  
227 population off Wicklow Head in 1997 (De Grave and Whitaker, 1997), the Wicklow Reef

228 Special Area of Conservation (SAC) was designated (*inter alia*) specifically for the presence  
229 of a subtidal *S. alveolata* reef based on the fact that it is “an extremely unusual feature and  
230 may be the first record for Britain and Ireland” (NPWS, 2014). Subsequent sampling of the  
231 region off Wicklow Head confirmed the presence of subtidal *S. alveolata* in the local area,  
232 but not necessarily at the exact location of the SAC. Furthermore, it is not known if it forms  
233 reefs. Other positive subtidal records exist from grab samples for outer Galway Bay, the Aran  
234 Islands, Carnsore Point and the Shannon Estuary.

235

### 236 3.1.2. Intertidal populations

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

251

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

268

269 The recent sampling that was carried out between 2013-2018 (Figures 2, 4d) provides the  
270 most up-to-date assessment of the distribution and abundance of *S. alveolata* around the Irish  
271 coastline. Sampling in the previously-identified distribution gaps confirmed that large  
272 swathes of coastline were devoid of *S. alveolata* (discussed in detail in Firth et al., 2020).  
273 Despite intensive sampling during this period and the filling in of important data gaps (i.e.  
274 Galway Bay, northwest and to a lesser degree Lough Swilly and the Dingle Peninsula), most  
275 regions remain relatively poorly sampled with <50 records each. Galway Bay was the most  
276 intensively sampled region, and was split based on relative differences in SACFOR

277 abundance categories. Galway Bay North exhibited high prevalence (67%) of the higher  
278 SACFOR categories (i.e. Abundant/Common) and low prevalence of negative observations  
279 (4%) (Figure 4d). Conversely, Galway Bay South exhibited low prevalence (5%) of the  
280 higher SACFOR categories and high prevalence of negative observations (74%) (Figure 4d).  
281 Of the 35 records from the northwest, 77% exhibited the higher SACFOR categories. Whilst  
282 few records (<10 each) were available for the Dingle and Lough Swilly, both regions  
283 supported populations exhibiting the higher SACFOR categories.

284

285

### 286 **3.2. Characterising the epibiotic and infaunal communities associated with *Sabellaria***

#### 287 ***alveolata***

288 A total of 40 taxa were recorded across all seven locations comprising 22 algae, eight  
289 molluscs, four annelids, three arthropods and one taxon each of lichen, cnidarian and  
290 bryozoan. Of these, 36 taxa (90%) were recorded on *S. alveolata* reefs (13 unique, including  
291 11 algae) and 25 taxa (63%) were recorded on rock (four unique) (Table S1). *Sabellaria*  
292 *alveolata* reef supported significantly greater algal richness ( $F_{1,251} = 191.1$ ,  $P < 0.0001$ ) and  
293 algal abundance ( $F_{1,251} = 112.1$ ,  $P < 0.0001$ ) than rock at the majority of locations (Figure  
294 5a,b). Conversely, rock supported significantly greater molluscan grazer richness ( $F_{1,251} =$   
295  $215.7$ ,  $P < 0.0001$ ) and abundance ( $F_{1,251} = 179.8$ ,  $P < 0.0001$ ) than *S. alveolata* reef at all  
296 locations (Figure 5c,d).

297

### 298 **3.3 Comparison of infaunal communities among *S. alveolata* reef phases and sand**

299 Excluding *S. alveolata*, 77 infaunal taxa were recorded across both locations comprising 36  
300 arthropods, 26 annelids, 10 molluscs and five 'other phyla' (comprising Cnidaria, Sipuncula,  
301 Nemertea and Nematoda). Of these, 75 taxa (97%) were recorded on *S. alveolata* reefs (67  
302 unique) and 10 were recorded in sand (two unique) (Table S2). The results varied among

303 response variables and locations. At Duncannon, overall mean richness was statistically  
304 higher in retrograding compared with prograding reef patches (Figure 6a). There were no  
305 significant differences in abundances between prograding and retrograding reef patches at  
306 Duncannon (Figure 6b). At Inverin, mean richness was similar between retrograding and  
307 prograding reef patches for the majority of groups compared; except arthropoda and other  
308 taxa, which were significantly higher in retrograding than prograding reef patches (Figure  
309 6c). In general, sand supported significantly lower richness and abundance than retrograding  
310 reef patches (Figure 6c,d).

311

312

#### 313 4. DISCUSSION

314

315 Through combining the best available historical and contemporary data, spanning 182 years,  
316 we provide a comprehensive account of broad-scale distribution and abundance of a data  
317 deficient species in a previously data deficient region. We increased the number of records  
318 25-fold from 40 in the OBIS database (OBIS, 2018) to 981; importantly many of these were  
319 absences (67%), enabling us to reliably determine discontinuities in the distribution and  
320 imbalances in the dataset. Despite filling an important knowledge gap for a species of  
321 conservation concern, sampling intensity was imbalanced both spatially and temporally. For  
322 example, 221 records for Northern Ireland make up 23% of our database. The Northern Irish  
323 coastline has received a disproportionate degree of sampling compared with the much longer  
324 coastline of the Republic of Ireland. Similarly, Galway Bay is the only region that has been  
325 sampled with high intensity (and recently), revealing that the north shoreline exhibits a  
326 greater percentage (67%) of higher SACFOR records than the south shoreline (5%). This is  
327 likely to be due to the much-reduced wave energy, and thus greater accumulation of finer  
328 silty sediments on the south shoreline, which in turn is less suitable for tube building than the

329 larger-grained sandy environment that characterises the north shoreline (O'Connor et al.,  
330 1993). Without intensive sampling, such observations would not be possible.

331

332 A number of locations have been identified as requiring better protection. Despite Duncannon  
333 exhibiting the most extensive stretches of reef in Ireland that are located within the River  
334 Barrow and River Nore SAC (NPWS, 2011, for which *S. alveolata* reefs are specifically  
335 listed as features of interest), this was the only location where a winkle (*Littorina littorea* L.  
336 1758) picker was observed kicking off large chunks of *S. alveolata* reef to access winkles.  
337 Similarly, Preston and Portig (2001) identified winkle collection as a considerable threat to *S.*  
338 *alveolata* at locations in the northeast (Glasdrumman and Ringboy/Minerstown). Further  
339 information on damage caused by harvesting and trampling (Dubois et al., 2002; Plicanti et  
340 al., 2016), or local human activities such as shellfish farming (Dubois et al., 2006) would be  
341 beneficial for identifying locations in need of protection and management, as well as public  
342 awareness efforts (e.g. information boards).

343

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

353

354 *S. alveolata* reefs in Ireland were typically characterised by a mosaic of development phases  
355 at small spatial scales (<1m), rather than being dominated by either progradation or  
356 retrogradation phase, as can be seen on the larger reefs in Mont-Saint-Michel Bay (Gruet,  
357 1986; Curd et al., 2019). These mosaic reefs were found to support greater algal diversity and  
358 abundance compared with adjacent rock. In addition to algae living as epibionts directly on  
359 the surface of the *S. alveolata* reefs, many macroalgal species can be attached directly to rock  
360 and protrude up through cracks in the reef. Despite these algae being attached to the rock,  
361 they are likely to still benefit from a combination of physical habitat amelioration and  
362 associational defence (Bertness et al., 1999) from grazing provided by the reef structure.

363

364 Mosaics of habitat patches, with varying amounts of primary or secondary producers, can  
365 make a major contribution to ecosystem functioning (Giller et al., 2004), with habitat patch  
366 diversity perhaps being more important than species diversity per se in open ecosystems.  
367 Biogenic habitats are noted for their structural complexity, facilitating diverse communities  
368 through habitat and refuge provision (Hughes et al., 2014; Walls et al., 2018; Bertolini et al.,  
369 2020). Had it been possible to sample large enough patches that were dominated by the  
370 progradation phase, it is unlikely that such patterns would have been observed, and it is  
371 assumed that few algae (or indeed other organisms) would have been attached to the reefs.  
372 Prograding reefs comprise tightly-packed tubes containing live individuals and consist almost  
373 entirely of feeding apertures (Wilson, 1968, 1971), which greatly reduce the probability of  
374 successful settlement by larvae of other species and inhibit overgrowth by adjacent organisms  
375 (Jackson, 1977).

376

377 Grazer diversity and abundance was higher on rock compared with *S. alveolata* reefs. A  
378 recent study by Muller et al. (2021) found no grazers represented in the infaunal community

379 associated with *S. alveolata* reefs. Similar inverse patterns of predator/prey abundance have  
380 been observed in mussel beds due to reduced predation pressure within mussel beds  
381 (Witman, 1985). These processes do not necessarily translate when it comes to grazer/algae  
382 relationships. For example, O'Connor and Crowe (2008) found that algae were more  
383 abundant and diverse within mussel beds than on adjacent rock; but experimental testing of  
384 grazing patterns revealed that grazing intensity was similar between the two habitats  
385 suggesting that grazing pressure was not the underlying driver. Crowe et al. (2011) factorially  
386 manipulated limpet grazing and mussel cover, and showed that whilst mussels provided a  
387 refuge (particularly for furoid germlings) from grazing activity of limpets, other grazing  
388 gastropods were actually found in greater abundance in mussel beds (a pattern also observed  
389 by Wangkulankul et al., 2016), and that there was some evidence of an inverse relationship  
390 between abundance of limpets and other grazers. This highlights that limpets are key grazers  
391 in this system as they are throughout the North-east Atlantic (Hawkins, 1981; Coleman et al.,  
392 2006; Jenkins et al., 2005), and that their grazing activity cannot be matched by other grazers  
393 (O'Connor and Crowe, 2005). Whilst it is probable that *Sabellaria* reefs provides a refuge for  
394 grazing activity from grazers (particularly limpets), experimental manipulation is necessary  
395 before any conclusions can be drawn about the role of grazers in driving epibiotic  
396 biodiversity patterns.

