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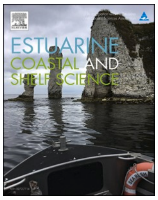

Northward range expansions are not the full story: A case study of *Sabellaria alveolata* in Great Britain

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ABSTRACT

Warming oceans are causing changes in the distribution of numerous species. If greenhouse gas production continues to follow current trends, further distribution changes will result. It is often assumed that range shifts into higher latitudes may mitigate threats to susceptible species. *Sabellaria alveolata* is an important intertidal ecosystem engineer and protected by the UK Biodiversity Action Plan. In this study we created a habitat suitability model for *S. alveolata* around Great Britain and quantified changes in coastal suitability with increasing sea surface temperatures (SST) using Representative Concentration Pathway (RCP) scenarios modelled by the International Panel on Climate Change. The model included maximum and minimum SST, substrate, slope, kinetic energy due to waves and currents, photosynthetically active radiation, and the coefficient of light attenuation. The model performed very well (AUC = 0.932, 50.2% of deviance explained) and all variables explaining comparable deviance (up to 10%). Recent SST was then combined with predicted SST increases, leading to suitable habitat locations expanding across the southern and western GB coastlines and resulting in larger patches, hence potential for connectivity. Some northern extension was observed; however, this was limited and patchy. The greatest extensions were seen on the south coast, with most of the south coast becoming a continuous network with excellent suitability. With an increase of 1.2 °C, the extent of coast in the excellent suitability class was increased by 5.75% compared to 2020, and by 38.1% with 3.2 °C. Despite the importance of winter temperature in driving *S. alveolata* distribution, over-riding environmental constraints prevented any major northward migration. The assertion that potential for range shifts to higher latitudes may mitigate the effects of climate change depends on niche availability which may not always be realised.

1. Introduction

Climate change through oceanic warming is causing shifts in species distributions around the globe (Pinsky et al., 2013; Burrows et al., 2014; Hiddink et al., 2015) and is associated with a loss of biodiversity (Slingenberg et al., 2009). Global warming will “more likely than not exceed 1.5 °C between 2030 and 2052”, if carbon emissions continue at their rate in 2021 (IPCC et al., 2021). Organisms can adapt to warming conditions through modifications to behaviour, genetic adaptation and/or phenotypic plasticity (Somero, 2010; Merila and Hendry, 2014). However, warming oceans are resulting in shifts to the distributions of many marine species (Poloczanska et al., 2013) through within range changes, range shift (Curd et al., 2022), and range fragmentation (Mestre et al., 2017) which are reported to be moving towards polar regions (Monzon et al., 2011). A key question is to what extent can these mechanisms mitigate the biodiversity loss driven by climate change, particularly amongst species that are of high ecosystem value or threatened.

Benthic communities are used as indicators of climate change impacts, due to their sessility or low mobility, and relatively long lifespan (Weinert et al., 2021). For instance, Hiddink et al. (2015) reported a 3.8–7.3 km. yr^{-1} movement of benthic species to the northwest of the North Sea in response to warming temperatures. One of the most widely distributed and abundant benthic groups, polychaetes have more than twelve thousand species reported across the globe (Appeltans et al., 2012). Polychaete assemblages have similar variation in distribution as the entirety of benthic fauna (Fauchald, 1973), and are therefore considered to be representative of marine biodiversity (Olsgard et al., 2003). Polychaetes engineer ecosystems through the production of temperate biogenic reefs, which are reported to be among the most

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threatened habitats globally (Beck et al., 2011), hence, the predominant reef forming polychaete in Europe, *Sabellaria alveolata*, (the honeycomb worm) is granted protection status along the European coastline, by both the EU Habitats Council Directive, and the Biodiversity Action Plan in the UK (Schlund et al., 2016).

Sabellaria alveolata is found at the intertidal zone, discontinuously from Morocco to Scotland (Muir et al., 2016), selectively utilizing the sediment load of the water column to build the tubes they inhabit (Le Cam et al., 2011). To become successfully established, *S. alveolata* require clean, continually washed substrates, and so are found in turbulent waters (Holt et al., 1998), with an abundance of sediment grains in the water column to build their tube structures (Wilson, 1970), which can develop into large reefs (Jones et al., 2018). The largest known reef structure is in the Bay of Mont-Saint-Michel, France, covering 250 ha (Dubois et al., 2007; Desroy et al., 2011). When *S. alveolata* reefs are established on soft substrates, these reefs are known to host greater concentrations of benthic invertebrates (Gore et al., 1978; Dubois et al., 2002), which have a higher biodiversity than the areas without *S. alveolata* (Dohner et al., 2005) due to the provision of trophic and spatial niches (Dubois et al., 2002, 2006; Jones et al., 2018). Marine species richness and density is highest with sediments engineered by *S. alveolata* reefs when compared to non-engineered sediments (Holt et al., 1998; Dias and Paula, 2001; Dubois et al., 2002; Jones et al., 2018). Such ecosystem engineering is especially significant in the intertidal zone and other extreme zones (Jones et al., 1997), due to their ability to modify and stabilise beach sediment and protect against mechanical extremes of weather conditions (Wells, 1970; Rees, 1976). *S. alveolata* is tolerant to heat, by modulating cellular membrane lipids, though this is limited to below 25 °C (Muir et al., 2016). Other extreme weather conditions negatively affect survival of *S. alveolata*, due to wave erosion and potential dismantling during storm events (Wilson, 1971). Cool summer or winter temperatures also increase mortality (Firth et al., 2011). Crucially, all *S. alveolata* reefs, living or dead, provide important ecosystem services and functions, and reefs that are reported as degraded do not reflect the health of the worms within that reef (Curd et al., 2019).

In this study, the role of environmental factors on current *S. alveolata* distribution was investigated around the coast of Great Britain (GB). Following this, an investigation into the impact of projected SST increases was conducted. We hypothesise that minimum SST sets the maximum latitude for *S. alveolata*, due to the increase in mortality recorded in Firth et al. (2011), and that habitat suitability for *S. alveolata* will expand north with increasing SST associated with climate change. We aim to explore how these changes occur across the rest of GB, as this is at the leading edge of *S. alveolata* extent, and the impacts these changes may have on populations towards the centroid of the extent.

2. Methods

2.1. Data sources and preliminary processing

Inclusion of factors was based on data temporal and spatial resolution, and the hydrodynamics of the environments *S. alveolata* are known to occupy, specifically wave, and tidal current kinetic energies, slope, photosynthetically active radiation (PAR), coefficient of light attenuation (KDPAR), substrate, and maximum and minimum seabed temperatures. Data sources for *S. alveolata* distribution and environmental covariates are outlined in Table S1. Due to availability and consistency of data available, the Republic of Ireland and the Shetland Islands were not included. All data were freely available, and datasets were selected for their resolution and spatial coverage.

