

# Isles of Scilly Seagrass – State of the Meadows 2023

September 2024

Natural England Commissioned Report NERC492

## About Natural England

Natural England is here to secure a healthy natural environment for people to enjoy, where wildlife is protected, and England's traditional landscapes are safeguarded for future generations.

## Further Information

This report can be downloaded from the [Natural England Access to Evidence Catalogue](#). For information on Natural England publications or if you require an alternative format, please contact the Natural England Enquiry Service on 0300 060 3900 or email [enquiries@naturalengland.org.uk](mailto:enquiries@naturalengland.org.uk).

## Copyright

This publication is published by Natural England under the [Open Government Licence v3.0](#) for public sector information. You are encouraged to use, and reuse, information subject to certain conditions.

Natural England images and photographs are only available for non-commercial purposes. If any other photographs, images, or information such as maps, or data cannot be used commercially this will be made clear within the report.

For information regarding the use of maps or data see our guidance on [how to access Natural England's maps and data](#).

© Natural England 2024

Catalogue code: NERC492

## Report Details

### Author(s)

Prof James Bull

Dr Emma Kenyon

### Natural England Project Manager

Jules Webber

### Contractor

In partnership with [Project Seagrass](#)

### Keywords

LIFE Recreation ReMEDIES, Eelgrass, Isles of Scilly, Monitoring, Project Seagrass, Seagrass, *Zostera marina*

### Acknowledgements

*Co-funded by the European Union. Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or CINEA. Neither the European Union nor the granting authority can be held responsible for them.*



#### **LIFE Recreation ReMEDIES (LIFE18 NAT/UK/000039)**

*Reducing and Mitigating Erosion and Disturbance impacts affecting the Seabed.*

### Citation

James Bull & Emma Kenyon. 2023. Isles of Scilly Seagrass – State of the Meadows 2023. [NERC492]. Natural England.

# Foreword

The LIFE Recreation ReMEDIES: ‘Reducing and Mitigating Erosion and Disturbance Impacts affecting the Seabed’ project (LIFE 18 NAT/UK/000039) runs from July 2019 - October 2024. The aim of the project is to improve the condition of seabed habitats, including seagrass beds, in five Special Areas of Conservation (SACs) between Essex and Isles of Scilly. This will be achieved by restoration, demonstration and reducing recreational pressures. Promoting awareness, communications and inspiring better care of sensitive seabed habitats will be key. Natural England (lead partner) is working with Marine Conservation Society, Ocean Conservation Trust, Plymouth City Council/TECF and the Royal Yachting Association. The project is financially supported by LIFE, a financial instrument of the European Commission.

Targeted project delivery for the Isles of Scilly has included workshops with local stakeholders to raise awareness and capture local knowledge about seagrass in Scilly. This report will make a vital contribution to the aims of the LIFE Recreation ReMEDIES project by providing condition data for the review of the status of seagrass beds on the Isles of Scilly since the baseline completed at the start of the project. It draws upon existing data and evidence available from Natural England and the supplier over the last 30 years. The report will also draw together summaries and recommendations from recent 2022 commissioned seagrass projects to help inform future seagrass monitoring, research, and conservation actions.

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

## Contents

1	Executive summary .....	6
2	Introduction.....	8
2.1	Seagrass.....	8
2.2	Wasting disease .....	8
2.3	Epiphytes .....	9
2.4	Non-native invasive species .....	9
2.5	Isles of Scilly .....	10
2.6	Long-term eelgrass monitoring .....	13
2.7	Eelgrass spatial distribution and extent monitoring .....	14
3	Methods.....	15
3.1	Long-term eelgrass monitoring .....	15
3.2	Analytical methods.....	16
3.3	Eelgrass spatial distribution and extent monitoring .....	18
4	Results .....	18
4.1	Long-term eelgrass monitoring .....	18
4.2	Eelgrass spatial distribution and extent monitoring .....	29
5	Conclusions and recommendations .....	40
5.1	Conclusions .....	40
5.2	Recommendations .....	42
6	References .....	43
7	Appendices.....	47
7.1	Appendix 1 – Spatial and temporal heterogeneity.....	47
7.2	Appendix 2 – Summary data for the current year.....	54

# 1 Executive summary

The LIFE Recreation ReMEDIES project, led by Natural England, aims to protect sensitive seabed habitats, including eelgrass (*Zostera marina*) beds, which are easily damaged and slow to recover. This analysis will make a vital contribution to the aims of the LIFE Recreation ReMEDIES project by providing condition data of eelgrass at five key beds across the islands at the end of the project. It draws upon the experience, survey methodology, and results of a long-term eelgrass monitoring programme (28 years) on Scilly. This analysis is a follow-up to that undertaken at the start of ReMEDIES, to assess change in the condition of the eelgrass.

We analyse novel data from spatially replicated surveys of a comparatively un-impacted, temperate eelgrass habitat, amongst the Isles of Scilly, UK. The five sites assessed were Broad Ledges Tresco, Higher Town Bay, Little Arthur, Old Grimsby Harbour, and West Broad Ledges. Metrics include eelgrass shoot density and morphology, wasting disease, and epiphyte cover, as well as informal assessment of the invasive non-native, *Sargassum muticum*. We also provide summaries of recently commissioned projects developing novel wave modelling, remote sensing, and habitat suitability modelling approaches for eelgrass. These were designed to improve understanding of eelgrass extent, using the Isles of Scilly as a focus.

While shoot density showed no statistically significant changes over time at four survey sites, at Higher Town Bay it has declined by 37 % since long-term monitoring began in 1996, or by 8 % since the initial ReMEDIES assessment in 2020. The cause is unknown but not thought to be boat activity, as monitoring is at the opposite end of the long bay to moorings. Morphology was also found to differ between sites with little overall trend through time. Shoot density and morphology were combined into leaf area index (LAI). This broadly followed the same pattern as shoot density, with a substantial decline at Higher Town Bay but relatively stable elsewhere. The proportion of quadrats located on eelgrass versus bare sand is used as a measure of patchiness. This showed little long-term change, except for Old Grimsby Harbour where a decline of 68 % over the duration of the long-term monitoring has occurred. However, this has stabilised, or even begun to reverse over the lifetime of the ReMEDIES project. Across the whole length of the survey, wasting disease prevalence and epiphyte cover both differ substantially between survey sites. Long-term changes in wasting disease and epiphyte cover have been observed but without any clear, linear trend. Finally, *Sargassum muticum* was noted at all surveyed sites but at low levels not expected to negatively impact on eelgrass.

Improved wave forecasting and remote sensing of eelgrass resulted in a habitat suitability model showing close agreement with boat-based ground truthing. Several areas, particularly in the western parts of the central lagoon in Scilly, are highly suitable environments for eelgrass but currently under-occupied. This includes Old Grimsby Harbour which, given recent cessation of declines, could be a good candidate site for localised eelgrass restoration attempts.

The synthesis of these findings indicates a generally stable picture of extensive eelgrass in excellent condition across Scilly. There are concerning declines at Higher Town Bay but cause for cautious optimism at Old Grimsby Harbour. Key recommendations include continuation of long-term in-water monitoring, as well as the adoption of modelling and experimental approaches to determine causes of localised decline set against wider resilience.

## 2 Introduction

At its inception in 2019, the LIFE Recreation ReMEDIES project, led by Natural England, aimed to protect sensitive seabed habitats including eelgrass beds – a critically endangered EU Red Listed Habitat – which are easily damaged and slow to recover. The project facilitated the installation of new advanced mooring systems, locally developed voluntary codes, targeted training, and habitat restoration in five areas across southern England, including the Isles of Scilly SAC. Targeted project delivery for the Isles of Scilly included workshops with local stakeholders to raise awareness and capture local knowledge about eelgrass on Scilly. This report contributes to the baseline monitoring of the ReMEDIES project on Scilly by assessing the condition of the eelgrass at five key eelgrass beds across the islands. It compares a survey undertaken in 2020, shortly after the start of ReMEDIES (Bull & Kenyon, 2021) with a follow-up survey towards the end of the project, undertaken in 2023. This report also draws upon the experience, survey methodology, and past results of the long-term monitoring programme of eelgrass on Scilly (28 years). Finally, condition monitoring is presented in the context of exciting, new approaches for eelgrass data acquisition, including high resolution wave modelling, use of remotely operated vehicles, and habitat suitability modelling and recommendations are made for future monitoring, research, and conservation.