397

398 The 77 infaunal taxa comprised a combination of intertidal, subtidal and terrestrial taxa (i.e.  
399 fly larvae), highlighting that the reefs support a unique combination of taxa from a range of  
400 different environments (Dubois et al., 2002). None of the taxa recorded were of particular  
401 note in terms of rarity or conservation value, although some may be considered important as  
402 either fishing bait (ragworms, *Nereis* and *Nephtys*) or due to their commercial importance  
403 (*Mytilus edulis* L. 1758). *Sabellaria alveolata* reefs and their surrounding sedimentary

404 habitats are known to support species of commercial importance (Dubois et al., 2006; Plicanti  
405 et al., 2016; Schimmenti et al., 2015), and the worms themselves are also collected as fishing  
406 bait, particularly in the Mediterranean (Gambi et al., 1992). By comparison with continental  
407 Europe, harvesting and bait collection are not currently considered to be especially  
408 detrimental activities in Ireland. The harvesting of winkles (*L. littorea*), purple urchins  
409 (*Paracentrotus lividus* Lamarck, 1816) and mussels (*Mytilus* spp.) are perhaps the most  
410 prevalent activities (Cummins et al., 2002; Fahy et al., 2008), and may have detrimental  
411 impacts on *S. alveolata* reefs.

412  
413 *Sabellaria alveolata* populations fluctuate naturally over time (Gruet, 1986), exhibiting  
414 different life history characteristics, with some colonies growing rapidly while others appear  
415 more senescent, mainly due to very patchy settlements of juveniles onto the reef. Little  
416 experimental work has explored the natural drivers of change, but it has been asserted that  
417 algal blooms and competition for space with competitors such as filter-feeding barnacles and  
418 mussels (Multer and Milliman, 1967) can lead to the weakening of reef structures rendering  
419 them more susceptible to erosion by waves (Wilson, 1971). Extreme climatic events  
420 (extensive colds or intense storms) are known to have long-term effects on reef structures  
421 (Crisp, 1964; Firth et al., 2015, 2020), with long-term and wide-reaching cascading effects.  
422 Furthermore, anthropogenic drivers such as trampling, harvesting of organisms from the reefs  
423 and collection of the worms for bait are all known to expedite the retrogradation process  
424 (Cunningham et al., 1984; Plicanti et al., 2016). Irrespective of morphological type or phase,  
425 all types of reefs (even dead ones) carry out important ecosystem functions and services  
426 (Sheehan et al., 2015; Gribben et al., 2017). Therefore, even the most 'degraded' reefs may  
427 provide an important structuring function, providing substrate for colonisation of benthic  
428 organisms (Dubois et al., 2002; Jones et al., 2018). They have an important legacy effect

429 through potentially serve as catalysts for future large and prograding reefs due to gregarious  
430 settlement of larvae that are attracted to the tube sand and its cement (Wilson, 1968; Pawlik,  
431 1988).

432

433 Assessing variability in habitat distribution and abundance is also important at a time when  
434 the implementation of some marine policies (such as the establishment of marine reserves  
435 and protected sites such as Special Areas of Conservation (SACs)) assumes a degree of  
436 stability in the features being protected. The Wicklow Reef SAC provides an interesting  
437 example of this. The location was designated for the presence of *S. alveolata*, but a report  
438 from the National Parks and Wildlife Service (NPWS, 2013) pointed out that the occurrence  
439 of *S. alveolata* within this site may be questionable and that the highly dynamic nature of this  
440 area is unlikely to support a stable biogenic reef composed of *S. alveolata* for any length of  
441 time. This highlights the importance of sustained observations, particularly relating to the  
442 designation of sites for the conservation of ephemeral or variable species or habitats.

443 Incidentally, during the writing of this paper, the Irish government announced plans to  
444 expand Ireland's Marine Protected Area network to 30% by 2030 (currently at 2.13%,  
445 Gov.ie., 2021). The results from this study will feed into this consultation.

446

447 With such fine-scale mapping of the distribution of this important reef-forming species, it is  
448 anticipated that this will be of significant use to those tasked with the management and  
449 protection of these habitats. This is particularly important as it comes at a time when cross-  
450 border management is very likely to become challenged due to potential changes in  
451 legislation, for example the exit of the UK from the European Union on 1<sup>st</sup> January 2021  
452 (Boyes and Elliott, 2016; Hawkins, 2017). The vast majority of environmental policy and  
453 legislation in the Republic of Ireland, Northern Ireland, and the UK as a whole, is governed

454 by legal frameworks and regulations set at the European Union level. The island of Ireland is  
455 an excellent example of the need for joint coordinated national responses to achieve effective  
456 resource management between the two jurisdictions (Stokes et al., 2006; Knights et al.,  
457 2015). This highlights the importance of achieving a potential future: a “one island - two  
458 systems” governance framework (Boyes and Elliott, 2016). This is a wider issue that applies  
459 at other national boundaries globally (Hawkins, 2017).

460

## 461 5. CONCLUSIONS

462 Through combining the best available historical and contemporary data, an important  
463 knowledge gap has been filled in the distribution and abundance of a data deficient species in  
464 a data deficient region. Absence of evidence is not evidence of absence: information on both  
465 positive and negative observations collated from a variety of sources can inform estimates of  
466 detectability of species, indicate decline in population or range size, and, ultimately, inform  
467 reassessment to data-sufficient categories (Good et al., 2006). This is particularly true for  
468 biogenic habitat-forming species, for which the mechanisms underpinning reef dynamics are  
469 not fully understood. This type of research could easily be carried out for other data deficient  
470 species and regions. Through doing this, the information gathered could inform future IUCN  
471 assessments. Undoubtedly, species and habitats that are currently classed as ‘Data deficient’  
472 on the IUCN Red Lists would be re-assigned - in many cases to ‘least concern’ (as we  
473 suspect is the case for *S. alveolata*). The data contained in the wide variety of sources that  
474 were used here provide the raw material for data mining and data archaeology. In this current  
475 setting of the global pandemic and cuts in state-funded science, historical and unpublished  
476 data, in addition to data from citizen science projects (Vye et al., 2020) represent potentially  
477 invaluable resources for sustained monitoring, management and conservation (Hawkins et al.,  
478 2013).

479

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493

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893 Table 1. SACFOR scale of abundance used to record *Sabellaria alveolata*. Adapted from  
 894 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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909 **Figures**

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

915  
916 Figure 2. Map illustrating the presence (full circles) and absence (empty circles) of *Sabellaria*  
917 *alveolata* around Ireland. All records for intertidal (green circles) and subtidal (orange  
918 circles) observations between 1836 and 2018 are shown. (a-f) Maps of the six discretely-  
919 bounded populations in Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway  
920 Bay and the northwest. For zoomed-in maps, only data from 2013-2018 are shown.

921  
922 Figure 3. (a) Photo of the *Sabellaria alveolata* reefs at Duncannon, Co. Wexford. (b) Image  
923 showing extent (~14ha in 2015) of the reefs at Duncannon. The conservation of *S. alveolata*  
924 reefs at Duncannon was specifically mentioned as a target in the River Barrow and River  
925 Nore Special Area of Conservation (site code: 2162) Conservation Objectives (NPWS, 2011).

926  
927 Figure 4. Summary of the relative frequency of occurrence of the various SACFOR scores for  
928 each of the six discretely-bounded populations: Lough Swilly, the northeast, south coast,  
929 Dingle Peninsula, Galway Bay (separated into north and south), and the northwest. (a) all  
930 intertidal records collated from all sources spanning the entire sampling period 1836-2018.  
931 The numbers on the right represent the total number of all records spanning the entire study  
932 period for each regional population. (b) all intertidal records collected by Crisp and  
933 Southward in the 1950s; (c) all intertidal records collected during the MarClim project 2003-

934 2004; (d) all intertidal records collected by co-authors of this paper 2013-2018. Note the scale  
935 on the X-axis changes in each panel. These three temporal sub-sets of data were selected  
936 because they had sufficient geographic coverage and reported SACFOR estimates. The  
937 numbers on the right in b-c represent the % of all records for each region represented by that  
938 temporal subset. Note that other records for each region exist outside these temporal subsets.  
939

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

944

945 Figure 6. Mean (a) infaunal richness and (b) infaunal abundance among progradation (black  
946 bars) and retrogradation phases (white bars) of *Sabellaria alveolata* reefs at Duncannon (n=5  
947 ± SE). Mean (c) infaunal richness and (d) infaunal abundance among progradation and  
948 retrogradation phases of *S. alveolata* reefs and adjacent sand (grey bars) at Inverin (n=3 ±  
949 SE). *Sabellaria alveolata* was not included in calculations of either richness or abundance of  
950 all species or annelids. NS = Not significant; \*\* P < 0.01. For Inverin, letters above bars  
951 denote significant differences between treatments.