Occurrence data was utilized from Curd et al. (2020), who gathered this data with various methods including targeted surveys, personal communications with authors and national biodiversity information systems. For this project, only points from 49.9°–57.9° N and longitude: 6.4° W – 1.4° E were selected (the coast of GB), and only those from 2000 to 2020. Where the same site was sampled multiple times, only the most recent record was retained. Consistent with Curd et al. (2022) we removed presence records found on the east coast of the UK, as it is reported that *S. alveolata* has always been absent from the North Sea (Nunes et al., 2021).

The physical factors of the water column were included as wave and tidal current energies. Wave energy was selected as it disturbs the seabed a result of surface waves in shallow water, and tidal current energy affects the water column and character of the seabed. PAR and KDPAR were selected as proxies for turbidity of the water column; higher light levels indicate lower turbidity. Slope was included as an angle from the horizontal, with horizontal at 0°, which is as a function of change in depth. This was incorporated as there are reports of *S. alveolata* occurrences at both the very lowest part of the shore (Wilson, 1971; Mettam et al., 1994) and as high up the shore as on coastal defence structures (Firth et al., 2015). Minimum and maximum temperatures have been reported as significant factors in other models conducted for this species (Firth et al., 2015, 2021a, 2021b; Curd et al., 2022). Similarly, substrate was included in response to literature (Firth et al., 2021a). Due to the availability of data, Folk class 5 (BGS, 2021) was included here (see Table S2). The classes were mud, sand, coarse grained sediment (CGS), mixed grain sediment (MGS) and rocks and boulders (R&Bs) (Table S2, Fig. S3).

Slope was extracted in ArcGIS 9.3 software (ESRI), using the Spatial Analyst 9.3 extension. Both seabed and terrestrial data layers from Ordinance Survey Terrain 50 Digital Terrain Model were used, to ensure full coverage of the intertidal, as one dataset alone was insufficient. Presence records at the coarser substrate classes were limited, and so MGS and R&Bs were combined with CGS; this made no qualitative difference to the model performance. Excluding these two classes was also considered, and this made no qualitative difference to our findings but resulted in gaps in our prediction maps. Temperature was included as SST due to the spatial and temporal availability and was calculated as an average of one day over the 20 years from 2000 to 2020, from what is considered the coldest ("Tmin") and warmest ("Tmax") months in British coastal waters; the 14th of February, and the 31st of August, as both august and September are considered the warmest months. This varies regionally throughout GB and therefore it is not feasible to select the absolute warmest and coldest days for the entire coast without tailoring this to each individual coordinate for the entire 20-year timeframe. Hence, these two dates were selected as they fall within or close to extremes of temperature for GB. This data was then converted from Kelvin to Celsius. IPCC projections for oceanic warming were used to make future projections of habitat suitability. Two projections were included: the "best case" scenario of RCP 2.6 and "business as usual" scenario of RCP 8.5, for both 2050 and 2100. Table 1 displays the RCP scenario and oceanic warming. RCP 4.5 was not utilized due to their overlap with other scenarios. Hereafter, these will only be referred to by the amount of warming, to avoid confusion. These temperatures scenarios were applied to both Tmin and Tmax.

No other variables required cleaning or processing before use but were collated by projecting onto the British National Grid coordinate reference system. For building the model, occurrence points were used to clip all environmental variable data layers using QGIS (QGIS, 2021). Where occurrence points were missing corresponding environmental variable values, the closest neighbour was substituted within a 1 km

Table 1
Projected sea surface temperature rise for each RCP and time frame. Due to overlap with other scenarios. RCP 4.5 and 6.0 were not run. Information from Genner et al. (2017).

RCP Scenario	2050	2100
2.6	0.8 °C	1.2 °C
4.5	1.2 °C	1.5 °C
8.5	1.5 °C	3.2 °C

direct line. For making predictions, a GB wide version of the same data was used.

2.2. Habitat suitability model construction

The association between *S. alveolata* and environmental predictor variables was modelled using a Generalised Additive Model (GAM). The response variable was presence and absence of *S. alveolata*, modelled as a binomial distribution. Continuous explanatory variables were as follows: slope, tidal current kinetic energy (KeC), wave energy (KeW), photosynthetically active radiation (PAR) and the coefficient of light attenuation (KDPAR). Local environmental predictors were fitted using cubic smoothing splines. Seabed substrate (five levels) was fitted as a categorical explanatory variable, both as a main effect and interacting with each of the continuous explanatory variables. Latitude and longitude were fitted using 2-dimensional tensor interactors. Initially, collinearity between environmental variables was assessed using pairwise Spearman correlation, with a cut-off of $r_s < 0.8$ for inclusion in the model (Dormann et al., 2013).

The GAM was built using R version 4.0.2 (R, 2021), with the "mgcv" package (Wood, 2011). Model analysis was conducted using the "ROCR" package (Sing et al., 2005). The performance of the model established using the Akaike Information Criterion value (AIC) and Area Under the Curve (AUC) quantification, based on the receiver operating characteristic (ROC) (Fielding and Bell, 1997). AIC is a comparative statistic, used to assess the parsimony of different models, to aid in selection. Models with comparatively lower AICs are more parsimonious. AUC is an absolute measure of model performance, with models returning AUC values > 0.9 considered to have performed well, 0.7–0.9 reflecting moderate performance, and 0.5–0.7 reflecting a poorly performing model. The outcome of the GAM models are probability or suitability values, ranging between 0 and 1; 1 reflecting the most suitable habitat or highest probability of finding *S. alveolata*. Probability values from the models were mapped using QGIS (QGIS, 2021).

All R code used in this study is included as Supplementary Material (Section 2).

