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TITLE:

**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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Highlights

- Improving the knowledge base of data deficient species will enable greater protection.
- We identified knowledge gaps for the distribution 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.

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.

Keywords

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

1. INTRODUCTION:

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

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

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

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

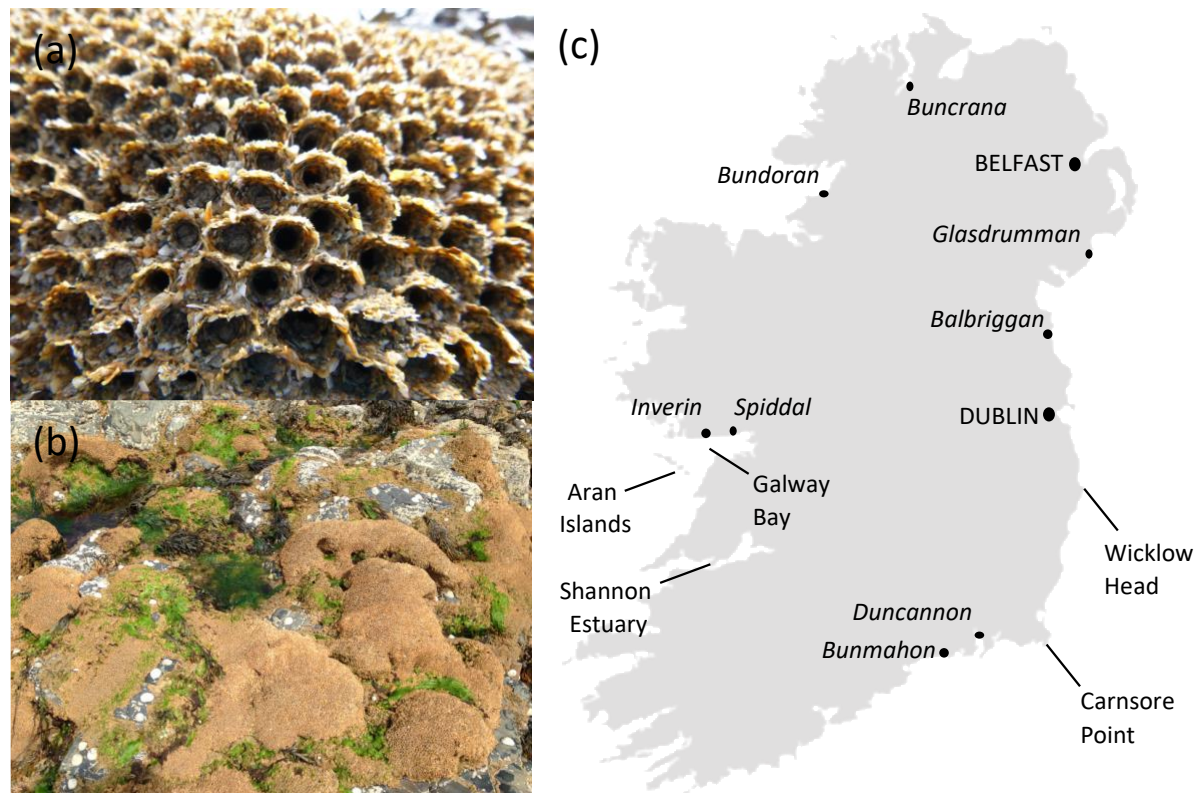


Figure 1. (a) Photo of the honeycomb structure of the tubes of *Sabellaria alveolata*. (b) Photo of the reef structures attached to rocks – note the mosaic structure with algae growing on the reef structures and limpets and barnacles on the patches of bare rock in between the reef structures. (c) Map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

Despite being recognised as an ecologically important habitat and designated for protection under international legislation such as the EU Habitats Directive (EEC/92/43), *S. alveolata* reefs are listed in the IUCN European Red List of Habitats as ‘Data deficient’ (Bertocci et al., 2017; Gubbay et al., 2017). Whilst a small number of regions have been subject to experimental research (e.g. northern France (Dubois et al., 2002) and Sicily (Bertocci et al., 2017)), little is known about its distribution or ecology outside of the UK, where there is a strong natural history heritage and a tradition of sustained observations (Wilson, 1971; Hawkins et al., 2013, 2016; Mieszkowska et al., 2014). There was an early interest from