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959 **TITLE:**

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

962

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997

## 998 **Abstract**

999 Data that can be used to monitor biodiversity through time are essential for conservation and  
1000 management. The reef-forming worm, *Sabellaria alveolata* (L. 1767) is currently classed as  
1001 ‘Data deficient’ due to an imbalance in the spread of data on its distribution. Little is known  
1002 about the distribution of this species around Ireland. Using data archaeology, we collated past  
1003 and present distribution records and discovered that *S. alveolata* has a discontinuous  
1004 distribution with large gaps in distribution. Many regions lack data and should be targeted for  
1005 sampling. Biodiversity surveys revealed that *S. alveolata* supported diverse epibiotic algal  
1006 communities. Retrograding (declining) reefs supported greater infaunal diversity than  
1007 prograding (growing) reefs or sand, suggesting that *S. alveolata* is a dynamic ecosystem  
1008 engineer that has a lasting legacy effect. Similar research should be carried out for other data

1009 deficient species, habitats and regions. Such data are invaluable resources for management  
1010 and conservation.

1011

1012 **Keywords**

1013 Baseline data, Biodiversity, Biogenic habitat, Marine Protected Area, Reef, Sustained  
1014 observations

1015

1016 **1. INTRODUCTION:**

1017 Biodiversity loss in the face of global environmental change is one of the greatest challenges  
1018 of our time. Increasingly, extinctions are being documented coupled with predictions of the  
1019 sixth mass extinction, primarily as a result of anthropogenic activities (Wake and  
1020 Vredenburg, 2008). In 2021, the Convention on Biological Diversity (CBD) will adopt a  
1021 post-2020 global biodiversity framework as a stepping stone towards the 2050 Vision of  
1022 'Living in harmony with nature'. Understanding the level of extinction risk faced by poorly-  
1023 mapped species and why interspecific differences in risk arise remains one of the greatest  
1024 challenges facing conservation biology. Assessment frameworks for threatened species are  
1025 crucial to identifying risk and monitoring progress toward CBD targets (Jones et al., 2011).  
1026 One of the most well-known is the International Union for Conservation of Nature (IUCN)  
1027 Red List (Bland et al., 2017; IUCN, 2020). Despite recent improvement in the taxonomic  
1028 coverage of the IUCN Red List (Bland et al., 2015), ~15% of the >65,000 species assessed  
1029 are still classified as data deficient due to a lack of information on taxonomy, geographic  
1030 distribution, population status, or threats (IUCN, 2020). A taxon in this category may be well  
1031 studied, and its biology well known, but appropriate data on abundance and/or distribution  
1032 may be lacking resulting in this 'data deficient' classification.

1033

1034 In the marine environment, biogenic reefs formed by corals, bivalves and polychaetes have  
1035 long been recognised for their role in ecosystem functioning and the consequent services that  
1036 they provide (Beck et al., 2011; Lemasson et al., 2017). The concept that biogenic reefs  
1037 promote biodiversity is also well known (e.g. corals: Cornell and Karlson, 2000; Buhl-  
1038 Mortenson et al., 2010; mussels: D'Anna et al., 1985; oysters: Lenihan, 1999). Diversity  
1039 patterns can vary with reef development phases (Grigg, 1983), especially in dynamic reef  
1040 building species such as sand or honeycomb worms such as *Phragmatopoma*, *Gunnarea* and  
1041 *Sabellaria* (Gruet, 1986; Dubois et al., 2002; Curd et al., 2019). Temperate biogenic reefs are  
1042 probably among the most threatened habitats globally (Beck et al., 2011). For example, in  
1043 Europe, biogenic reefs are listed under Annex 1 of the Habitats Directive, which records the  
1044 habitat types that are considered to be the most in need of conservation at a European level  
1045 (Holt et al., 1998). The European Red List of Habitats (Gubbay et al., 2017) identified that  
1046 60% of biogenic reef habitats in Europe were data deficient. Of those for which there were  
1047 sufficient data, 50% were considered to be either critically endangered or endangered.

1048  
1049 The honeycomb worm *Sabellaria alveolata* L. (Figure 1) is a warm-water reef-forming  
1050 species that is distributed from Morocco/Western Sahara to southwest Scotland (Gruet, 1986;  
1051 Curd et al., 2020; Lourenço et al., 2020). *Sabellaria alveolata* is a broadcast spawner that  
1052 produces planktotrophic larvae, which settle and metamorphose preferentially on the  
1053 cemented sand tubes of conspecific adults (Wilson, 1968), typically in areas where rocky  
1054 reefs abut sandy beaches supplying coarse sand for tube-building (Gruet, 1984). Colonies of  
1055 individuals can form biogenic structures ranging from small patches, hummocks, and veneers  
1056 to the largest biogenic reefs in Europe (5.52 and 6.76 ha, Bajjouk et al., 2020) in Mont-Saint-  
1057 Michel Bay, France (Holt et al., 1998; Lecornu et al., 2016). The worms, their biogenic  
1058 structures (hereafter 'reefs') and the associated biological communities play an important role

1059 in ecosystem functioning, delivering services such as nutrient cycling, biofiltration and wave  
1060 attenuation (Dubois et al., 2009; Lefebvre et al., 2009; Cugier et al., 2010; Jones et al., 2018).  
1061 On rock, *S. alveolata* can be ecologically dominant, overgrowing and displacing other  
1062 common rocky-reef assemblages developing at similar tidal levels such as mussels or brown  
1063 macroalgae (Wilson, 1971). Reefs undergo natural cycles of growth (progradation) and  
1064 decline (retrogradation) (*sensu* Curd et al., 2019 after Gruet, 1986) that are reflected in their  
1065 appearance and associated biodiversity. Prograding reefs are typically dominated by occupied  
1066 tubes and have few epibionts, whereas retrograding reefs are characterised by mosaics of  
1067 occupied and unoccupied tubes that show signs of reef erosion and extensive coverage of  
1068 epibionts and biofilms (Wilson, 1976; Curd et al., 2019).

1069

1070 Despite being recognised as an ecologically important habitat and designated for protection  
1071 under international legislation such as the EU Habitats Directive (EEC/92/43), *S. alveolata*  
1072 reefs are listed in the IUCN European Red List of Habitats as ‘Data deficient’ (Bertocci et al.,  
1073 2017; Gubbay et al., 2017). Whilst a small number of regions have been subject to  
1074 experimental research (e.g. northern France (Dubois et al., 2002) and Sicily (Bertocci et al.,  
1075 2017)), little is known about its distribution or ecology outside of the UK, where there is a  
1076 strong natural history heritage and a tradition of sustained observations (Wilson, 1971;  
1077 Hawkins et al., 2013, 2016; Mieszkowska et al., 2014). There was an early interest from  
1078 conservation agencies (Cunningham et al., 1984) and it is listed as a UK Priority Marine  
1079 Habitat (JNCC, 2008). Beyond the UK, whilst *S. alveolata* has been reported to occur on all  
1080 coasts of the island of Ireland (hereafter ‘Ireland’ including both the Republic of Ireland and  
1081 Northern Ireland), at the time of writing, only 40 records existed in the Oceanographic  
1082 Biodiversity Information System (OBIS) database in comparison to 2357 for Britain (OBIS,  
1083 2018). In Northern Ireland, *S. alveolata* was described as ‘unknown, not well mapped’ in the

1084 UK National Ecosystem Assessment 2011. Furthermore, a Web of Science search for  
1085 ‘*Sabellaria alveolata*’ and ‘Ireland’ produced a single paper (Culloty et al., 2010). Clearly,  
1086 there is a lack of information on this important habitat around Ireland.

1087

1088 Recognising the importance of *S. alveolata* and the paucity of information on its distribution  
1089 and ecology in Ireland, our goals were to:

1090 (1) identify regions with insufficient data that should be targeted for future sampling;

1091 (2) describe the biodiversity (epibiotic and infaunal) associated with reefs. For epibiota, we  
1092 hypothesised that algal richness and abundance would be higher on *S. alveolata* reef than on  
1093 rock, and that grazer richness and abundance would be greater on rock than on *S. alveolata*  
1094 reef, and for infauna, that richness and abundance would be higher in retrograding than in  
1095 prograding reefs; and

1096 (3) present a potential framework for data gathering that could potentially be applied to  
1097 other habitats, species and regions. This information could be used to inform assessments  
1098 of the status of data deficient species and habitats, thus providing potentially invaluable  
1099 resources for sustained monitoring, management and conservation.