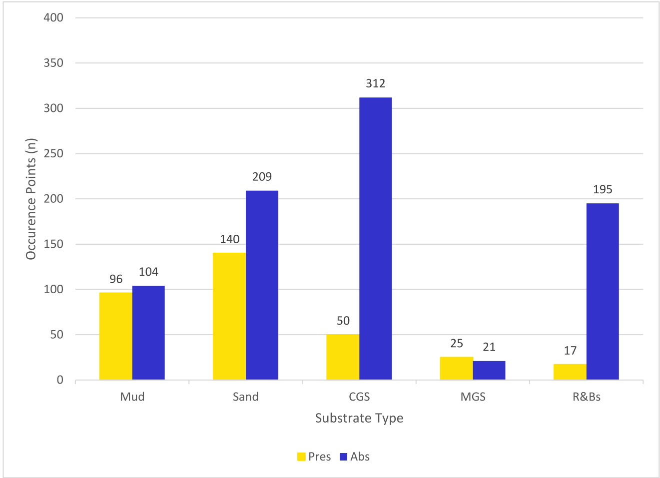

Fig. 1. Presence and absence points sorted by substrate class. Bars are labelled with the number of presence or absence records. The total number of records taken at either MGS or R&Bs is less than a third of those found at other substrate types (5% and 10% respectively).

Table 2
Descriptive statistics of each version of the model run without one descriptive factor. The full GAM includes all descriptive factors. ΔAIC is the comparison of the other model versions from the full version as this measure is comparative.

Removed Factor	R^2	Deviance explained	AUC	AIC	ΔAIC
Substrate	0.439	40.8%	0.903	642.1	67.4
KDPAR	0.460	43.6%	0.912	631.1	56.4
Wave	0.491	47.0%	0.922	600.6	25.9
Current	0.497	46.0%	0.920	602.1	27.5
Tmin	0.511	48.9%	0.929	591.5	16.8
Tmax	0.512	48.2%	0.927	585.8	11.1
PAR	0.516	49.2%	0.928	582.6	7.96
Slope	0.517	48.2%	0.929	594.4	19.7
None removed	0.529	50.2%	0.932	574.7	

3. Results

3.1. Habitat suitability model performance

A total of 1169 presence/absence data points were used to assemble the GAM model, with locations outlined in Fig. S1. The study area (latitude: 49.9°–57.9° N and longitude: 6.4° W – 1.4° E) was chosen as it matches the general distribution of *S. alveolata* records in GB. Of the records, there were 328 presences, and 841 absences.

Occurrence records were not made equally across all substrate types, as shown in Fig. 1, but were adequately balanced for a binomial GAM. R&Bs had the lowest number of presence records associated (n = 17). MGS had the lowest total of records associated (n = 46). The highest number of absences were reported with CGS (n = 312), and the highest number of presences with sand (n = 140). Hence, we pooled CGS, MGS and R&Bs in our modelling. Hereafter, substrate is referred to as substrate 1 for mud, substrate 2 for sand and substrate 3 for the combined classes CGS, MGS and R&Bs.

The Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) for our full model (trading off the true positive rate against the false positive rate) is shown in Fig. S2. It is considered that the closer the curve is to the upper left-hand corner, more accurate the test (Fielding and Bell, 1997). Fig. S2 shows the full model performed well, with an AUC of 0.932, R^2 of 0.529.

Statistical support for each variable included in the model is outlined in Table 2, including R^2, AUC and the difference in AIC value (ΔAIC) when compared to the full model with all variables included. Based on R^2, AUC and ΔAIC, substrate is the most influential variable, with removal leading to a drop of 0.09 to R^2, a loss of 9.4% explained deviance, and ΔAIC = 67.4. The remaining variables were less influential, with none individually accounting for more than a seven percent drop in R^2 or deviance or a two percent reduction in AUC. However, based on ΔAIC, removal of all single variables except PAR (ΔAIC = 7.96) did make a substantial change to model fit, with ΔAIC >10.

The suitability of factors for *S. alvealota* was plotted for each variable by substrate level (Fig. 2). Relationships for each variable displayed different patterns at each substrate class. P-values for these relationships can be found in Table S3.

Slope. On mud (substrate 1), increasing slope led to a decrease in suitability, whereas on the other substrates an apparently reversing relationship was poorly supported, with 95 % confidence ribbons that did not exclude the possibility of no relationship.

Water movement. On mud, there was no relationship between KeW and suitability, but on the other substrates relationships followed the same sigmoid pattern, with rapid increases in suitability after 100 Nm^2s^{-1}. With KeC, on mud (substrate 1), there is a slight, negative relationship. However, on sand (substrate 2), there is high suitability around $100Nm^2s^{-1}$, but at either extreme (1 or $10{,}000Nm^2s^{-1}$), low suitability is found. With coarser substrates (substrate 3), a negative monotonic relationship is seen, with the highest suitability found at or below $1Nm^2s^{-1}$, rapidly decreasing until $100Nm^2s^{-1}$, though the lowest suitability remains at around 0.3, whereas with substrate 2, the lowest probabilities were 0.

Light. Relationships between PAR and suitability were minimal, with the exception of a small decrease in suitability with increasing light levels on sand (substrate 2). KDPAR showed a strong positive relationship across the lowest values (<1%), with reversals in this trend

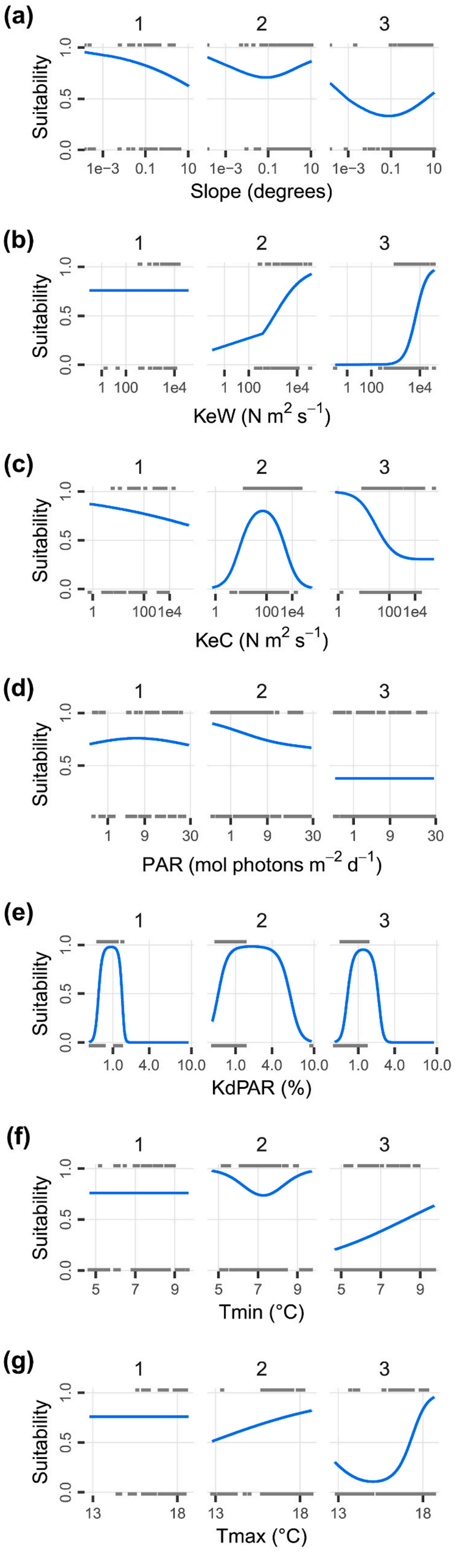

Fig. 2. Confidence intervals for each factor, split by substrate (1 = mud, 2 = sand, 3 = CGS, MGS and R&Bs). Solid blue lines show fitted responses. Density of data is shown as rug plots at the top and bottom of plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

apparent at higher values.