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

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

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

2. METHODS

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

The distribution of *S. alveolata* around Ireland was recently described by Firth et al. (2020). This paper focused on describing the most important environmental variables (i.e. wave height, tidal amplitude, stratification index, then substrate type) underpinning distribution patterns and abundance changes over time. The dataset used in that paper comprised data from a range of sources including grey literature, museum specimens, published papers and publicly-available databases combined with records from field sampling (including intensive targeted sampling in the 1950s (by Denis Crisp and Alan Southward: Southward and Crisp, 1954); 2003-2004 (the MarClim Project: Simkanin et al., 2005; Merder et al., 2018); and by co-authors of this paper between 2013-2018). Using the same dataset, here, we focus in on the six previously-identified discretely bounded regional populations. We examined the spread of both records and SACFOR abundance categories (S=Superabundant, A=Abundant, C=Common, F=Frequent, O=Occasional, R=Rare, and Not Seen). This enabled us to identify any spatial or temporal imbalances in the spread of distributional data. All data were mapped using ArcGIS (ESRI, 2016).

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

To test the hypothesis that *S. alveolata* reefs support higher algal richness and abundance and lower molluscan grazer richness and abundance than adjacent emergent rock (hereafter rock), a minimum of ten (and in most locations twenty) quadrats (25 cm × 25 cm) were randomly placed on both habitat types at eight locations between March and September 2016: Glasdrumman, Balbriggan, Duncannon, Bunmahon, Spiddal, Inverin, Bundoran and Buncrana (Figure 1c). These locations were selected based on their broad geographic

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

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

2.3. Statistical analyses

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

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

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

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

3. RESULTS

3.1. Identifying regions with insufficient data on the distribution of S. alveolata around Ireland

A total of 981 records were collated between 1836 and 2018: 319 (33%) of these were 'positive' observations (i.e. present) and 662 (67%) were 'negative' observations (i.e. absent/not seen). The vast majority of the records (954) were from intertidal habitats with very few records from subtidal habitats (27). Unsurprisingly, sampling effort varied spatially 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.