1100

## 1101 2. METHODS

1102

### 1103 ***2.1. Identifying regions with insufficient data on the distribution of *S. alveolata* around*** 1104 ***Ireland***

1105 The distribution of *S. alveolata* around Ireland was recently described by Firth et al. (2020).

1106 This paper focused on describing the most important environmental variables (i.e. wave  
1107 height, tidal amplitude, stratification index, then substrate type) underpinning distribution  
1108 patterns and abundance changes over time. The dataset used in that paper comprised data  
1109 from a range of sources including grey literature, museum specimens, published papers and

1110 publicly-available databases combined with records from field sampling (including intensive  
1111 targeted sampling in the 1950s (by Denis Crisp and Alan Southward: Southward and Crisp,  
1112 1954); 2003-2004 (the MarClim Project: Simkanin et al., 2005; Merder et al., 2018); and by  
1113 co-authors of this paper between 2013-2018). Using the same dataset, here, we focus in on  
1114 the six previously-identified discretely bounded regional populations. We examined the  
1115 spread of both records and SACFOR abundance categories (S=Superabundant, A=Abundant,  
1116 C=Common, F=Frequent, O=Occasional, R=Rare, and Not Seen). This enabled us to identify  
1117 any spatial or temporal imbalances in the spread of distributional data. All data were mapped  
1118 using ArcGIS (ESRI, 2016).

1119

## 1120 ***2.2. Characterising the epibiotic and infaunal communities associated with Sabellaria*** 1121 ***alveolata***

1122 To test the hypothesis that *S. alveolata* reefs support higher algal richness and abundance and  
1123 lower molluscan grazer richness and abundance than adjacent emergent rock (hereafter rock),  
1124 a minimum of ten (and in most locations twenty) quadrats (25 cm × 25 cm) were randomly  
1125 placed on both habitat types at eight locations between March and September 2016:  
1126 Glasdrumman, Balbriggan, Duncannon, Bunmahon, Spiddal, Inverin, Bundoran and  
1127 Buncrana (Figure 1c). These locations were selected based on their broad geographic  
1128 coverage of the Irish coastline, and because they had sufficient *S. alveolata* reef cover to  
1129 enable a high level of replication. Prograding reefs dominated by progradation phase are not  
1130 common in Ireland, and thus only retrograding reefs were sampled for epibiotic communities.  
1131 In each quadrat, percentage cover of algae was estimated (points occupied under a 10 × 10  
1132 grid), and all mobile grazers were identified and counted.

1133

1134 To test the hypothesis that infaunal richness and abundance would be higher in retrograding  
1135 than prograding reefs, five samples of prograding reefs and five samples from retrograding  
1136 reefs were taken at Duncannon, Co. Wexford and Inverin, Co. Galway (Figure 1c) in August  
1137 2013 and May 2015 respectively. These locations were selected because they supported large  
1138 patches ( $>1\text{ m}^2$ ) comprising both prograding and retrograding phase types. Prograding  
1139 patches were defined as having occupied tubes comprising  $>70\%$  of the area with no visible  
1140 damage to the surface. Retrograding patches were defined as having  $>70\%$  of tubes appearing  
1141 to be unoccupied by the worms. All samples were collected from the centre of patches ( $\sim 1$   
1142  $\text{m}^2$ ) to avoid edge effects. At Inverin, reefs were compared with the adjacent sand ( $>1\text{ m}$   
1143 away from the reef) as an additional habitat comparison. Each sample was taken using a 10  
1144 cm diameter circular corer to approximately 15 cm depth, and was preserved in 70%  
1145 Industrial Methylated Spirits. In the laboratory, reef samples were carefully picked apart and  
1146 washed through  $500\mu\text{m}$  mesh. All individuals retained were identified to the lowest  
1147 taxonomic level. Due to problems transporting samples from Inverin, only three were  
1148 processed from each habitat type.

1149

### 1150 **2.3. Statistical analyses**

1151 Epifauna: Comparison of algal abundance and richness, and molluscan grazer abundance and  
1152 richness were made between reef types (prograding; retrograding) and locations (8) were  
1153 compared using linear-mixed effects (lme) models including reef type and location as fixed  
1154 and random factors respectively, and estimated using restricted maximum likelihood  
1155 (REML). Optimal model selection for each metric was based on Akaike Information  
1156 Criterion (AIC) (Zuur et al., 2009) and models were validated to check for normality and  
1157 homogeneity of the residuals. Tukey post-hoc contrasts were used to compare differences  
1158 between reef types within locations.

1159

1160 Infauna: Multiple one-factor analysis of variance (ANOVA) tests were used to compare  
1161 richness and abundance among habitat types (prograding reef; retrograding reef; sand  
1162 (Inverin only)) at Duncannon and Inverin locations, which were considered separately.  
1163 Richness and abundance measures were calculated for 5 taxonomic classifications: (1) All  
1164 taxa; (2) Annelida; (3) Arthropoda; (4) Mollusca; and (5) Other. Prior to ANOVA, tests for  
1165 homogeneity of variance were performed using Levene's test (*car* package). Tukey post-hoc  
1166 contrasts were used to compare habitat types at Inverin.

1167

1168 All statistical analyses were performed in R (R Core Team, 2020).

1169

### 1170 3. RESULTS

1171

#### 1172 *3.1. Identifying regions with insufficient data on the distribution of S. alveolata around* 1173 *Ireland*

1174 A total of 981 records were collated between 1836 and 2018: 319 (33%) of these were  
1175 'positive' observations (i.e. present) and 662 (67%) were 'negative' observations (i.e.  
1176 absent/not seen). The vast majority of the records (954) were from intertidal habitats with  
1177 very few records from subtidal habitats (27). Unsurprisingly, sampling effort varied spatially  
1178 and temporally, resulting in an imbalance of records among regions and sampling periods.

1179

##### 1180 *3.1.1. Subtidal populations*

1181 Of the 27 subtidal records available (orange dots in Figure 2), only a single record from Clare  
1182 Island (Southern, 1912) reported a negative observation (not seen); the rest were all positive  
1183 observations, largely from grab sampling. Due to the discovery of a subtidal reef-forming  
1184 population off Wicklow Head in 1997 (De Grave and Whitaker, 1997), the Wicklow Reef

1185 Special Area of Conservation (SAC) was designated (*inter alia*) specifically for the presence  
1186 of a subtidal *S. alveolata* reef based on the fact that it is “an extremely unusual feature and  
1187 may be the first record for Britain and Ireland” (NPWS, 2014). Subsequent sampling of the  
1188 region off Wicklow Head confirmed the presence of subtidal *S. alveolata* in the local area,  
1189 but not necessarily at the exact location of the SAC. Furthermore, it is not known if it forms  
1190 reefs. Other positive subtidal records exist from grab samples for outer Galway Bay, the Aran  
1191 Islands, Carnsore Point and the Shannon Estuary.

1192

### 1193 3.1.2. Intertidal populations

1194 Of the 954 intertidal records collated, 293 (31%) were positive observations and 661 (69%)  
1195 were negative observations. *S. alveolata* has a discontinuous distribution around the Irish  
1196 coastline, with six discretely-bounded populations found in the northeast (Coney Island, Co.  
1197 Down to Howth, Co. Dublin), south coast (Cullenstown, Co. Wexford to Galley Head, Co.  
1198 Cork), Dingle Peninsula, Galway Bay (Black Head, Co. Clare to Cloghmore, Co. Galway),  
1199 northwest (Killala Bay, Co. Mayo to Fintra Beach, Co. Donegal) and Lough Swilly (Figure  
1200 2). The northernmost population was found at Portsalon, Co. Donegal (55.21°N), and two  
1201 coincident leading range edges were identified on the north coast (Dunree, Lough Swilly, Co.  
1202 Donegal) and the east coast (Greencastle Rocks, Carlingford Lough, Co. Down). The reefs  
1203 located at Duncannon, Co. Wexford represent the largest (~14ha in 2015, compared to  
1204 previous estimate of 20ha (NPWS, 2011)) and best example of intertidal reefs (in terms of  
1205 both condition and extent) in Ireland (Figure 3); and one of the only locations dominated by  
1206 prograding reefs. It is also the only location surveyed that was assigned the Superabundant  
1207 SACFOR category.

1208

1209 Sampling effort varied spatially and temporally (Figure 4). Over the longer term, the  
1210 northeast and the south coasts appeared to be subjected to intensive sampling (123 and 148  
1211 records respectively, Figure 4a). In both regions, however, the majority of the records were  
1212 collected prior to 2013. Data collected between 2013-2018 for the northeast and south coasts  
1213 only represented 22% and 14% of records respectively for each region across the entire study  
1214 period. This suggests that these regions were under-sampled in the most recent intensive  
1215 sampling. Due to the availability of sufficient historical data at the same locations over time,  
1216 long-term comparisons were possible for both regions. Locations in the northeast had few  
1217 records in the higher SACFOR categories (figures 2, 4), and populations were very ‘dynamic’  
1218 through time with evidence of population increases, declines, extirpations and recolonisations  
1219 throughout the region (discussed in detail in Firth et al., 2020). In contrast, the south coast  
1220 exhibited greater stability over time, with many locations exhibiting persistently higher  
1221 SACFOR abundance categories through time (Figure 4). The remaining regions were  
1222 generally poorly sampled (<70 records in total), with most regions either having very few  
1223 records in total (i.e. Lough Swilly (13) and Dingle (21)) or very few older records (all except  
1224 northeast and south). This limited any meaningful temporal comparison.