### 2.1 Seagrass

Seagrasses are globally dispersed along coastlines, covering c. 0.3 to 0.6 million km<sup>2</sup> (Duarte & Chiscano, 1999; Duarte, 2002). Much of the value of seagrass meadows lies in their high levels of primary productivity, acting as a carbon and nutrient sink, providing a shelter for invertebrates or juveniles of fish species, and protecting shorelines via wave attenuation and stabilization of sediments (Costanza et al., 1997; Duarte & Chiscano, 1999, Gillanders, 2007; Potouroglou et al., 2017). However, seagrasses are currently in rapid decline worldwide, due to a range of anthropogenic impacts, disease, and climate change (Orth et al., 2006; Waycott et al., 2009). This decline is also substantial and very concerning across the UK (Green et al., 2021). As a result, there is considerable interest in understanding the drivers of seagrass population dynamics and a general appreciation that multiple spatial scales are important; for example, local density at the sub-metre scale (Olesen & Sand-Jensen, 1994a, 1994b; Bull et al., 2012), the influence of clonal expansion over tens of metres (Reusch et al., 1999; Kendrick et al., 2005; Zipperle et al., 2011), or even metapopulations spanning oceans (Rozenfeld, 2008).

*Zostera marina* (eelgrass) is the predominant seagrass species of the north Atlantic and is the focus of this report, which is almost exclusively sub-tidal around the Isles of Scilly.

### 2.2 Wasting disease

In the 1930s, a 'wasting disease' (*Labyrinthula zosterae*) substantially reduced populations of eelgrass. Along the Atlantic coasts of Europe and North America, up to 90% loss was



estimated (Muehlstein, 1989), with dramatic knock-on effects to fishing industries and waterfowl populations (Orth et al., 2006). Wasting disease continues to affect eelgrass beds, but with no outbreaks as dramatic as the epidemic of the 1930s (Short et al., 1988). Various theories have been put forward to explain the occurrence of wasting disease (review in den Hartog, 1987). In particular, environmental stresses, especially high summer temperatures, have been suggested as a likely trigger for epidemics (Rasmussen, 1977).

Wasting disease was reported to have reappeared around the Isles of Scilly in the early 1990s, and this was a key motivation for the long-term condition monitoring analyzed in this report (Fowler, 1992). Signs of disease were quantified by its characteristic leaf lesions (den Hartog, 1989; Burdick et al., 1993). Presence of the causative agent was not tested for directly (for example, by culturing or PCR). However, results from population dynamic modelling are consistent with these signs of disease being caused by an infectious agent (Bull et al., 2012).

## 2.3 Epiphytes

Epiphytes form an integral part of a typical seagrass ecosystem, potentially accounting for a substantial component of biomass, but can also directly compete with seagrass for light (Lobelle et al., 2013). In the surveys reported here, attempts were not made to identify specific epiphyte species. Rather, all visible epiphytes were treated as a functional group, likely to have a similar effect on eelgrass growth by restricting light reaching the photosynthetic surface of leaves. In reality, the epiphytic community of *Z. marina* is typical of many seagrasses, including algae as well as a range of invertebrate species (Borowitzka, 2007). There is known to be substantial spatial and temporal heterogeneity in epiphyte distributions on the leaves of *Z. marina* (Cullinane et al., 1985; Johnson et al., 2005); a phenomenon also found in other seagrass genera, such as *Amphibolis* (Lethbridge et al., 1988) and *Posidonia* (Piazzi & Cinelli, 2000).

## 2.4 Non-native invasive species

The main non-native species of note observed amongst eelgrass in the Isles of Scilly is *Sargassum muticum*, wireweed. This invasive species was first recorded on the Isle of Wight in 1973 ([www.marlin.ac.uk](http://www.marlin.ac.uk)) and has since spread throughout much of the UK and Ireland. *S. muticum* is regularly encountered by eelgrass survey teams in the Isles of Scilly. As such, there is legitimate concern that it has potential to compete with native species, including eelgrass. The counterpoint to this possibility is that *S. muticum* requires hard substrate to grow on, so is likely to be highly spatially restricted across the sand- and sediment-dominated substrates where eelgrass grows in the Isles of Scilly. While not formally quantified as part of the long-term condition monitoring reported here, surveyors report no obvious increases in its prevalence and distribution, nor evidence that it is directly outcompeting eelgrass at scale.

## 2.5 Isles of Scilly

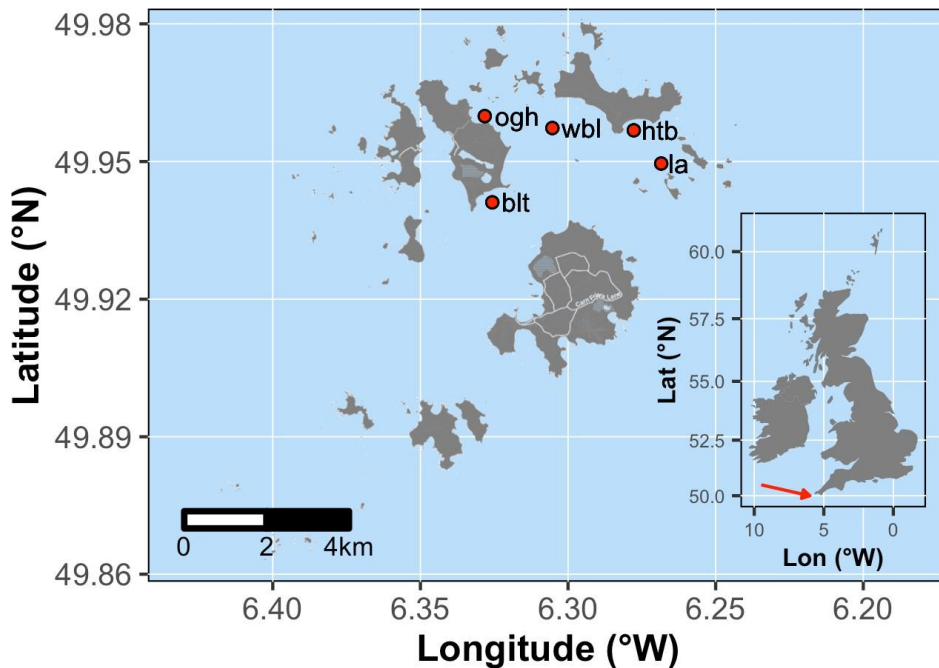
One of the main surviving eelgrass habitats around the UK is located in the shallow, relatively sheltered waters between the numerous islands and rocks that make up the Isles of Scilly, UK. Lying approximately 25 miles southwest from Land's End, Cornwall, the Isles of Scilly are to the extreme west of the United Kingdom (Figure 1). They comprise an archipelago of approximately 200 granite islands and rocks, separated by shallow sea. The five main islands (St. Mary's, St. Martin's, Tresco, St. Agnes, and Bryher) are permanently inhabited, supporting tourism, fishing and small-scale farming.

The Isles of Scilly SAC was designated in 2005 for the following features (and sub-features):

- 1) mudflats and sandflats not covered by seawater at low tide (intertidal sand and muddy sand);
- 2) reefs (circalittoral rock, infralittoral rock, intertidal rock);
- 3) sandbanks which are slightly covered by seawater all the time (subtidal coarse sediments, subtidal mixed sediments, subtidal sand, and subtidal seagrass beds);
- 4) intertidal mudflats and sand flats (sand communities);
- 5) grey seals (*Halichoerus grypus*); and
- 6) shore dock (*Rumex rupestris*).