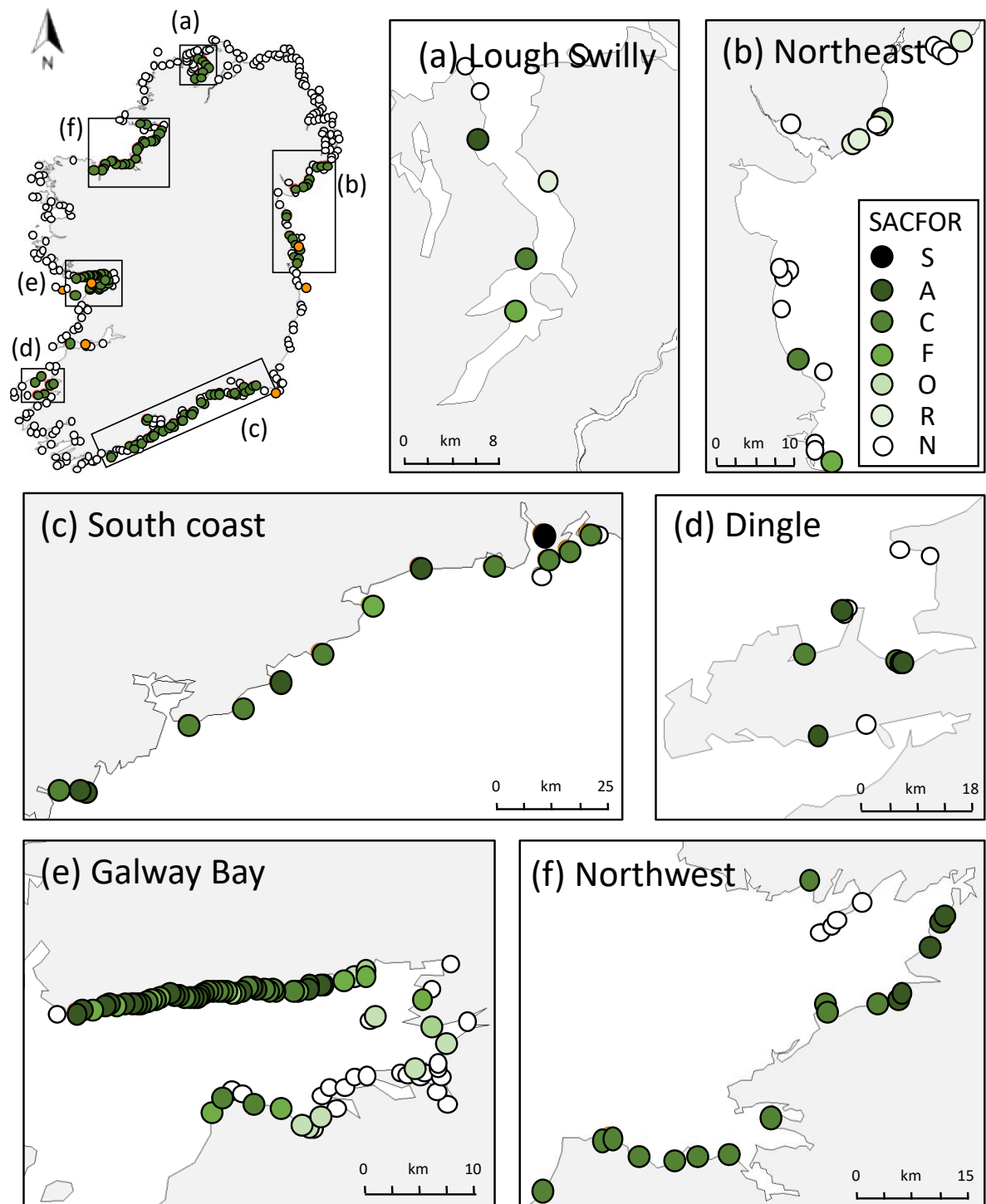


Figure 2. Map illustrating the presence (full circles) and absence (empty circles) of *Sabellaria alveolata* around Ireland. All records for intertidal (green circles) and subtidal (orange circles) observations between 1836 and 2018 are shown. (a-f) Maps of the six discretely-bounded populations in Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway 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.