Temperature. On mud (substrate 1), there was no relationship between suitability and minimum SST (Tmin); on sand (substrate 2) there was a reversing relationship; but on coarser substrates (substrate 3) there was a positive relationship with Tmin. Finally, on mud (substrate 1) there was no evidence of a relationship between suitability and maximum SST (Tmax); on sand (substrate2) there was a weak positive relationship with Tmax; and on coarser substrates (substrate 3) there was a positive relationship with Tmax, particularly above c. 15 °C.

Looking across substrate types as a whole, *S. alveolata* habitat suitability is determined primarily by light attenuation (KDPAR) on mud (substrate 1); by light attenuation and water movement (waves and current) on sand (substrate 2); and by light attenuation, water movement, and sea surface temperature (SST) on coarser substrates (substrate 3).

3.2. Suitability changes with increasing SST

Suitability was classified from ARG UK (2010): poor <0.5, below average 0.5–0.59, average 0.6–0.69, good 0.7–0.79 and excellent >0.8. Three areas were outlined on the maps, which have noteworthy changes, and good data coverage. Area A includes the Isle of Man, and the mainland area where England meets Scotland on the western coast. Area B contains most of Wales, and Area C covers the Isle of Wight and the adjacent coast of the southern mainland.

Present-day scenario (0°C). Fig. 3 shows 10.67% of the coastline was considered suitable for *S. alveolata* (p=>0.6) (Table 3). Areas of suitability are found along the east and west coasts, with sparse patches in northern Scotland and along the south coast close to the Isle of Wight. The longest stretches of continuous suitability are seen on the north coast of area B, and along the east coast of England.

Warming of 0.8°C. Fig. 4 shows suitable areas increase by 9.66% from the 0 °C scenario. Suitable areas in the lower part of area A are increased, though the upper part remained mostly unchanged. Suitability of the east coast of England disappeared. The southern coast of England sees increased size and number of suitable patches (e.g., area C). Area B saw the greatest expansion of suitability, particularly in the lower half. The suitable areas also become more connected here.

Warming of 1.2°C. Fig. 5 shows differences between the suitability of 0.8 and 1.2 are minimal, as the overall suitability increases by 5.97%. This is reflected in the suitability of area B, wherein the trend remains similar, with an increase from good to excellent at some points. Area A saw an increase in suitability of some lower parts, though these are few. The most dramatic change occurred on the southern coastline, where the patchy suitable areas expanded, and moved up in class (i.e., from average to good, and good to excellent). The suitable areas in northern Scotland remain unchanged except for small areas on the eastern coast, which became excellent.

Warming of 1.5°C. Fig. 6 again shows the difference between 1.2 and 1.5 were minimal, with an increase in suitability (>0.6) of 3.89%. These changes occur in the previously outlined areas; area C, lower area B and lower area A. The southeast coast also increases in suitability, moving through the classes rather than expanding.

Warming of 3.2°C. With the most extreme predicted increase (Fig. 7), the largest increase in suitability is seen with this scenario, of 26.12%. This is reflected in the increase in suitability of the eastern coast of Scotland, and dramatic expansion of excellent class locations across the entire south coast, which can clearly be seen in area C. Area B becomes an area of continuous excellent locations, excluding 3 points. Area A follows this trend, though there are more areas that remain unsuitable than for area B. This reflects both an increase in suitability of previously unsuitable (<0.6) areas, and an increase in suitable areas, for example from average to excellent. The Outer Hebrides, which until this projection, remained mostly unchanged from the 0 °C prediction, now have several areas that are excellent or good. Several locations in the north of the Scottish mainland also become suitable.