1225

1226 The recent sampling that was carried out between 2013-2018 (Figures 2, 4d) provides the  
1227 most up-to-date assessment of the distribution and abundance of *S. alveolata* around the Irish  
1228 coastline. Sampling in the previously-identified distribution gaps confirmed that large  
1229 swathes of coastline were devoid of *S. alveolata* (discussed in detail in Firth et al., 2020).  
1230 Despite intensive sampling during this period and the filling in of important data gaps (i.e.  
1231 Galway Bay, northwest and to a lesser degree Lough Swilly and the Dingle Peninsula), most  
1232 regions remain relatively poorly sampled with <50 records each. Galway Bay was the most  
1233 intensively sampled region, and was split based on relative differences in SACFOR

1234 abundance categories. Galway Bay North exhibited high prevalence (67%) of the higher  
1235 SACFOR categories (i.e. Abundant/Common) and low prevalence of negative observations  
1236 (4%) (Figure 4d). Conversely, Galway Bay South exhibited low prevalence (5%) of the  
1237 higher SACFOR categories and high prevalence of negative observations (74%) (Figure 4d).  
1238 Of the 35 records from the northwest, 77% exhibited the higher SACFOR categories. Whilst  
1239 few records (<10 each) were available for the Dingle and Lough Swilly, both regions  
1240 supported populations exhibiting the higher SACFOR categories.

1241

1242

### 1243 ***3.2. Characterising the epibiotic and infaunal communities associated with Sabellaria*** 1244 ***alveolata***

1245 A total of 40 taxa were recorded across all seven locations comprising 22 algae, eight  
1246 molluscs, four annelids, three arthropods and one taxon each of lichen, cnidarian and  
1247 bryozoan. Of these, 36 taxa (90%) were recorded on *S. alveolata* reefs (13 unique, including  
1248 11 algae) and 25 taxa (63%) were recorded on rock (four unique) (Table S1). *Sabellaria*  
1249 *alveolata* reef supported significantly greater algal richness ( $F_{1,251} = 191.1$ ,  $P < 0.0001$ ) and  
1250 algal abundance ( $F_{1,251} = 112.1$ ,  $P < 0.0001$ ) than rock at the majority of locations (Figure  
1251 5a,b). Conversely, rock supported significantly greater molluscan grazer richness ( $F_{1,251} =$   
1252  $215.7$ ,  $P < 0.0001$ ) and abundance ( $F_{1,251} = 179.8$ ,  $P < 0.0001$ ) than *S. alveolata* reef at all  
1253 locations (Figure 5c,d).

1254

### 1255 ***3.3 Comparison of infaunal communities among S. alveolata reef phases and sand***

1256 Excluding *S. alveolata*, 77 infaunal taxa were recorded across both locations comprising 36  
1257 arthropods, 26 annelids, 10 molluscs and five 'other phyla' (comprising Cnidaria, Sipuncula,  
1258 Nemertea and Nematoda). Of these, 75 taxa (97%) were recorded on *S. alveolata* reefs (67

1259 unique) and 10 were recorded in sand (two unique) (Table S2). The results varied among  
1260 response variables and locations. At Duncannon, overall mean richness was statistically  
1261 higher in retrograding compared with prograding reef patches (Figure 6a). There were no  
1262 significant differences in abundances between prograding and retrograding reef patches at  
1263 Duncannon (Figure 6b). At Inverin, mean richness was similar between retrograding and  
1264 prograding reef patches for the majority of groups compared; except arthropoda and other  
1265 taxa, which were significantly higher in retrograding than prograding reef patches (Figure  
1266 6c). In general, sand supported significantly lower richness and abundance than retrograding  
1267 reef patches (Figure 6c,d).

1268  
1269

#### 1270 4. DISCUSSION

1271

1272 Through combining the best available historical and contemporary data, spanning 182 years,  
1273 we provide a comprehensive account of broad-scale distribution and abundance of a data  
1274 deficient species in a previously data deficient region. We increased the number of records  
1275 25-fold from 40 in the OBIS database (OBIS, 2018) to 981; importantly many of these were  
1276 absences (67%), enabling us to reliably determine discontinuities in the distribution and  
1277 imbalances in the dataset. Despite filling an important knowledge gap for a species of  
1278 conservation concern, sampling intensity was imbalanced both spatially and temporally. For  
1279 example, 221 records for Northern Ireland make up 23% of our database. The Northern Irish  
1280 coastline has received a disproportionate degree of sampling compared with the much longer  
1281 coastline of the Republic of Ireland. Similarly, Galway Bay is the only region that has been  
1282 sampled with high intensity (and recently), revealing that the north shoreline exhibits a  
1283 greater percentage (67%) of higher SACFOR records than the south shoreline (5%). This is  
1284 likely to be due to the much-reduced wave energy, and thus greater accumulation of finer  
1285 silty sediments on the south shoreline, which in turn is less suitable for tube building than the

1286 larger-grained sandy environment that characterises the north shoreline (O'Connor et al.,  
1287 1993). Without intensive sampling, such observations would not be possible.

1288

1289 A number of locations have been identified as requiring better protection. Despite Duncannon  
1290 exhibiting the most extensive stretches of reef in Ireland that are located within the River  
1291 Barrow and River Nore SAC (NPWS, 2011, for which *S. alveolata* reefs are specifically  
1292 listed as features of interest), this was the only location where a winkle (*Littorina littorea* L.  
1293 1758) picker was observed kicking off large chunks of *S. alveolata* reef to access winkles.  
1294 Similarly, Preston and Portig (2001) identified winkle collection as a considerable threat to *S.*  
1295 *alveolata* at locations in the northeast (Glasdrumman and Ringboy/Minerstown). Further  
1296 information on damage caused by harvesting and trampling (Dubois et al., 2002; Plicanti et  
1297 al., 2016), or local human activities such as shellfish farming (Dubois et al., 2006) would be  
1298 beneficial for identifying locations in need of protection and management, as well as public  
1299 awareness efforts (e.g. information boards).

1300

1301 In the short-term (within 1-2 years), intensive sampling is recommended at all sub-regional  
1302 boundary edges to determine the true boundaries. We also recommend that the poorly  
1303 sampled Lough Swilly and Dingle Peninsula, and the vulnerable northeast are subjected to  
1304 intensive sampling in the short-term. Following this, we recommend that a network of key  
1305 locations (spanning all regions) are identified for sustained observations of fixed areas over  
1306 medium (5–10 years), and long (20–30 years) timescales. Using a hierarchical sampling  
1307 approach (1m, 5m, 10m, and landscape) over fixed areas will yield information about  
1308 changes in the nature, extent and ecology of reefs over time. This would be invaluable for  
1309 informing managers about any spatio-temporal changes in condition and extent.

1310

1311 *S. alveolata* reefs in Ireland were typically characterised by a mosaic of development phases  
1312 at small spatial scales (<1m), rather than being dominated by either progradation or  
1313 retrogradation phase, as can be seen on the larger reefs in Mont-Saint-Michel Bay (Gruet,  
1314 1986; Curd et al., 2019). These mosaic reefs were found to support greater algal diversity and  
1315 abundance compared with adjacent rock. In addition to algae living as epibionts directly on  
1316 the surface of the *S. alveolata* reefs, many macroalgal species can be attached directly to rock  
1317 and protrude up through cracks in the reef. Despite these algae being attached to the rock,  
1318 they are likely to still benefit from a combination of physical habitat amelioration and  
1319 associational defence (Bertness et al., 1999) from grazing provided by the reef structure.

1320

1321 Mosaics of habitat patches, with varying amounts of primary or secondary producers, can  
1322 make a major contribution to ecosystem functioning (Giller et al., 2004), with habitat patch  
1323 diversity perhaps being more important than species diversity per se in open ecosystems.  
1324 Biogenic habitats are noted for their structural complexity, facilitating diverse communities  
1325 through habitat and refuge provision (Hughes et al., 2014; Walls et al., 2018; Bertolini et al.,  
1326 2020). Had it been possible to sample large enough patches that were dominated by the  
1327 progradation phase, it is unlikely that such patterns would have been observed, and it is  
1328 assumed that few algae (or indeed other organisms) would have been attached to the reefs.  
1329 Prograding reefs comprise tightly-packed tubes containing live individuals and consist almost  
1330 entirely of feeding apertures (Wilson, 1968, 1971), which greatly reduce the probability of  
1331 successful settlement by larvae of other species and inhibit overgrowth by adjacent organisms  
1332 (Jackson, 1977).

1333

1334 Grazer diversity and abundance was higher on rock compared with *S. alveolata* reefs. A  
1335 recent study by Muller et al. (2021) found no grazers represented in the infaunal community

1336 associated with *S. alveolata* reefs. Similar inverse patterns of predator/prey abundance have  
1337 been observed in mussel beds due to reduced predation pressure within mussel beds  
1338 (Witman, 1985). These processes do not necessarily translate when it comes to grazer/algae  
1339 relationships. For example, O'Connor and Crowe (2008) found that algae were more  
1340 abundant and diverse within mussel beds than on adjacent rock; but experimental testing of  
1341 grazing patterns revealed that grazing intensity was similar between the two habitats  
1342 suggesting that grazing pressure was not the underlying driver. Crowe et al. (2011) factorially  
1343 manipulated limpet grazing and mussel cover, and showed that whilst mussels provided a  
1344 refuge (particularly for furoid germlings) from grazing activity of limpets, other grazing  
1345 gastropods were actually found in greater abundance in mussel beds (a pattern also observed  
1346 by Wangkulankul et al., 2016), and that there was some evidence of an inverse relationship  
1347 between abundance of limpets and other grazers. This highlights that limpets are key grazers  
1348 in this system as they are throughout the North-east Atlantic (Hawkins, 1981; Coleman et al.,  
1349 2006; Jenkins et al., 2005), and that their grazing activity cannot be matched by other grazers  
1350 (O'Connor and Crowe, 2005). Whilst it is probable that *Sabellaria* reefs provides a refuge for  
1351 grazing activity from grazers (particularly limpets), experimental manipulation is necessary  
1352 before any conclusions can be drawn about the role of grazers in driving epibiotic  
1353 biodiversity patterns.