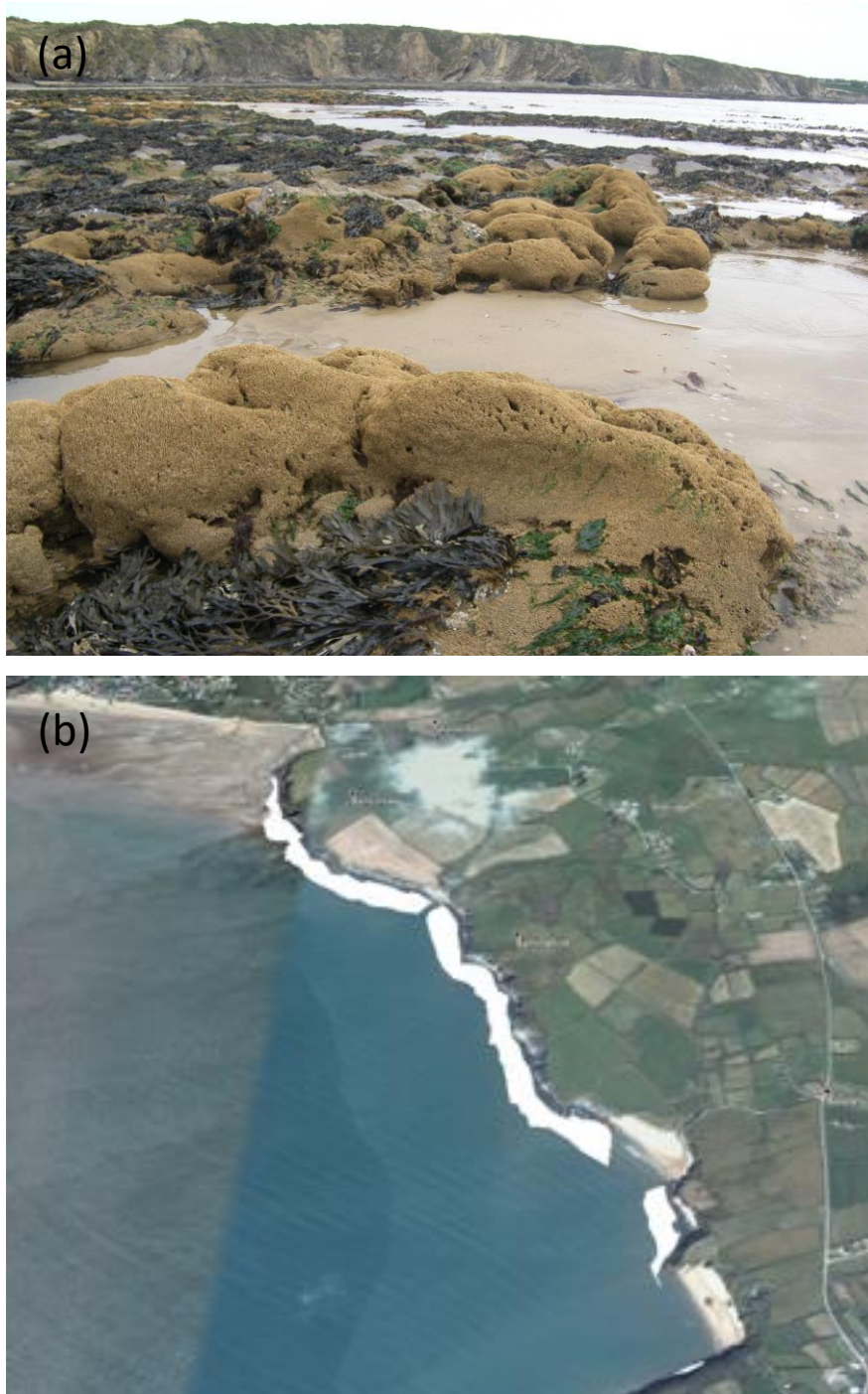


Figure 3. (a) Photo of the *Sabellaria alveolata* reefs at Duncannon, Co. Wexford. (b) Image showing extent (~14ha in 2015) of the reefs at Duncannon. The conservation of *S. alveolata* reefs at Duncannon was specifically mentioned as a target in the River Barrow and River Nore Special Area of Conservation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

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.