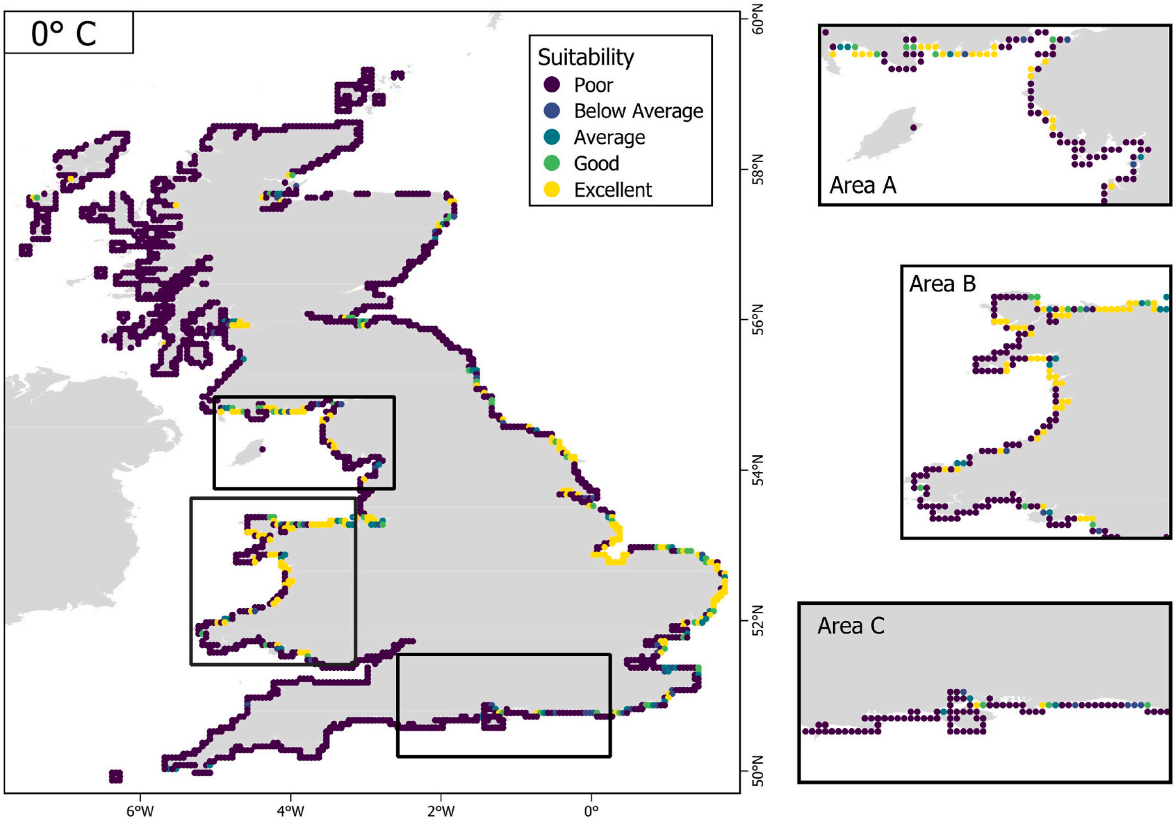

Fig. 3. Habitat suitability of GB with no SST increase applied.

Table 3
Percentage of coastline in each suitability class with different SST increase.

Suitability Class	0 °C	0.8 °C	1.2 °C	1.5 °C	3.2 °C
Poor	87.83	78.17	72.20	68.31	42.19
Below Average	1.50	5.73	5.37	3.52	2.04
Average	2.04	4.68	4.03	4.68	9.41
Good	2.79	2.94	6.82	5.95	2.41
Excellent	5.83	8.48	11.58	17.53	43.94

Finally, we summarised predicted temperature-induced changes in habitat suitability over latitude (Fig. 8). In the current scenario (0 °C warming) there is a clear latitudinal peak at mid-latitudes of the UK, around 53°N. With mild to moderate warming (up to 1.5 °C), the main increases in habitat suitability are seen in the south of the UK, with levelling up across the southern and mid-latitudes in terms of suitability, and almost no northward range expansion. At the highest modelled temperature increase (3.2 °C), the greatest increase in habitat suitability was still at the lower latitudes but the east coast of Scotland (around 58°N) and, to a lesser extent, the Outer Hebrides begins to show increases in suitability within areas that are tightly limited by substrate suitability.

4. Discussion

The aim of this study was to explore how the suitability of the GB coastline would change for *Sabellaria alveolata* with increasing SST due to climate change. This study utilized 1169 *S. alveolata* occurrence points, to test the relationship between minimum (Tmin) and maximum (Tmax) SST, substrate type, slope, wave (KeW) and current (KeC) energies, photosynthetically active radiation (PAR) and the coefficient of light attenuation (KDPAR), and how these influenced *S. alveolata* extents. The model performed well (AUC 0.932, R^2 0.529, Table 2) and was then used to predict future suitability of the GB coast with increasing SST.

The model found substrate to be highly influential; removal of this factor led to a 10% reduction in deviance explained and a 0.09 reduction in R^2. This has meant that the model labelled some areas where *S. alveolata* have been found between 2000 and 2020 to be unsuitable, as the local substrate was either CGS, MGS or R&Bs. This indicates that the model predictions may be conservative in these areas, which could be significant for the leading-edge extension. Additionally, this study is focussed on modelling habitat suitability and how this evolves with increased SST, not on predicting where to find *S. alveolata*. This is relevant as in the projection with no warming applied, areas of excellent and good suitability were found in patches along the east coast of England. This is interesting as it is known that *S. alveolata* is not found in the North Sea (Nunes et al., 2021). Our model suggests this may remain the case, as all suitability disappears when any SST increases are applied.

Data availability and resolution was a limiting factor of this model. For the intertidal around GB, datasets are often absent, or as part of a lower resolution dataset. For example, folk class 5 was used for substrate in this model, in part because no higher folk classes were available at the GB scale. However, as *S. alveolata* selects particles from the water column based on size and shape (Lo Bue et al., 2022), it is unlikely that a higher division would improve model performance. Further, the model could have been improved with a higher resolution of KDPAR and KeW data, which would have helped to further capture the complexity of the GB coast, particularly around the complex shapes of the Scottish coastline.

Our model identified minimum SST (Tmin) as being slightly more impactful than maximum SST (Tmax) ($\Delta AIC = 16.8$ vs. 11.1, Table 2). This agrees in part with Firth et al. (Firth et al., 2015, 2021a, 2021b), Lecornu et al. (2016) and Holt et al. (1998), who report that lower temperatures were found to be most significant for range extent