1354

1355 The 77 infaunal taxa comprised a combination of intertidal, subtidal and terrestrial taxa (i.e.  
1356 fly larvae), highlighting that the reefs support a unique combination of taxa from a range of  
1357 different environments (Dubois et al., 2002). None of the taxa recorded were of particular  
1358 note in terms of rarity or conservation value, although some may be considered important as  
1359 either fishing bait (ragworms, *Nereis* and *Nephtys*) or due to their commercial importance  
1360 (*Mytilus edulis* L. 1758). *Sabellaria alveolata* reefs and their surrounding sedimentary

1361 habitats are known to support species of commercial importance (Dubois et al., 2006; Plicanti  
1362 et al., 2016; Schimmenti et al., 2015), and the worms themselves are also collected as fishing  
1363 bait, particularly in the Mediterranean (Gambi et al., 1992). By comparison with continental  
1364 Europe, harvesting and bait collection are not currently considered to be especially  
1365 detrimental activities in Ireland. The harvesting of winkles (*L. littorea*), purple urchins  
1366 (*Paracentrotus lividus* Lamarck, 1816) and mussels (*Mytilus* spp.) are perhaps the most  
1367 prevalent activities (Cummins et al., 2002; Fahy et al., 2008), and may have detrimental  
1368 impacts on *S. alveolata* reefs.

1369  
1370 *Sabellaria alveolata* populations fluctuate naturally over time (Gruet, 1986), exhibiting  
1371 different life history characteristics, with some colonies growing rapidly while others appear  
1372 more senescent, mainly due to very patchy settlements of juveniles onto the reef. Little  
1373 experimental work has explored the natural drivers of change, but it has been asserted that  
1374 algal blooms and competition for space with competitors such as filter-feeding barnacles and  
1375 mussels (Multer and Milliman, 1967) can lead to the weakening of reef structures rendering  
1376 them more susceptible to erosion by waves (Wilson, 1971). Extreme climatic events  
1377 (extensive colds or intense storms) are known to have long-term effects on reef structures  
1378 (Crisp, 1964; Firth et al., 2015, 2020), with long-term and wide-reaching cascading effects.  
1379 Furthermore, anthropogenic drivers such as trampling, harvesting of organisms from the reefs  
1380 and collection of the worms for bait are all known to expedite the retrogradation process  
1381 (Cunningham et al., 1984; Plicanti et al., 2016). Irrespective of morphological type or phase,  
1382 all types of reefs (even dead ones) carry out important ecosystem functions and services  
1383 (Sheehan et al., 2015; Gribben et al., 2017). Therefore, even the most 'degraded' reefs may  
1384 provide an important structuring function, providing substrate for colonisation of benthic  
1385 organisms (Dubois et al., 2002; Jones et al., 2018). They have an important legacy effect

1386 through potentially serve as catalysts for future large and prograding reefs due to gregarious  
1387 settlement of larvae that are attracted to the tube sand and its cement (Wilson, 1968; Pawlik,  
1388 1988).

1389

1390 Assessing variability in habitat distribution and abundance is also important at a time when  
1391 the implementation of some marine policies (such as the establishment of marine reserves  
1392 and protected sites such as Special Areas of Conservation (SACs)) assumes a degree of  
1393 stability in the features being protected. The Wicklow Reef SAC provides an interesting  
1394 example of this. The location was designated for the presence of *S. alveolata*, but a report  
1395 from the National Parks and Wildlife Service (NPWS, 2013) pointed out that the occurrence  
1396 of *S. alveolata* within this site may be questionable and that the highly dynamic nature of this  
1397 area is unlikely to support a stable biogenic reef composed of *S. alveolata* for any length of  
1398 time. This highlights the importance of sustained observations, particularly relating to the  
1399 designation of sites for the conservation of ephemeral or variable species or habitats.

1400 Incidentally, during the writing of this paper, the Irish government announced plans to  
1401 expand Ireland's Marine Protected Area network to 30% by 2030 (currently at 2.13%,  
1402 Gov.ie., 2021). The results from this study will feed into this consultation.

1403

1404 With such fine-scale mapping of the distribution of this important reef-forming species, it is  
1405 anticipated that this will be of significant use to those tasked with the management and  
1406 protection of these habitats. This is particularly important as it comes at a time when cross-  
1407 border management is very likely to become challenged due to potential changes in  
1408 legislation, for example the exit of the UK from the European Union on 1<sup>st</sup> January 2021  
1409 (Boyes and Elliott, 2016; Hawkins, 2017). The vast majority of environmental policy and  
1410 legislation in the Republic of Ireland, Northern Ireland, and the UK as a whole, is governed

1411 by legal frameworks and regulations set at the European Union level. The island of Ireland is  
1412 an excellent example of the need for joint coordinated national responses to achieve effective  
1413 resource management between the two jurisdictions (Stokes et al., 2006; Knights et al.,  
1414 2015). This highlights the importance of achieving a potential future: a “one island - two  
1415 systems” governance framework (Boyes and Elliott, 2016). This is a wider issue that applies  
1416 at other national boundaries globally (Hawkins, 2017).

1417

## 1418 **5. CONCLUSIONS**

1419 Through combining the best available historical and contemporary data, an important  
1420 knowledge gap has been filled in the distribution and abundance of a data deficient species in  
1421 a data deficient region. Absence of evidence is not evidence of absence: information on both  
1422 positive and negative observations collated from a variety of sources can inform estimates of  
1423 detectability of species, indicate decline in population or range size, and, ultimately, inform  
1424 reassessment to data-sufficient categories (Good et al., 2006). This is particularly true for  
1425 biogenic habitat-forming species, for which the mechanisms underpinning reef dynamics are  
1426 not fully understood. This type of research could easily be carried out for other data deficient  
1427 species and regions. Through doing this, the information gathered could inform future IUCN  
1428 assessments. Undoubtedly, species and habitats that are currently classed as ‘Data deficient’  
1429 on the IUCN Red Lists would be re-assigned - in many cases to ‘least concern’ (as we  
1430 suspect is the case for *S. alveolata*). The data contained in the wide variety of sources that  
1431 were used here provide the raw material for data mining and data archaeology. In this current  
1432 setting of the global pandemic and cuts in state-funded science, historical and unpublished  
1433 data, in addition to data from citizen science projects (Vye et al., 2020) represent potentially  
1434 invaluable resources for sustained monitoring, management and conservation (Hawkins et al.,  
1435 2013).

1436

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1450

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1850 Table 1. SACFOR scale of abundance used to record *Sabellaria alveolata*. Adapted from  
 1851 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

1852

### 1853 **Figures**

1854 Figure 1. (a) Photo of the honeycomb structure of the tubes of *Sabellaria alveolata*. (b) Photo  
 1855 of the reef structures attached to rocks – note the mosaic structure with algae growing on the  
 1856 reef structures and limpets and barnacles on the patches of bare rock in between the reef  
 1857 structures. (c) Map of Ireland with locations that are mentioned in this paper. The names in  
 1858 italics are the locations where the biodiversity surveys were carried out.

1859

1860 Figure 2. Map illustrating the presence (full circles) and absence (empty circles) of *Sabellaria*  
 1861 *alveolata* around Ireland. All records for intertidal (green circles) and subtidal (orange  
 1862 circles) observations between 1836 and 2018 are shown. (a-f) Maps of the six discretely-  
 1863 bounded populations in Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway  
 1864 Bay and the northwest. For zoomed-in maps, only data from 2013-2018 are shown.

1865

1866 Figure 3. (a) Photo of the *Sabellaria alveolata* reefs at Duncannon, Co. Wexford. (b) Image  
1867 showing extent (~14ha in 2015) of the reefs at Duncannon. The conservation of *S. alveolata*  
1868 reefs at Duncannon was specifically mentioned as a target in the River Barrow and River  
1869 Nore Special Area of Conservation (site code: 2162) Conservation Objectives (NPWS, 2011).  
1870

1871 Figure 4. Summary of the relative frequency of occurrence of the various SACFOR scores for  
1872 each of the six discretely-bounded populations: Lough Swilly, the northeast, south coast,  
1873 Dingle Peninsula, Galway Bay (separated into north and south), and the northwest. (a) all  
1874 intertidal records collated from all sources spanning the entire sampling period 1836-2018.  
1875 The numbers on the right represent the total number of all records spanning the entire study  
1876 period for each regional population. (b) all intertidal records collected by Crisp and  
1877 Southward in the 1950s; (c) all intertidal records collected during the MarClim project 2003-  
1878 2004; (d) all intertidal records collected by co-authors of this paper 2013-2018. Note the scale  
1879 on the X-axis changes in each panel. These three temporal sub-sets of data were selected  
1880 because they had sufficient geographic coverage and reported SACFOR estimates. The  
1881 numbers on the right in b-c represent the % of all records for each region represented by that  
1882 temporal subset. Note that other records for each region exist outside these temporal subsets.  
1883

1884 Figure 5. Mean (a) algal richness, (b) algal % cover, (c) molluscan grazer richness, (d)  
1885 molluscan grazer abundance per quadrat (0.25 x 0.25cm) on emergent rock and *Sabellaria*  
1886 *alveolata* reefs at eight locations around Ireland (n = 10 or 20 ± SE). NS = Not significant; \*\*  
1887 P < 0.01.