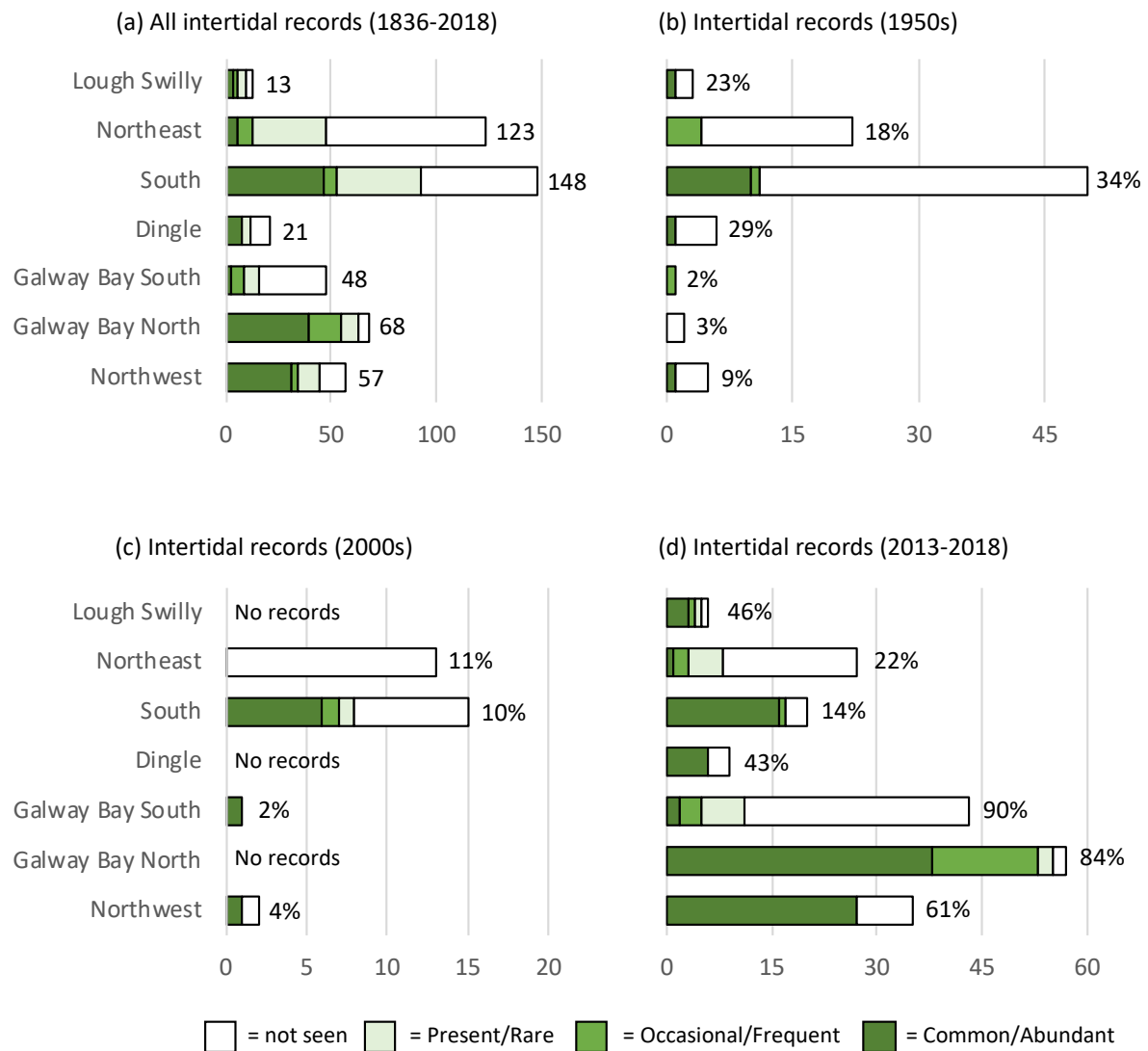


Figure 4. Summary of the relative frequency of occurrence of the various SACFOR scores for each of the six discretely-bounded populations: Lough Swilly, the northeast, south coast, Dingle Peninsula, Galway Bay (separated into north and south), and the northwest. (a) All intertidal records collated from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

numbers on the right in b-c represent the % of all records for each region represented by that temporal subset. Note that other records for each region exist outside these temporal subsets.

The recent sampling that was carried out between 2013-2018 (Figures 2, 4d) provides the most up-to-date assessment of the distribution and abundance of *S. alveolata* around the Irish coastline. Sampling in the previously-identified distribution gaps confirmed that large swathes of coastline were devoid of *S. alveolata* (discussed in detail in Firth et al., 2020). Despite intensive sampling during this period and the filling in of important data gaps (i.e. Galway Bay, northwest and to a lesser degree Lough Swilly and the Dingle Peninsula), most regions remain relatively poorly sampled with <50 records each. Galway Bay was the most intensively sampled region, and was split based on relative differences in SACFOR abundance categories. Galway Bay North exhibited high prevalence (67%) of the higher SACFOR categories (i.e. Abundant/Common) and low prevalence of negative observations (4%) (Figure 4d). Conversely, Galway Bay South exhibited low prevalence (5%) of the higher SACFOR categories and high prevalence of negative observations (74%) (Figure 4d). Of the 35 records from the northwest, 77% exhibited the higher SACFOR categories. Whilst few records (<10 each) were available for the Dingle and Lough Swilly, both regions supported populations exhibiting the higher SACFOR categories.