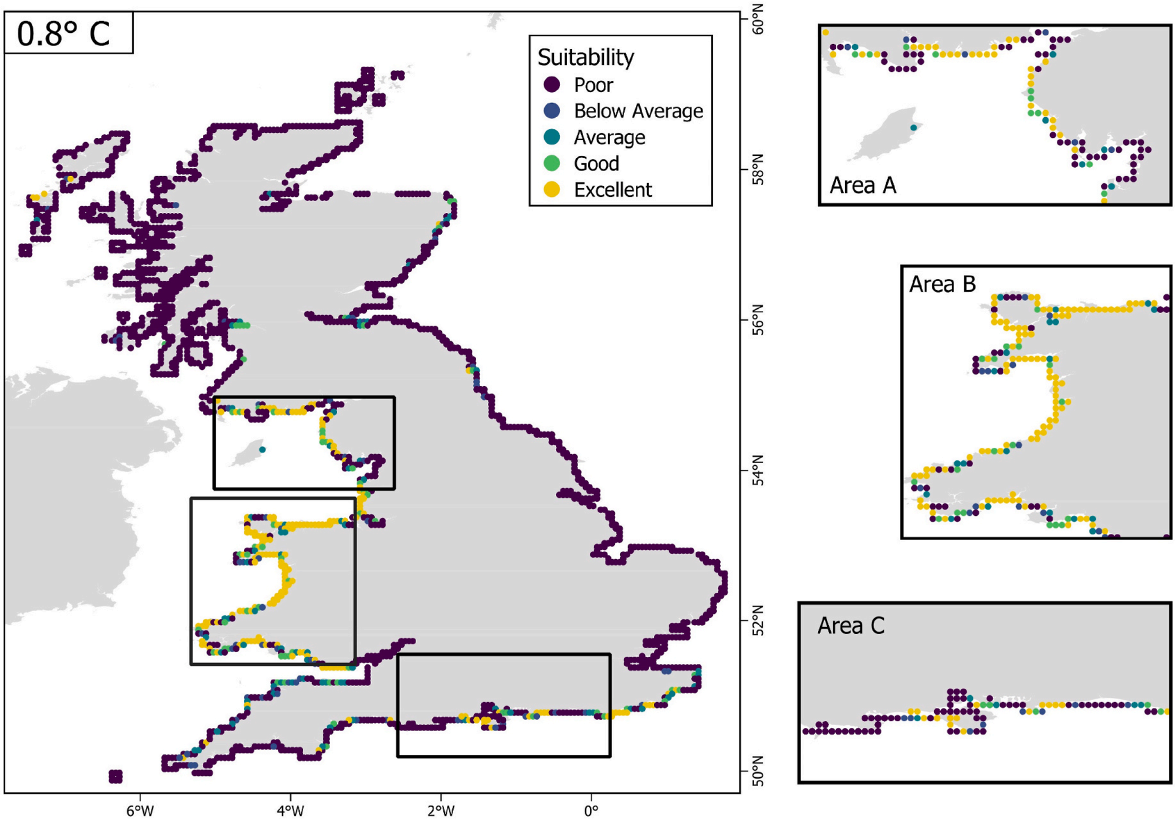

Fig. 4. Habitat suitability of GB with 0.8 °C SST increase.

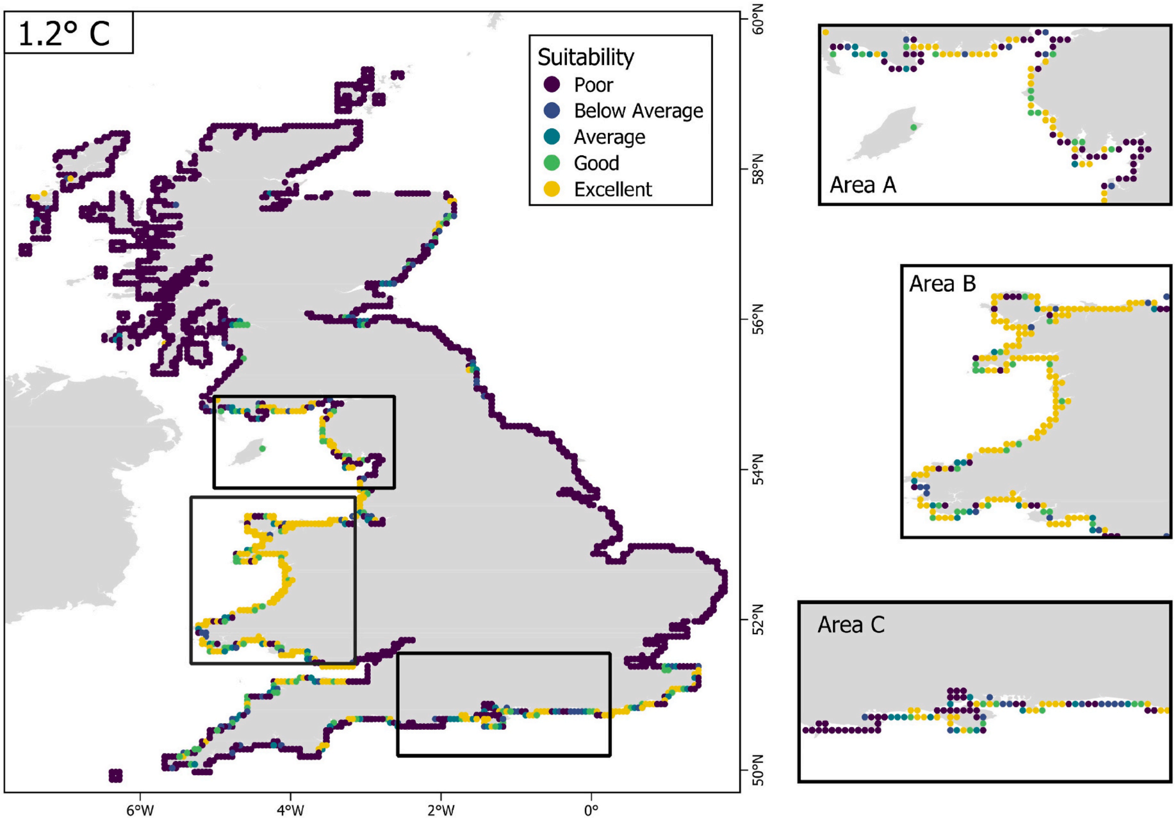

Fig. 5. Habitat suitability of GB with 1.2 °C SST increase.