In this sub-tidal environment, there are no large grazing species, such as the geese that affect inter-tidal eelgrass populations (Zipperle et al., 2010; van der Teide et al., 2012), or the marine turtles and sirenians of tropical seagrass habitats (Thayer et al., 1984; Fourqurean et al., 2012). In addition, the Isles of Scilly are an archipelago (Figure 1), where seagrass has been assessed to be amongst the best condition in the UK (Jones & Unsworth, 2016). Here, eelgrass grows substantially as a natural monoculture, and it has been possible to make rare baseline observations of an eelgrass ecosystem not thought to be in serious overall decline.

Five eelgrass survey locations were established in the early 1990s (Figure 1). These point locations clearly do not cover the whole extent of seagrass around the archipelago (e.g., see Jackson et al., 2011) but were intended to represent a range of environmental conditions encountered across the Isles of Scilly seagrass meadows.



**Figure 1.** Locations of the five long-term eelgrass monitoring sites around the Isles of Scilly. Red points indicate sites. Clockwise from bottom-left: Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Inset map of the United Kingdom & Ireland. Red arrow indicates the position of the Isles of Scilly.

The following sections on site descriptions are closely based on the initial ReMEDIES Isles of Scilly eelgrass report (Bull & Kenyon, 2021), originally adapted from Cook (2011). There have been no major developments close to any of the five eelgrass survey sites during the term of the ReMEDIES project. However, there was substantial work to extend the main quay in Hugh Town, St. Mary's in recent years. The amount of associated traffic and disturbance is unknown.

## 2.5.1 Broad Ledges Tresco

Broad Ledges Tresco lies on the southern edge of Tresco and, together with Crab Ledge, Tobaccoman's Ledge, and Green Island to the east, forms part of the large intertidal area that fringes the southern coast of Tresco. There is a concrete pier that allows access to the island from the sea and is used by tourist boats at most states of the tide. The bay is used on an occasional basis as an anchoring point for smaller yachts. The area is open to the prevailing southwesterly winds and tidal streams. The seabed here comprises coarse sand, mixed with small gravel, pebbles and some cobbles, as well as some *Sargassum muticum* and small macroalgae, found attached to the small material. The site does have yachts anchoring but this is infrequent due to the more exposed nature of the location. The

bed is close to the works that took place in 2008 to repair and extend the pier at Carn Near. This site is accessible for in-water eelgrass monitoring at most tidal states although currents present a challenge at certain times.

### 2.5.2 Higher Town Bay

The bay is situated on the southern edge of St. Martin's and is bounded by Cruther's Point to the west and English Point to the east. A small stone harbour, which acts as one of the main access points to the island from the sea, is situated at the western end of the bay. The bay is also used as an anchorage for a number of small vessels and the fringing beach and dune system are a popular destination for tourists. The eelgrass bed is concentrated at the eastern end of the bay and runs from English Island, westwards along the edge of the bay. Occasional eelgrass shoots have been observed growing to within c. 50 m the harbour at the western end of the bay. Strong tidal streams flow across the bay and the bed is also exposed to the prevailing southwesterly winds. The sea floor here comprises medium sands which, given the strong tidal streams, is liable to erosion. This sediment movement and erosion is prevented in some places by the eelgrass rhizomes that help bind the sand and also promote accretion to the extent that the eelgrass forms prominent platforms that stand up to c. 30 cm above the surrounding sea floor. The strong tidal streams bring large fronds of loose macroalgae from the rocky ground of the Eastern Isles and although there are very few other species growing here, there are large loose fronds of transported material that overlie the eelgrass. This site is only accessible for in-water eelgrass monitoring during a narrow window of slack water, where eelgrass can be assessed by wading at low water.

### 2.5.3 Little Arthur

This bed lies in the Eastern Isles and to the east of Little Arthur, where it is sheltered from the prevailing southwesterly winds and strong currents that flow round the islands. A much larger expanse of eelgrass lies to the west of Little Arthur, but this is not accessible for in-water monitoring due to strong currents. However, that meadow has been the focus of a related study using aerial photography to infer population dynamics (Irvine et al., 2018), as well as remotely operated vehicle surveys (Bertelli et al., in press). The Eastern Isles are also home to a colony of grey seals (*Halichoerus grypus*) that attract boats of tourists who come to view them. Few of these boats, however, anchor here and impact the eelgrass bed. The majority of the substrate within the islands comprises bedrock and large boulders that are covered by dense growths of macroalgae. The eelgrass bed, however, lies in a small patch of medium sand and, despite the surrounding macroalgae, the eelgrass bed is relatively free from any covering vegetation. This is one of the deepest beds surveyed in the islands and although small in area, exists as a complete single bed with few significant patches of sand. In-water eelgrass monitoring is best conducted at either lower or high-water slack.

## 2.5.4 Old Grimsby Harbour

The bed lies towards the southern side of the natural harbour formed by the small bay on the eastern side of Tresco that forms one of the main access points to the island from the sea. Although this access is dependent on the state of the tide, a large number of boats use the stone quay situated in the centre of the western side of the bay. The bay is found on the eastern side of the island, and it provides shelter for both the visiting boats that anchor on the edge of the bay and local boats that use the permanent mooring buoys in the bay, from the prevailing southwesterly winds. These moorings are anchored to base weights by means of a heavy sinker chain with a large buoy on the surface. The chains have to be long enough to allow for the rise and fall of the tide, which means that at low water there is potentially a large amount of chain lying on the sea floor and over the eelgrass shoots. The seabed is somewhat variable over the long term, ranging from mainly medium sand in some years to fine sand or silt in other years. This is overlaid with patchy eelgrass, intermixed with some overlying loose macroalgae. This site is accessible for in-water eelgrass monitoring at any state of the tide, although care needs to be taken to avoid other water users.

## 2.5.5 West Broad Ledges

West Broad Ledge lies on the southwestern edge of St. Martin's and on the southern edge of the channel between St. Martin's and the island of Tean. This channel is used by pleasure boats navigating between the islands but not often as an anchoring point as boats generally choose to anchor further to the north of the access jetty. The seabed comprises medium and coarse sand with small gravel and pebbles on which some fronds of *S. muticum* and other species of small macroalgae are present. The eelgrass bed covers a wide area but is highly patchy in nature. The bed is also swept by strong tidal currents, especially on spring tides. This site is only accessible for in-water eelgrass monitoring at slack water, with high water being preferable.

## 2.6 Long-term eelgrass monitoring

Some form of monitoring of the Isles of Scilly eelgrass beds has been undertaken since the 1980s (reviewed by Bull & Kenyon, in press). This early work made numerous valuable contributions to our understanding of these beds, including the discovery of the signs of wasting disease in the archipelago, that was observed to be coincident with deterioration of the eelgrass. In the early 1990s, efforts were made to establish annual surveys, following consistent methodology. The long-term eelgrass monitoring analyzed here is a direct continuation of this process, with records that we regard as comparable beginning in 1996. The over-arching aim of that monitoring is to build a long-term evidence base of eelgrass condition.

The objectives of the annual long-term eelgrass monitoring in the Isles of Scilly are to record:

- 1) the density (shoot counts per quadrat) of eelgrass at five sites around the archipelago;
- 2) the number of leaves per shoot of eelgrass;
- 3) the maximum leaf length per shoot;
- 4) the amount of infection on eelgrass leaves, thought to indicate wasting disease; and
- 5) the amount of epiphyte cover on leaves.

Additionally, notes are taken on the presence and distribution of the non-native species, *Sargassum muticum*.