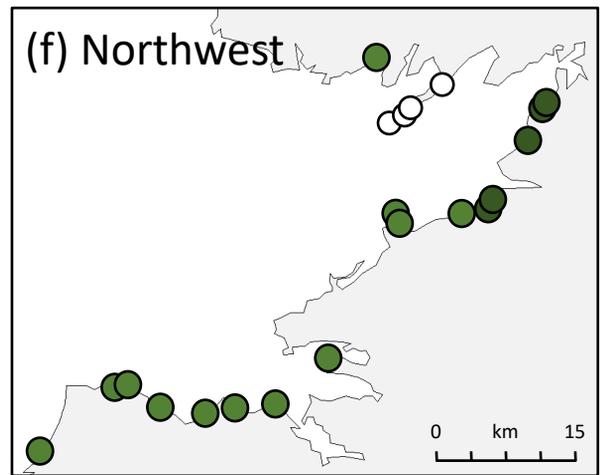
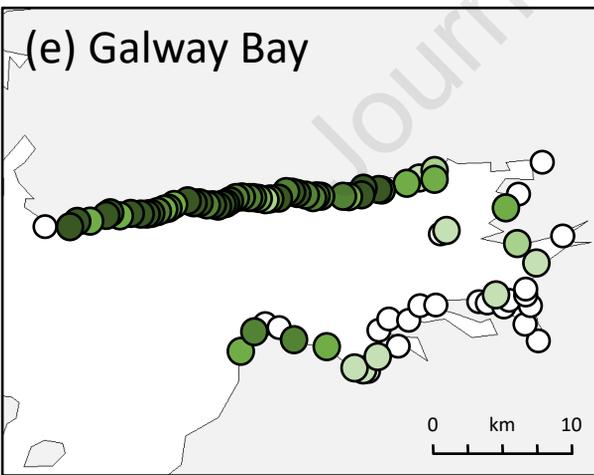
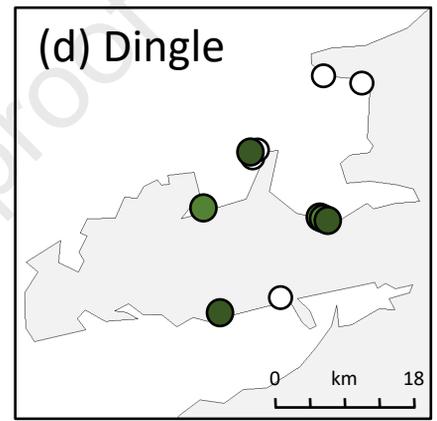
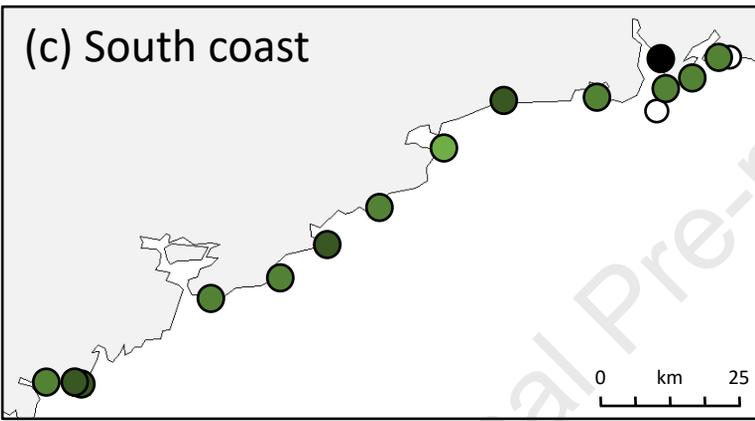
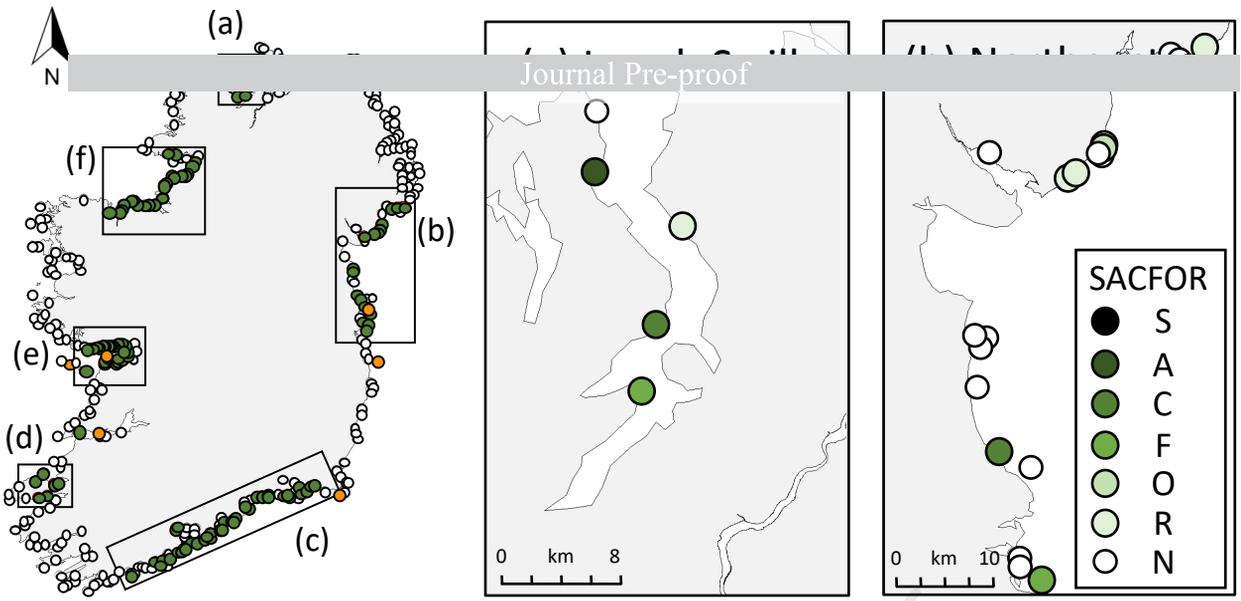
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1889 Figure 6. Mean (a) infaunal richness and (b) infaunal abundance among progradation (black  
1890 bars) and retrogradation phases (white bars) of *Sabellaria alveolata* reefs at Duncannon (n=5

1891  $\pm$  SE). Mean (c) infaunal richness and (d) infaunal abundance among progradation and  
1892 retrogradation phases of *S. alveolata* reefs and adjacent sand (grey bars) at Inverin (n=3  $\pm$   
1893 SE). *Sabellaria alveolata* was not included in calculations of either richness or abundance of  
1894 all species or annelids. NS = Not significant; \*\* P < 0.01. For Inverin, letters above bars  
1895 denote significant differences between treatments.

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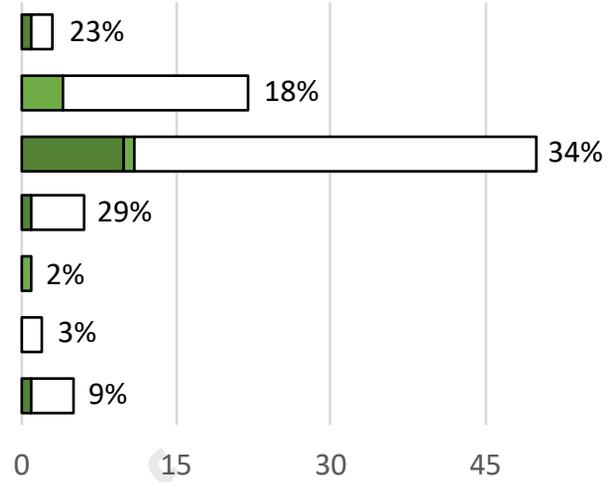
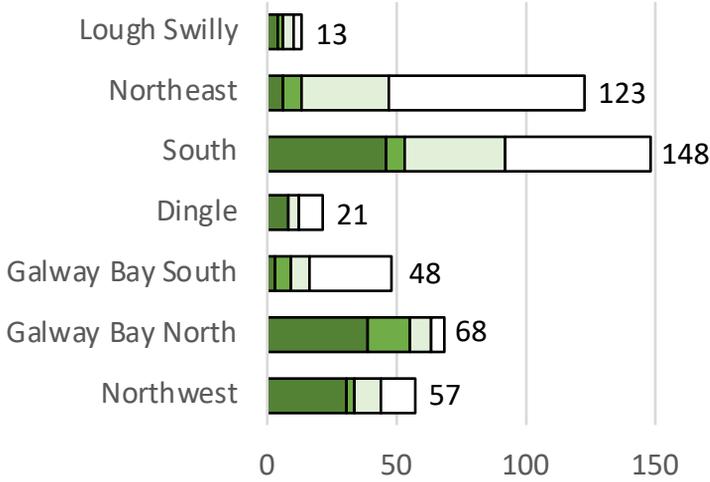