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

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

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

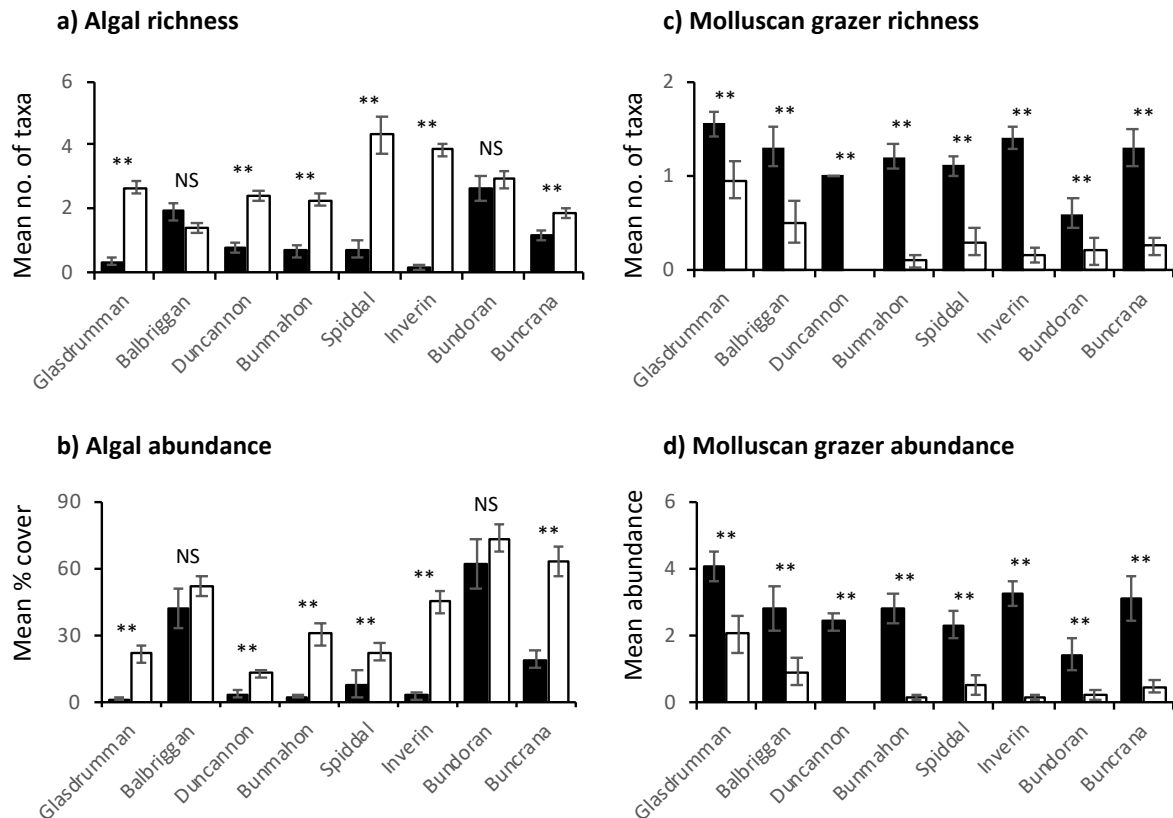


Figure 5. Mean (a) algal richness, (b) algal % cover, (c) molluscan grazer richness, (d) molluscan grazer abundance per quadrat (0.25 x 0.25cm) on emergent rock and *Sabellaria alveolata* reefs at eight locations around Ireland ($n = 10$ or $20 \pm SE$). NS = Not significant; ** $P < 0.01$.