## 2.7 Eelgrass spatial distribution and extent monitoring

By the early 2020's, the Isles of Scilly has gained international recognition as a UK hotspot of monitoring and research effort on eelgrass, e.g., Bowden et al. (2001) – biodiversity, Foden & Brazier (2007) – Water Framework Directive, Jackson et al. (2011) – mapping, Bull et al. (2012) – wasting disease, Lobelle et al. (2013) – epiphytes, Potouroglou et al. (2015) – life history, Jones & Unsworth (2016) – bioindicators, Irvine et al. (2018) – spatial patterning, Alotaibi et al. (2019) – population genetics, Bertelli et al. (2021) – dynamics, as well as featuring as a case study in the Seagrass Restoration Handbook UK & Ireland (Gamble et al., 2021), NERC's Sustainable Management of UK Marine Resources research programme ([www.smmr.org.uk](http://www.smmr.org.uk)), and the LIFE Recreation ReMEDIES project (<https://saveourseabed.co.uk>).

To help develop the eelgrass research momentum in the Isles of Scilly, as well as enhance capacity and capability for eelgrass monitoring elsewhere using Scilly as a case study, Natural England commissioned an integrated portfolio of projects focusing on novel (remote) data acquisition and modelling. These projects were completed in 2022 and presented through a series of Natural England Reports (Bertelli et al., in press – remotely operated vehicles, Conley et al., in press – wave modelling, Bertelli et al., in press – habitat suitability modelling).

Summaries of these commissioned projects are provided in this report. This is intended to provide supplementary evidence to inform condition of subtidal eelgrass in the Isles of Scilly, as well as brief critical evaluation of methods, consideration of heterogeneities in the data, and recommendations to inform future eelgrass monitoring, research, and conservation actions.

## 3 Methods

### 3.1 Long-term eelgrass monitoring

#### 3.1.1 Survey location

As far as possible, surveys in 2023 were carried out at the same five locations as in previous years (Figure 1 and Table 1). These have become known as ‘Broad Ledges Tresco’ (blt), ‘Higher Town Bay’ (htb), ‘Little Arthur’ (la), ‘Old Grimsby Harbour’ (ogh) and ‘West Broad Ledges’ (wbl). Once on site, the vessel was manoeuvred to the target coordinates for the survey. Final placement of the anchor was based on finding a sandy patch, devoid of eelgrass, as close as possible to the target. This was done to minimize the impact of the survey on the eelgrass. The resulting central datum for each survey was typically within 10-20 m of the target coordinates and the actual coordinates were recorded.

**Table 1.** Isles of Scilly eelgrass survey locations in 2023 at Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Sites	Latitude (°N)	Longitude (°W)
blt	49.93967	6.32942
htb	49.95737	6.27400
la	49.94888	6.26445
ogh	49.96027	6.32990
wbl	49.95675	6.30447

#### 3.1.2 Quadrat placement

Quadrat-based shoot counts were replicated 25 times at each of the five survey sites. To achieve this, pairs of random rectangular (‘x’ and ‘y’) coordinates were generated and translated into polar coordinates (‘distance’ and ‘bearing’). Any polar coordinates with distances greater than 30 m were discarded. This process continued until 25 polar coordinates within the maximum survey radius of 30 m were assigned to each survey site. The rectangular-polar conversion method ensures even sampling of a circular survey area, guarding against over sampling of the centre that would result from generating random polar coordinates.

#### 3.1.3 Shoot count

Shoot counts were made in 25 × 25 cm quadrats and shoot density was presented per quadrat. It would be possible to extrapolate to m<sup>-2</sup>, simply multiplying quadrat counts by 16, for easy comparison with other global studies presented at the metre scale. However,



this was not done here as it would imply knowledge of spatial heterogeneity at a different scale to that measured.

### **3.1.4 Shoot morphology**

In addition to shoot density, the number of leaves was recorded on every shoot. Furthermore, the length of the longest leaf on every shoot was recorded from a point at the base of the shoot, where leaves separate from the stem to the leaf tip. Canopy height per quadrat was defined as the median of the lengths of the longest leaf on each shoot in each quadrat.

### **3.1.5 Leaf area index**

Estimates of 'leaf area index' (LAI) per quadrat were calculated by multiplying the length of the longest leaf on a given shoot by the number of leaves on that shoot, summed over all shoots in a given quadrat. Since this is based on the longest leaf and, additionally, no leaf widths were measured, this metric is not traditional LAI (the area of leaf per unit area of ground) but serves as a relevant proxy for making comparisons within this dataset.

### **3.1.6 Wasting disease**

Proportions of individual leaves showing signs of wasting disease (lesions characterized by black spots and streaks, den Hartog, 1989) were scored for all leaves, based on an accepted categorisation: ['0' = 0 %], [0 % < '1' < 2 %], [2 % < '2' < 25 %], [25 % < '3' < 50 %], [50 % < '4' < 75 %] and [75 % < '5' < 100 %] (Burdick et al., 1993 – see Figure 1 therein for a diagrammatic representation of the categories).

### **3.1.7 Epiphytes**

Attempts were not made to identify specific epiphytes, but rather all visible epiphytes were treated as a functional group, likely to have a similar effect on eelgrass growth by restricting light available for photosynthesis. This is because identification of many epiphyte species, especially algae, is a highly specialized and time-consuming task, beyond the scope of this project. Here, the proportions were recorded of each eelgrass leaf covered in epiphytes of any type using the same percentage cover brackets as for recording signs of wasting disease.

## **3.2 Analytical methods**

We present analysis of spatial and temporal trends through the whole period of the Isles of Scilly eelgrass long-term monitoring (1996-present), in particular highlighting changes that have occurred during the period of the ReMEDIES project. Throughout, the Generalized Linear Model (GLM) framework is ideal. This form of analysis is sufficiently flexible to model all the different types of data recorded, rather than being limited by the assumption of Normally distributed residuals.



We used this approach to quantify trends through time at each survey site using a quadratic function of time, interacting with survey site as fixed effects. In time series data, individual census points often show correlation with previous time points (autocorrelation). This is particularly likely in the case of species where individuals persist in the same place for more than one year, as *Z. marina* does. Therefore, we also quantified and assessed autocorrelation in our GLMs. Spatial correlation between the five survey sites along with differences in the amount of within-site variation between sites (heteroscedacity) was modelled using an unstructured variance-covariance matrix, or by using a dispersal formula modelling survey site for heteroscedacity without correlation. These different variance-covariance structures were compared using AICc to quantify evidence ratios.

### 3.2.1 Shoot count

We combined information on presence or absence of eelgrass shoots within quadrats with information on shoot density within occupied quadrats. This was analyzed using a zero-inflated mixture model. This is a GLM that simultaneously quantifies the proportion of occupied quadrats assuming a binomial distribution (logit link function) of presence and absence, with quantification of non-zero shoot density assuming a zero-truncated negative binomial distribution (log link function).

### 3.2.2 Leaf count

Numbers of leaves per shoot were summarized by their median value per quadrat. Since this results in 0.5s, these were rounded using the 'round to the nearest even integer' approach (IEC Standard 60559), as this removes biases associated from the better known 'round 0.5s up' approach. The resulting non-negative integers were modelling using a zero-truncated generalized Poisson distribution GLM (log link function).

### 3.2.3 Continuous data

Maximum leaf length and leaf area index data (LAI) are continuous but with a lower boundary of zero. This results in skewed data distributions with increasing variance-mean ratios (i.e., variability in leaf lengths is greater among sets of longer leaves). We modelled this type of lower bounded data using gamma distribution GLMs (log link function).

### 3.2.4 Semi-quantitative data

Wasting disease and epiphyte cover were recorded on a 0-5 semi-quantitative scale, based on percentage brackets. Scores were back transformed to the midpoint of their percentage bracket. For example, a score of '3' equates to between 25 % and 50 % cover, so a '3' is back transformed to  $(25 + 50) / 2 = 37.5$  % cover, or 0.375 cover as a proportion. Proportion data were then analyzed using beta distribution GLMs (logit link function). Note that this is a change to equivalent analysis in previous annual reports, where 0-5 scores were simply averaged and divided by 5 to result in a score in the range 0-1, which was then treated as a proportion. The previous approach allowed for

comparisons between sites and over time, as the method was consistently applied, but over-estimated total cover.