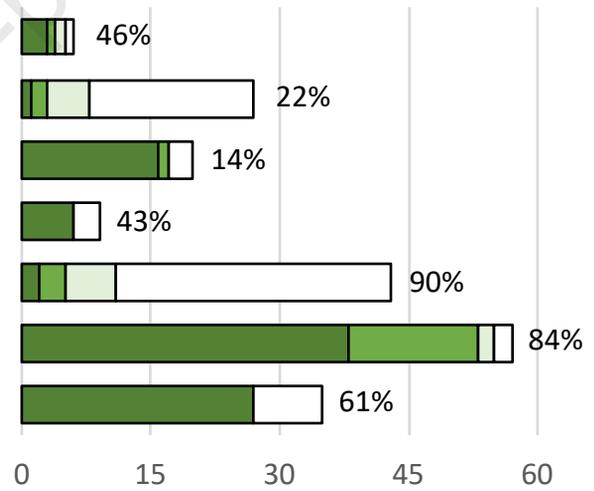
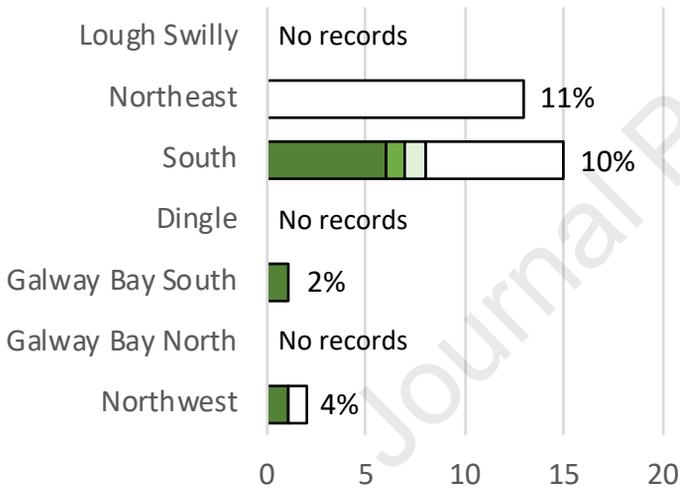
(a) All intertidal records (1836-2018)

(b) Intertidal records (1950s)



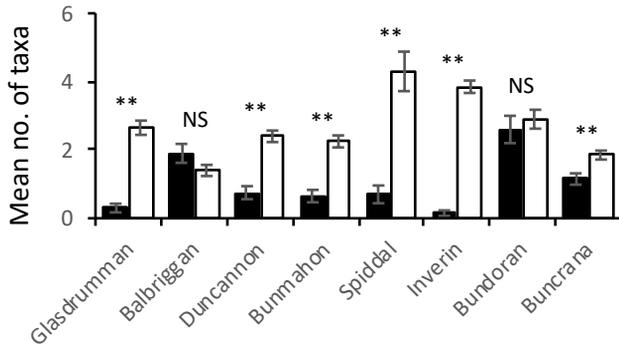
(c) Intertidal records (2000s)

(d) Intertidal records (2013-2018)

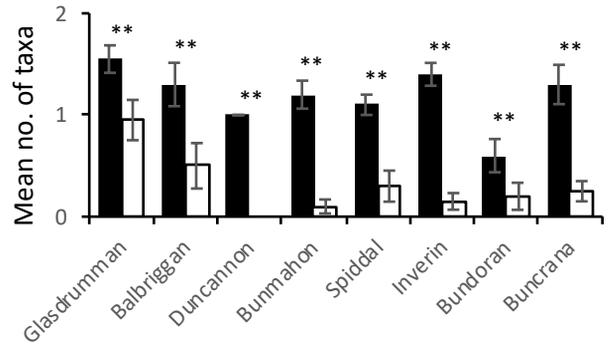


= not seen  
  = Present/Rare  
  = Occasional/Frequent  
  = Common/Abundant

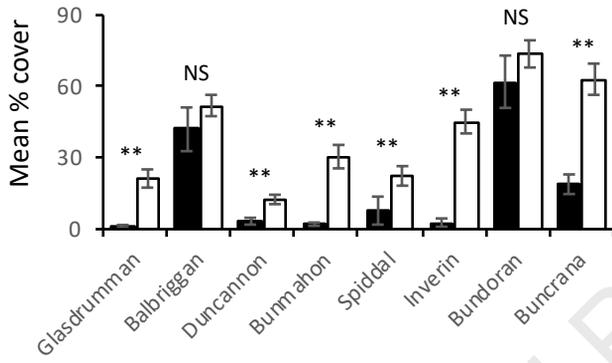
## a) Algal richness



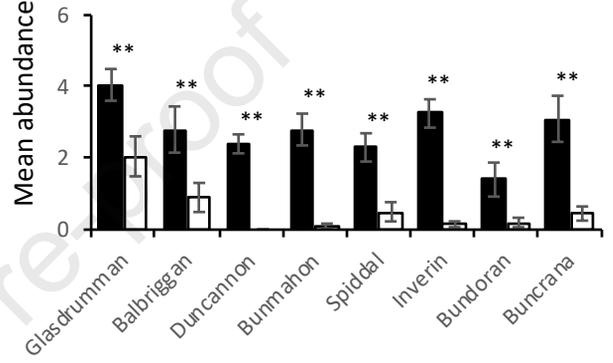
## c) Molluscan grazer richness



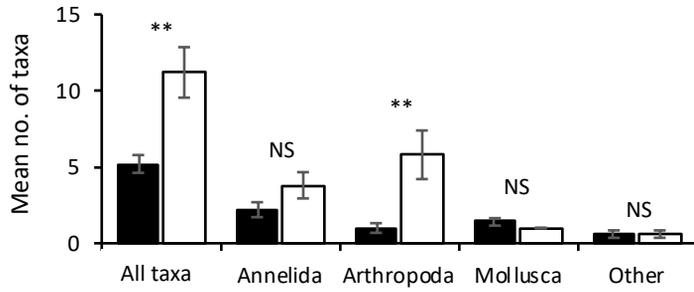
## b) Algal abundance



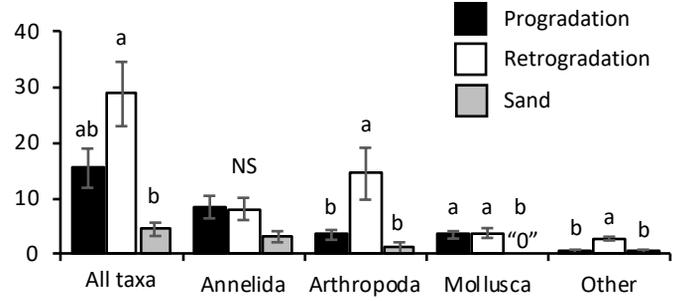
## d) Molluscan grazer abundance



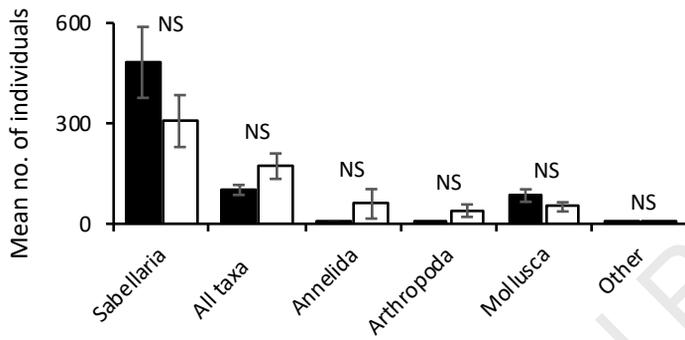
a) Richness - Duncannon



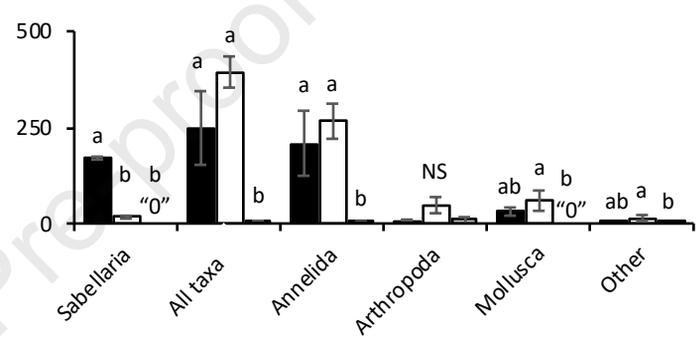
c) Richness - Inverin



b) Abundance - Duncannon



d) Abundance - Inverin



## Highlights

- Improving the knowledge base of data deficient species will enable greater protection.
- We identified knowledge gaps for the distribution of a data deficient species in a poorly mapped region.
- *S. alveolata* reefs supported diverse epibiotic algal assemblages.
- Retrograding (declining) reefs supported greater infaunal diversity than prograding (growing) reefs.
- Such research should be done for other data deficient species and habitats.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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