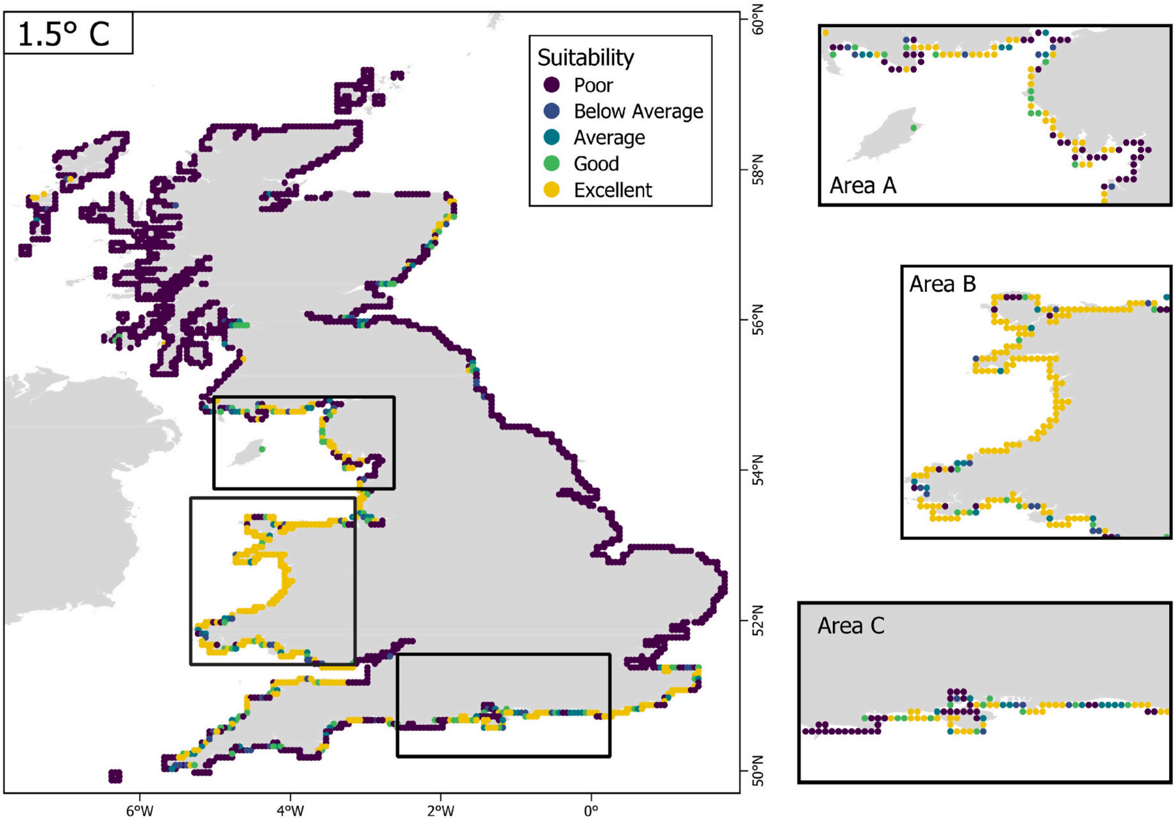

Fig. 6. Habitat suitability of GB with 1.5 °C SST increase.

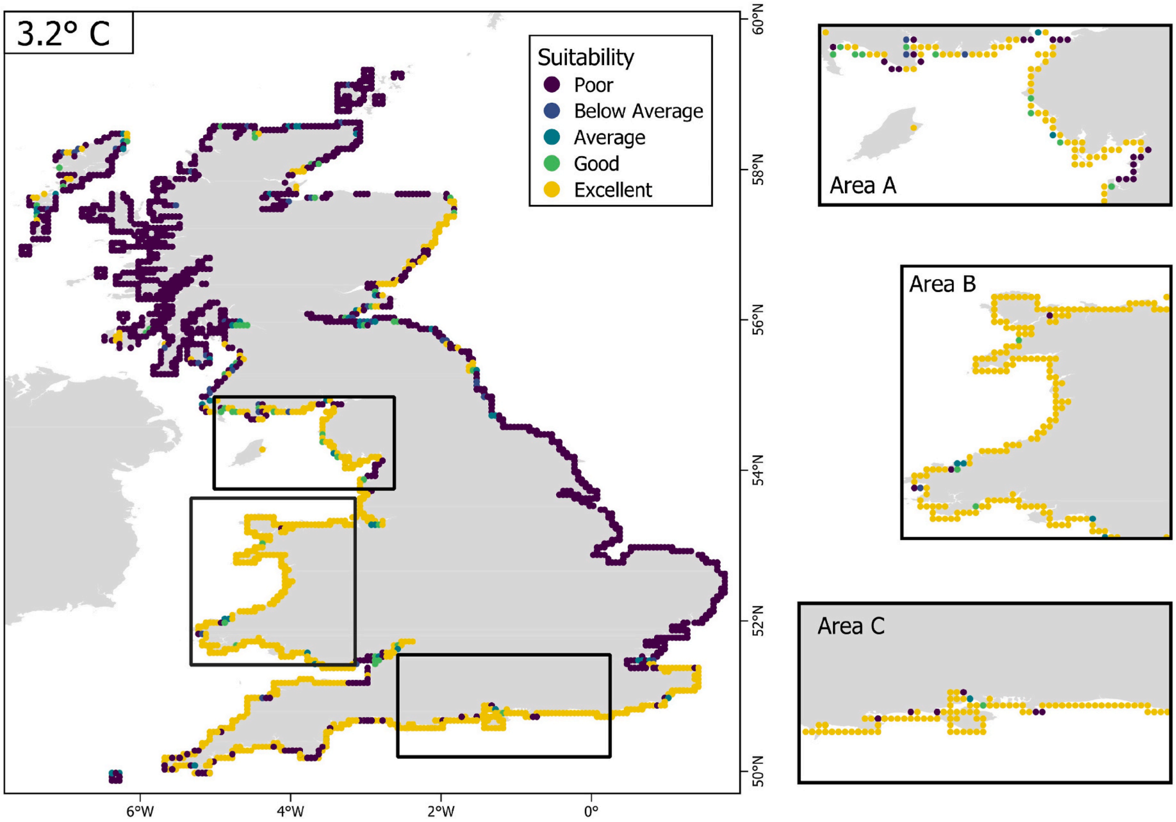

Fig. 7. Habitat suitability of GB with 3.2 °C SST increase.

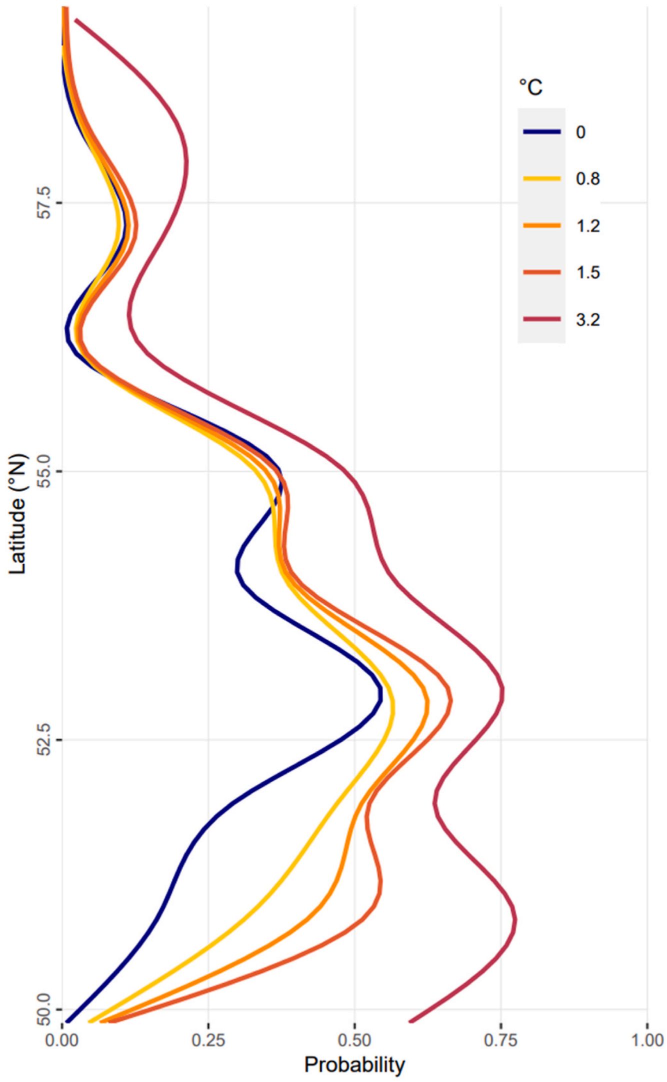

Fig. 8. *Suitability of GB coast for* Sabellaria alveolata *plotted by latitude.*

especially over multiple years and were significant in determining historical extents. Firth et al. (2021b) also found that substrate was more influential than temperature, despite using folk class 7 whereas here folk class 5 was utilized. *S. alveolata* are known to actively select the particles preferred for tube building from the surrounding water column, and are known to prefer rounded, smooth-surfaced grains, often of quartz or feldspar (Sanfilippo et al., 2019). Hence, rather than increasing the folk classification, including the mineralogy may have increased predictive power, and in this model, would have removed the uncertainty with CGS, MGS and R&Bs.