### 3.2.5 Software

All statistical analyses were undertaken using R version 4.3.1 (R Core Team, 2023). GLMs were constructed as Generalized Linear Mixed Models using the glmmTMB package. Code is available from the authors on request.

## 3.3 Eelgrass spatial distribution and extent monitoring

This report contains a summary of work, including analysis, presented in a series of reports commissioned by Natural England in 2022. Details of survey and analysis methods can be found in those reports (Bertelli et al., in press – remotely operated vehicles, Conley et al., in press – wave modelling, Bertelli et al., in press – habitat suitability modelling).

## 4 Results

### 4.1 Long-term eelgrass monitoring

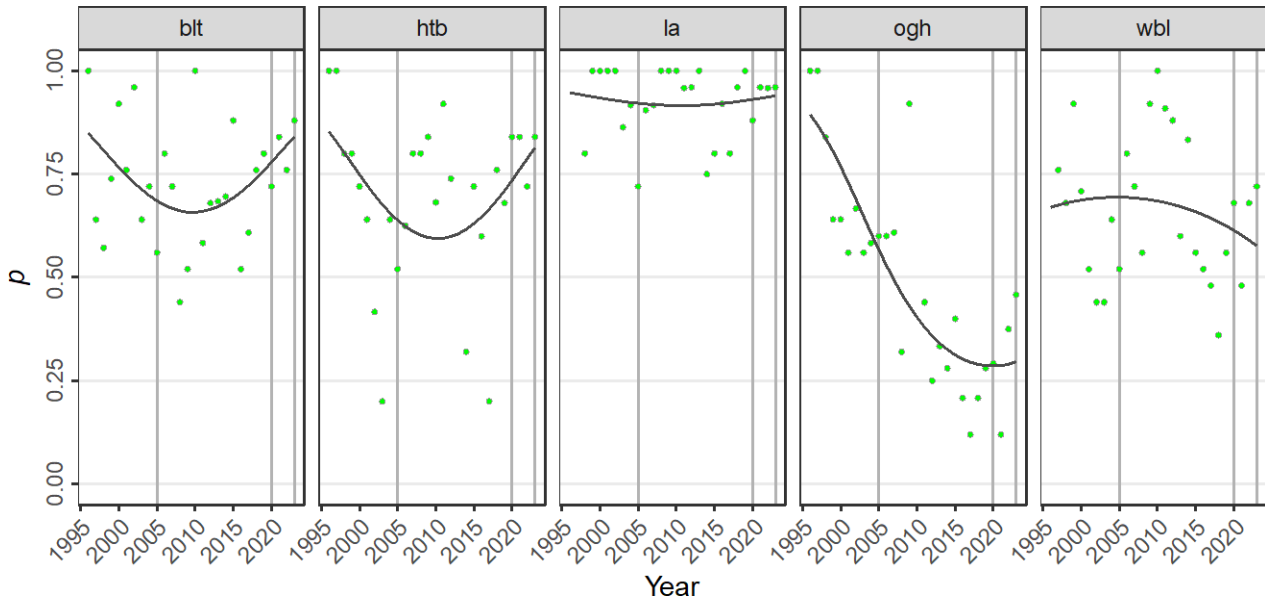
#### 4.1.1 Shoot count

Shoot count was assessed as quadrat occupancy (eelgrass present, absent), as well as counts where eelgrass shoots were present.

Before quantifying trends through time, we assessed spatial and temporal correlation, as well as heteroscedacity (differences in variation over time between sites). Quantifying spatial and temporal correlation, as well as heteroscedacity, is both informative ecologically, and an important pre-requisite for statistical analysis of trends. We report this aspect of the analysis in Appendix 1, as its relatively technical nature could distract from the focus on overall trends.

We quantified overall trends by fitting a quadratic model through time. This was separated into quadrat occupancy (present, absent), Figure 2, and non-zero shoot counts, Figure 3.

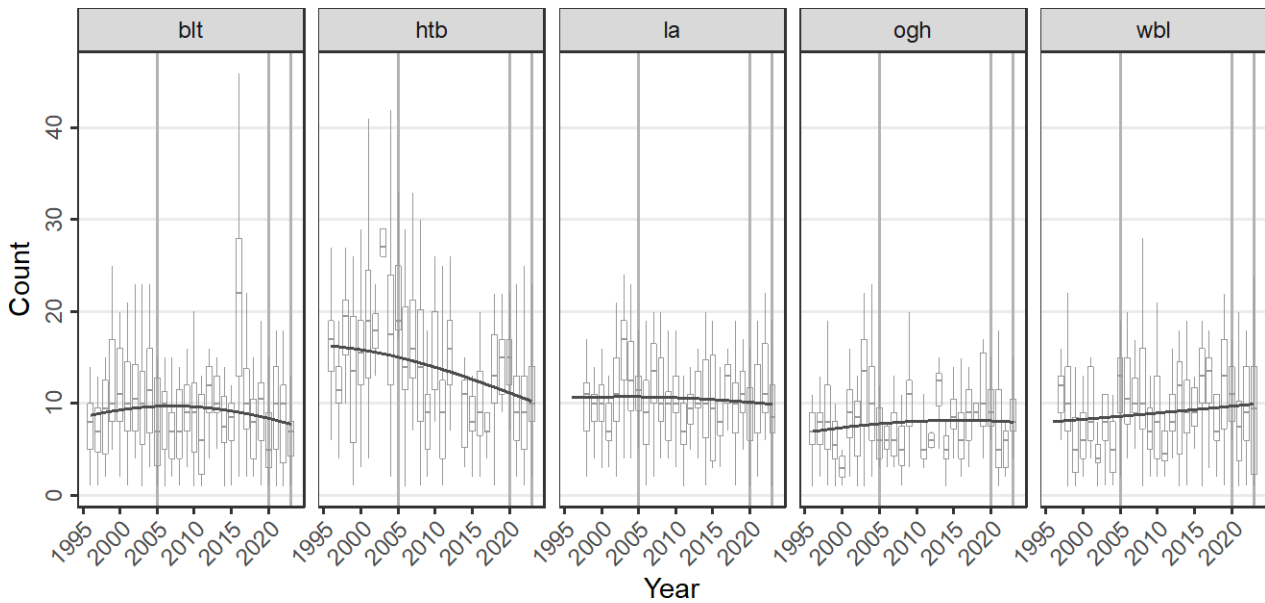
For quadrat occupancy, there was an initial decline, followed by recovery, at Broad Ledges Tresco (GLM quadratic term,  $p < 0.001$ ) and Higher Town Bay (GLM quadratic term,  $p < 0.001$ ). There was no significant trend in quadrat occupancy at Little Arthur (GLM linear term,  $p = 0.865$ ) and West Broad Ledges (GLM linear term,  $p = 0.140$ ). At Old Grimsby Harbour, a strong initial decline in quadrat occupancy slowed up to the point of some reversal towards the end of the long-term monitoring (GLM quadratic term,  $p < 0.001$ ). Old Grimsby Harbour has experienced 68 % loss in quadrat occupancy since 1996 but a 4 % increase since the initial ReMEDIES survey in 2020.



**Figure 2.** Time series plots of the proportion,  $p$ , of occupied quadrats recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys.

In quadrats where seagrass was present, shoot counts remained stable through time, with the exception of a decline at Higher Town Bay, which shows a decline of 37 % over the period of long-term monitoring (GLM linear term,  $p = 0.002$ ), or an 8 % decline since the initial ReMEDIES survey in 2020.

Time series over the period of long-term monitoring shown in Figure 3, with all pairwise site comparisons are shown in Table 2. Note that to compare levels between sites, we average over time for Higher Town Bay, so these pairwise comparisons don't take into account the decline at that site.