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

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

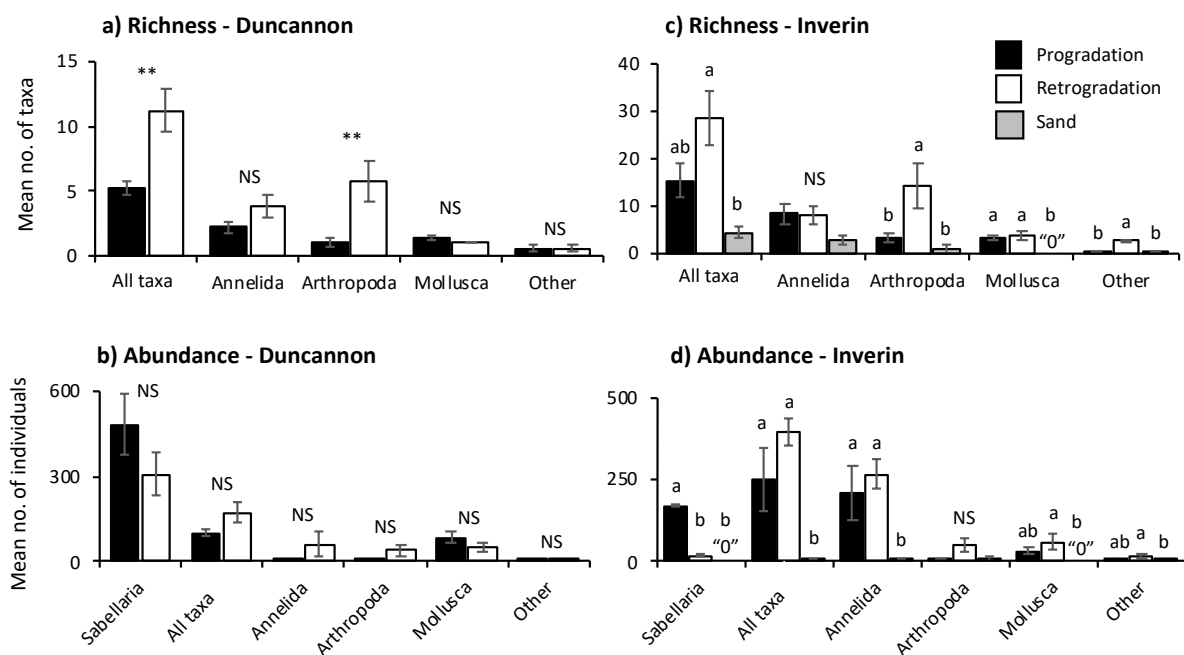


Figure 6. Mean (a) infaunal richness and (b) infaunal abundance among progradation (black bars) and retrogradation phases (white bars) of *Sabellaria alveolata* reefs at Duncannon ($n=5 \pm \text{SE}$). Mean (c) infaunal richness and (d) infaunal abundance among progradation and retrogradation phases of *S. alveolata* reefs and adjacent sand (grey bars) at Inverin ($n=3 \pm$

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

4. DISCUSSION

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

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

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

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

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

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

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

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

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

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

prevalent activities (Cummins et al., 2002; Fahy et al., 2008), and may have detrimental impacts on *S. alveolata* reefs.

Sabellaria alveolata populations fluctuate naturally over time (Gruet, 1986), exhibiting different life history characteristics, with some colonies growing rapidly while others appear more senescent, mainly due to very patchy settlements of juveniles onto the reef. Little experimental work has explored the natural drivers of change, but it has been asserted that algal blooms and competition for space with competitors such as filter-feeding barnacles and mussels (Multer and Milliman, 1967) can lead to the weakening of reef structures rendering them more susceptible to erosion by waves (Wilson, 1971). Extreme climatic events (extensive colds or intense storms) are known to have long-term effects on reef structures (Crisp, 1964; Firth et al., 2015, 2020), with long-term and wide-reaching cascading effects. Furthermore, anthropogenic drivers such as trampling, harvesting of organisms from the reefs and collection of the worms for bait are all known to expedite the retrogradation process (Cunningham et al., 1984; Plicanti et al., 2016). Irrespective of morphological type or phase, all types of reefs (even dead ones) carry out important ecosystem functions and services (Sheehan et al., 2015; Gribben et al., 2017). Therefore, even the most ‘degraded’ reefs may provide an important structuring function, providing substrate for colonisation of benthic organisms (Dubois et al., 2002; Jones et al., 2018). They have an important legacy effect through potentially serve as catalysts for future large and prograding reefs due to gregarious settlement of larvae that are attracted to the tube sand and its cement (Wilson, 1968; Pawlik, 1988).

Assessing variability in habitat distribution and abundance is also important at a time when the implementation of some marine policies (such as the establishment of marine reserves

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

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

Conclusions

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

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Table 1. SACFOR scale of abundance used to record *Sabellaria alveolata*. Adapted from 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 ² surface within a 30-minute search
A	Abundant: Numerous large patches almost always over 1 m ² , forming hummocks over 30 cm thick, covering over a total 1000 m ² surface within a 30-minute search.

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

Table S1. Inventory of taxa that were found on emergent rock and on *S. alveolata* reefs across all locations surveyed (Glasdrumman, Balbriggan, Duncannon, Bunmahon, Spiddal, 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	✓
	Total number of taxa	27	37

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Table S2. Inventory of taxa that were found in prograding and retrograding *S. alveolata* reefs and sand across the two locations (Duncannon, Co. Wexford (surveyed August 2013) and 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

Arthropoda	<i>Trypanosyllis coeliaca</i>	X	✓	X
	<i>Tubificoides pseudogaster</i>	✓	✓	X
	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
Total number of taxa	41	63	10

Figures

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

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

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

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

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

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

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

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