In our study we found that with each increase in SST applied, suitability of the GB coast increased, with the greatest increase found with 3.2 °C. This relationship is expected as it is proportional to the SST increase applied. Each SST increase between 0 °C to 1.5 °C resulted in between 5.43 and 6.34% increase in suitable locations ($>$0.6), with the greatest increase at 3.2 °C, with an increase in excellent class locations of 45.1% compared to 0 °C. These changes resulted in an increase in existing extent (patch size) as well as new sites becoming suitable. Curd et al. (2022) also found increased patch size with changing climatic factors towards the polar extent of *S. alveolata*, and stated that these patches could strengthen connectivity, allowing for enhanced resilience of distant populations. This could be crucial for new suitable areas found around the coast of Scotland, as these patches are small and distant, and may rely on the stronghold areas further south for genetic resilience.

A noticeable change seen with 3.2 °C of increased SST was the increase in suitability across the south coast of England, evolving from a few patches seen with the previous temperature applications, to an almost continuous network of excellent class locations. This finding agrees in part with the findings of Curd et al. (2022) in the same area, who reported an increase in patch size here. Curd et al. (2022) examined both terrestrial and marine factors, of which four factors had climate change predictions associated and were modelled for the present (2000–2020) and the future (2040–2049) at RCP 4.5. This is represented here by the 1.2 °C SST increase, though we did not find an increase in suitability comparable to Curd et al. (2022) at this level of warming, likely due to their inclusion of additional factors in their model that had climate change predictions applied; salinity, air temperature and wave height. These combined factors will have had a cumulative impact on their model, meaning more warming would need to be applied to this model to see proportional results. Thus, similar patterns are predicted here, but at a higher SST increase application.

An increase in suitability of the southern English coast would be significant for diversity and resilience of populations further north, though dispersal and connectivity around the GB coast would need to be examined, as there is a higher genetic diversity at the leading edge than toward the centroid of distribution in the Bay of Mont-Saint-Michel (Nunes et al., 2021), indicating a lack of connectivity and dispersal towards the leading edge in GB. Nunes et al. (2021) advise that the populations in the English Channel should be viewed as self-sustaining. Hence, expansions in this area may aid resilience of regional populations but are not likely to boost southerly populations (Nunes et al., 2021), which are at risk from the effects of climate change (Curd et al., 2022). This is especially concerning as warming is already reported around the trailing edge, and ocean warming is occurring in Europe at twice the global average rate (WMO, 2023).

The increase in south coast suitability partially agrees with McHenry et al. (2019), who studied 137 marine species in the US NES, USA. They built one model to examine the effects of increased temperature only (partial model), and a second (full) model examined how warming would impact their explanatory variables of surface and bottom salinity, surface and bottom temperature, and sea surface height. Both models used data equivalent to RCP8.5 (3.2 °C warming in this model). The findings from their partial model indicate that pelagic, demersal, and benthic species would experience an expansion in suitable habitat of an average ~7000 km^2, with a northward expansion of 65–75 km. Our model is comparable to this partial model. Their full model still found a modest northward migration of 45–60 km, but also found that the trailing and centroids would move north too, resulting in a contracted range, on average loosing 3000 km^2. Curd et al. (2022) also found an extension of range at the leading edge, towards the polar regions, and found the extent increasingly fragmented towards to equator at the trailing edge. These models demonstrate how temperature alone may not capture the complexity of the impacts of warming oceans. For example, McHenry et al. (2019) use sea surface height; as an intertidal species, *S. alveolata* is susceptible to sea level rise as increasing sea levels submerge reefs or lead to coastal squeezing, wherein species migrate further inshore to accommodate for the increased sea level, becoming trapped by the cliffs, unsuitable shores or urban constructions which prevent further inshore migration (Jackson and McIlvenny, 2011; Rilov et al., 2021). Therefore, despite an increase in the suitability of the present-day coastline with increased SST, fragmentation could still occur due to the topography of the GB coast and how this is impacted by rising sea levels; most presences recorded in this dataset occurred on slopes of $<10°$ from the horizontal ($n = 324$), which would experience changes in sea level very rapidly.

It was expected that *S. alveolata* would extend its range northwards with warming oceans, as the habitat suitability of the northern coastline is expected to increase (e.g., van Hal et al., 2010; Monzon et al., 2011; Keith et al., 2011; Genner et al., 2017; Curd et al., 2022). Our model predictions agree with this (Figs. 3–8, Table 3), as some suitable ($>$0.6) locations are seen to the north of the study area with increasing temperature applications, which were not seen in the 0 °C predictions. However, the northern extent did not rapidly extend with increasing temperatures until the 3.2 °C application, and then it was patchy and disconnected. This reflects the complex coastline and heterogenous conditions. Establishment here will depend on connectivity from other locations further south, which are predicted here to become more suitable and therefore may be the stronghold needed for norther expansions to occur. The topography of the islands of the Inner and Outer Hebrides has created areas of enhanced currents, turbulence eddies and separated flows in this region (Ellett and Edwards, 1983). This may help to explain why the current occurrences are fragmented and could hinder the norther expansion of *S. alveolata*, through preventing connectivity and dispersal; such hydrodynamic barriers have been reported in Ireland (Firth et al., 2021a). Northward extensions of ranges for species in response to changing climate only considers temperature changes and does not consider that there may be physical barriers already in place, such as hydrodynamics and as mentioned previously, topography.

CRediT authorship contribution statement

Camille Domy: Writing – original draft, Visualization, Software, Resources, Investigation, Formal analysis, Data curation. **Rebecca Stone:** Writing – original draft, Software, Resources, Methodology, Investigation, Data curation. **Ruth Callaway:** Supervision. **James C. Bull:** Writing – review & editing, Supervision.

Declaration of competing interest

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.

Data availability

All data and code used is outlined in the supplementary section; all data is free to access

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108543.

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