**Figure 3.** Time series plots of the non-zero shoot counts per 25 cm × 25 cm quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional 1.5 × IQR.

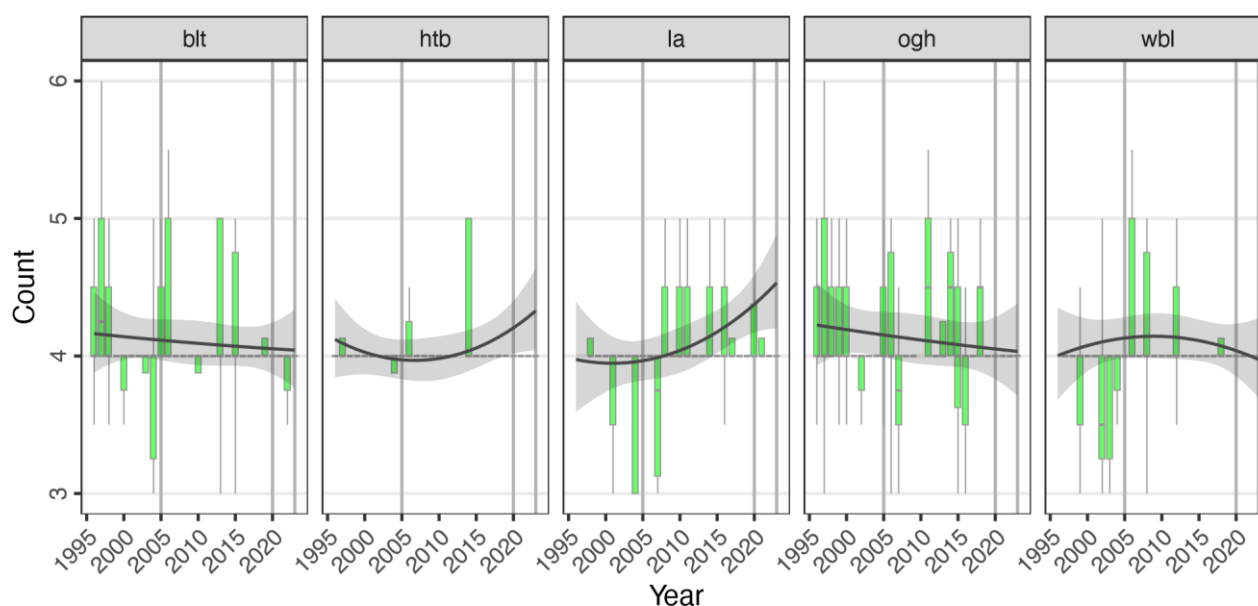
**Table 2.** Pairwise comparisons in non-zero shoot counts between survey sites. Estimates are on a natural logarithm scale. P-values are adjusted for multiple comparisons using the Tukey familywise method. Significantly different pairs of sites are highlighted in **bold**.

Contrast	Estimate	SE	z-score	p-value
<b>blt - htb</b>	<b>-0.410</b>	<b>0.077</b>	<b>-5.327</b>	<b>&lt; 0.001</b>
blt - la	-0.144	0.075	-1.918	0.307
blt - ogh	0.156	0.079	1.962	0.285
blt - wbl	0.012	0.078	0.148	1.000
<b>htb - la</b>	<b>0.265</b>	<b>0.075</b>	<b>3.543</b>	<b>0.004</b>
<b>htb - ogh</b>	<b>0.565</b>	<b>0.079</b>	<b>7.149</b>	<b>&lt; 0.001</b>
<b>htb - wbl</b>	<b>0.421</b>	<b>0.077</b>	<b>5.438</b>	<b>&lt; 0.001</b>
<b>la - ogh</b>	<b>0.300</b>	<b>0.077</b>	<b>3.876</b>	<b>0.001</b>
la - wbl	0.156	0.076	2.057	0.239
ogh - wbl	-0.144	0.080	-1.810	0.368

### 4.1.2 Shoot morphology

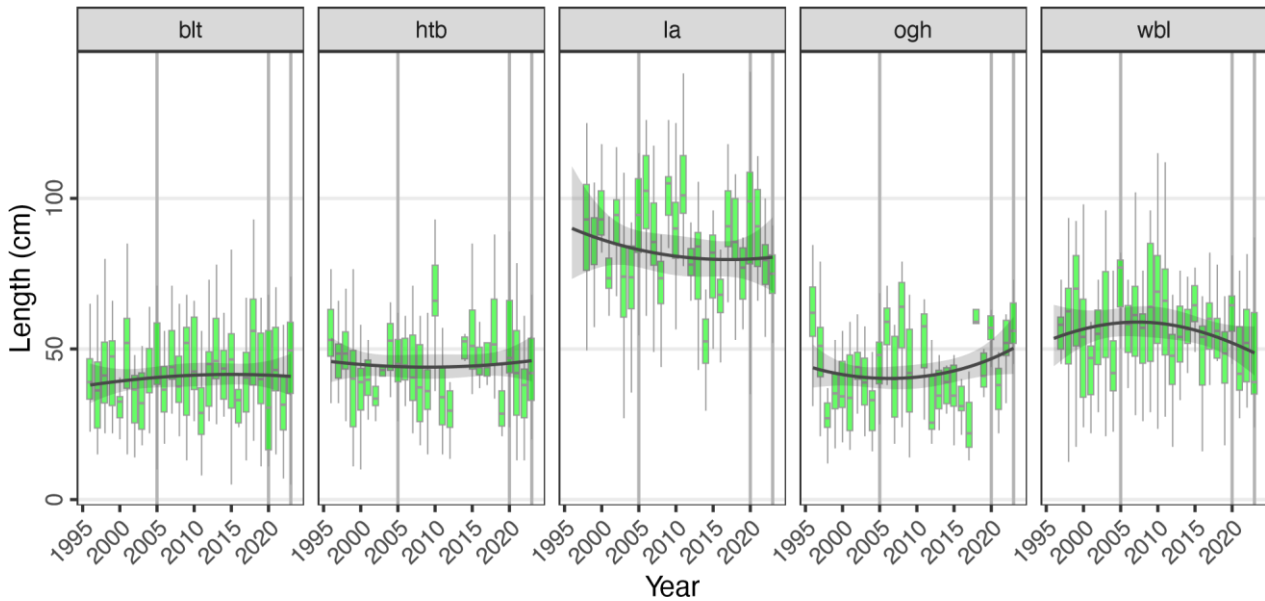
Shoot morphology was assessed through counts of the number of leaves per shoot and the length of the longest leaf per shoot (sometimes used as the basis of canopy height estimates).

The average number of leaves per shoot was very close to four (Figure 4). The only trend that was statistically supported was a small increase in the average number of leaves per shoot at Little Arthur (GLM linear term,  $p = 0.007$ ). Averaging over time for Little Arthur (so not taking into account the increase at that site), there is no statistical support for differences in the number of leaves per shoot between survey sites ( $\Delta AICc = -7.53$ ).



**Figure 4.** Time series plots of median leaf counts per 25 cm × 25 cm quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional  $1.5 \times IQR$ . Note, years that appear to show no box-whisker plot are cases where the median leaf count was consistently four across all quadrats.

Observed trends over time in the median longest leaf per shoot, per quadrat were not statistically supported ( $\Delta AICc = -12.0$ ). However, the average longest leaf values did differ between survey sites ( $\Delta AICc = 59.3$ ). Little Arthur had significantly longer leaves than any other site (Estimate = 81.9 cm, SE = 2.45 cm). Time series over the period of long-term monitoring shown in Figure 5, with all pairwise comparisons are shown in Table 3.



**Figure 5.** Time series plots of median longest leaf per shoot, per 25 cm × 25 cm quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional 1.5 × IQR.

**Table 3.** Pairwise comparisons in median longest leaf per shoot, per quadrat, between survey sites. Estimates are on a natural logarithm scale. P-values are adjusted for multiple comparisons using the Tukey familywise method. Significantly different pairs of sites are highlighted in **bold**.

Contrast	Estimate	SE	z-score	p-value
blt - htb	-0.097	0.046	-2.089	0.225
<b>blt - la</b>	<b>-0.702</b>	<b>0.045</b>	<b>-15.72</b>	<b>&lt; 0.001</b>
blt - ogh	-0.047	0.048	-0.993	0.859
<b>blt - wbl</b>	<b>-0.321</b>	<b>0.046</b>	<b>-6.956</b>	<b>&lt; 0.001</b>
<b>htb - la</b>	<b>-0.605</b>	<b>0.044</b>	<b>-13.71</b>	<b>&lt; 0.001</b>
htb - ogh	0.050	0.047	1.046	0.834
<b>htb - wbl</b>	<b>-0.224</b>	<b>0.046</b>	<b>-4.909</b>	<b>&lt; 0.001</b>
<b>la - ogh</b>	<b>0.654</b>	<b>0.046</b>	<b>14.35</b>	<b>&lt; 0.001</b>
<b>la - wbl</b>	<b>0.381</b>	<b>0.044</b>	<b>8.686</b>	<b>&lt; 0.001</b>
<b>ogh - wbl</b>	<b>-0.274</b>	<b>0.047</b>	<b>-5.805</b>	<b>&lt; 0.001</b>

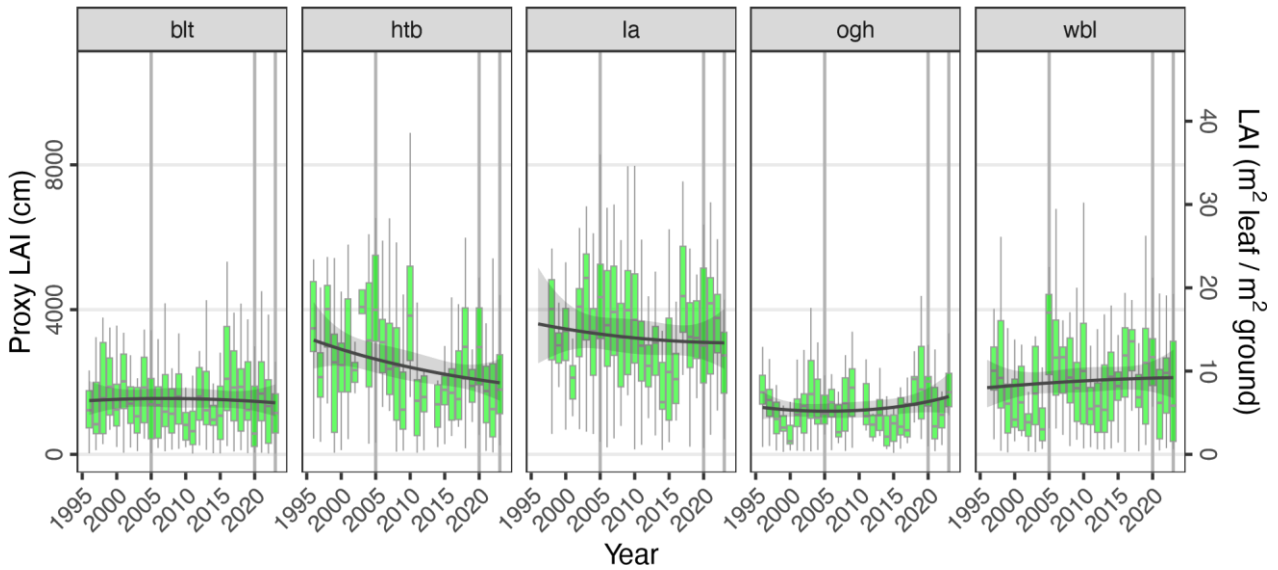
### 4.1.3 Leaf area index

We developed a proxy measure for leaf area index (LAI) based on the measurements taken during long-term monitoring. Since LAI is defined as the total leaf area (sometimes taken as one side of the leaf, and sometimes as both surfaces), it would be necessary to measure the length and width of every leaf to accurately calculate LAI. Here, we are able to multiply the length of the longest leaf on a given shoot by the number of leaves on that shoot and sum that over all shoots in a quadrat. This falls short in two respects: the longest leaf may not be representative of the total leaf lengths on a shoot, and no measures of width were taken.

In a focused study during the 2011 Isles of Scilly eelgrass survey, a subset of quadrats were exhaustively sampled by measuring the lengths and widths of every leaf (Bull et al., in prep.). This allowed us to calculate the correlation between true LAI and our proxy measure, as well as conversion factor based on type II (major axis) regression. The conversion factor (cm leaf length per  $25 \times 25$  cm quadrat  $\rightarrow$   $m^2$  two-sided leaf area per  $m^2$  ground) = 0.0044 (95 % c.i. = 0.0040, 0.0048). This was based on a high correlation value,  $r = 0.98$ , between proxy and true LAI, and strongly supported statistically (Major Axis Regression,  $p < 0.001$ ). We present LAI in both proxy and converted forms in Figure 6.

The only trend that was statistically supported was a decrease in LAI at Higher Town Bay (GLM linear term,  $p = 0.010$ ). Consistent with the finding for non-zero shoot density, there was a 37 % drop in LAI over the long-term monitoring period (1996-2023). Time series over the period of long-term monitoring shown in Figure 6, with all pairwise comparisons are shown in Table 4. Note that to compare levels between sites, we average over time for Higher Town Bay, so these pairwise comparisons don't take into account the decline at that site.





**Figure 6.** Time series plots of LAI recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional  $1.5 \times$  IQR. The lefthand y-axis shows our observed proxy for LAI (total cm of leaf per  $25 \times 25$  cm quadrat, based on multiplying the longest leaf per shoot by the number of leaves per shoot). The righthand y-axis shows a conversion to traditional LAI (total, two-sided, leaf area per  $m^2$  of ground).

**Table 4.** Pairwise comparisons in LAI between survey sites. Estimates are on a natural logarithm scale. P-values are adjusted for multiple comparisons using the Tukey familywise method. Significantly different pairs of sites are highlighted in **bold**.

Contrast	Estimate	SE	z-score	p-value
<b>blt - htb</b>	<b>-0.955</b>	<b>0.091</b>	<b>-10.47</b>	<b>&lt; 0.001</b>
<b>blt - la</b>	<b>-1.101</b>	<b>0.088</b>	<b>-12.53</b>	<b>&lt; 0.001</b>
blt - ogh	-0.236	0.094	-2.511	0.088
<b>blt - wbl</b>	<b>-0.553</b>	<b>0.092</b>	<b>-5.983</b>	<b>&lt; 0.001</b>
htb - la	-0.146	0.087	-1.688	0.441
<b>htb - ogh</b>	<b>0.719</b>	<b>0.093</b>	<b>7.773</b>	<b>&lt; 0.001</b>
<b>htb - wbl</b>	<b>0.402</b>	<b>0.091</b>	<b>4.412</b>	<b>&lt; 0.001</b>
<b>la - ogh</b>	<b>0.866</b>	<b>0.089</b>	<b>9.696</b>	<b>&lt; 0.001</b>

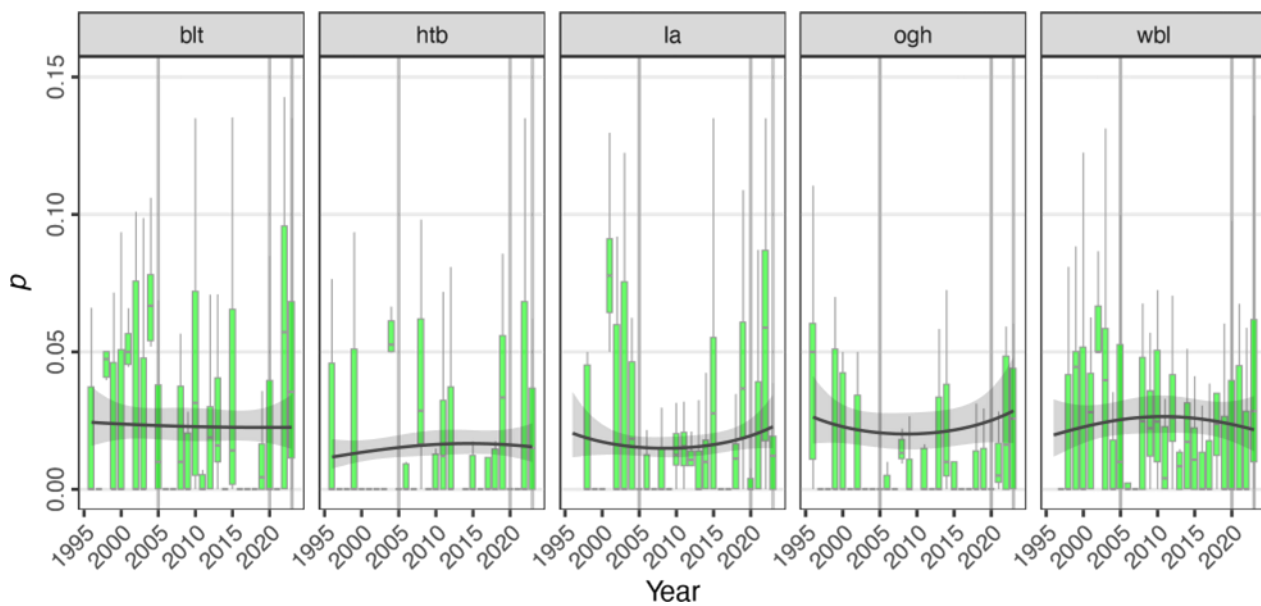
Contrast	Estimate	SE	z-score	p-value
----------	----------	----	---------	---------



la - wbl	0.548	0.088	6.244	< 0.001
ogh - wbl	-0.317	0.093	-3.400	< 0.001

#### 4.1.4 Wasting disease

Observed trends over time in wasting disease were not statistically supported ( $\Delta AICc = -14.0$ ). However, the average wasting disease values did differ between survey sites ( $\Delta AICc = 6.85$ ). Time series over the period of long-term monitoring shown in Figure 7, with all pairwise comparisons are shown in Table 5.



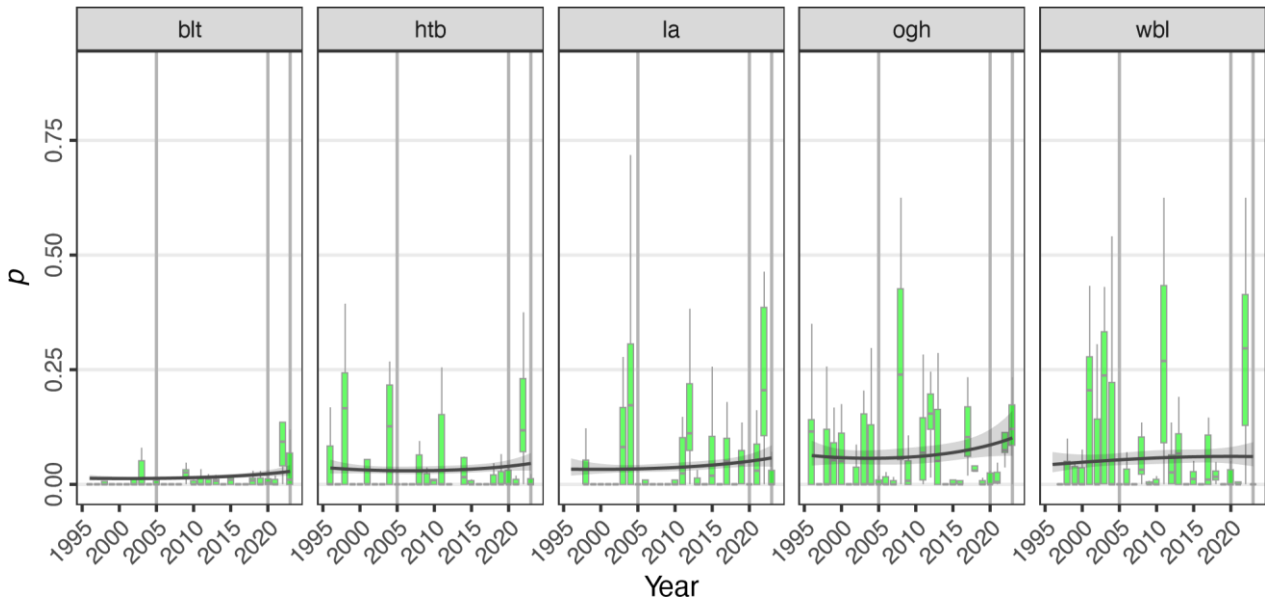
**Figure 7.** Time series plots of the proportion,  $p$ , wasting disease recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional  $1.5 \times IQR$ . Note, years that appear to show no box-whisker plot are cases where the median wasting disease was consistently zero across all quadrats; however, this does not mean no wasting disease was observed.

**Table 5.** Pairwise comparisons in wasting disease between survey sites. Estimates are on a natural logarithm scale. P-values are adjusted for multiple comparisons using the Tukey familywise method. Significantly different pairs of sites are highlighted in **bold**.

<b>Contrast</b>	<b>Estimate</b>	<b>SE</b>	<b>z-score</b>	<b>p-value</b>
<b>blt - htb</b>	<b>0.428</b>	<b>0.156</b>	<b>2.743</b>	<b>0.048</b>
blt - la	0.320	0.145	2.206	0.177
blt - ogh	0.019	0.172	0.110	1.000
blt - wbl	-0.060	0.151	-0.396	0.995
htb - la	-0.107	0.151	-0.711	0.954
htb - ogh	-0.409	0.177	-2.307	0.143
<b>htb - wbl</b>	<b>-0.488</b>	<b>0.157</b>	<b>-3.107</b>	<b>0.016</b>
la - ogh	-0.301	0.168	-1.795	0.376
la - wbl	-0.380	0.146	-2.600	0.070
ogh - wbl	-0.079	0.173	-0.456	0.991

#### 4.1.5 Epiphytes

The only trend that was statistically supported was a 75 % increase in epiphyte cover at Little Arthur over the period of long-term monitoring (GLM linear term,  $p = 0.027$ ). Time series over the period of long-term monitoring shown in Figure 8, with all pairwise sites comparisons are shown in Table 6. Note that to compare levels between sites, we average over time for Little Arthur, so these pairwise comparisons don't take into account the increase at that site.



**Figure 8.** Time series plots of the proportion,  $p$ , epiphyte cover recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Solid trend lines were fitted as quadratic functions of time. Grey confidence ribbons show 95 % confidence intervals. Vertical lines on each panel show the date of SAC designation (2005), as well as the initial (2020) and final (2023) ReMEDIES surveys. Annual box-whisker plots show distributions across quadrats, with the central line indicating the median, boxes spanning the interquartile range (IQR), and Tukey whiskers extending an additional  $1.5 \times$  IQR. Note, years that appear to show no box-whisker plot are cases where the median epiphyte cover was consistently zero across all quadrats; however, this does not mean no epiphytes were observed.

**Table 6.** Pairwise comparisons in epiphyte cover between survey sites. Estimates are on a natural logarithm scale. P-values are adjusted for multiple comparisons using the Tukey familywise method. Significantly different pairs of sites are highlighted in **bold**.

Contrast	Estimate	SE	z-score	p-value
<b>blt - htb</b>	<b>-0.744</b>	<b>0.174</b>	<b>-4.286</b>	<b>&lt; 0.001</b>
<b>blt - la</b>	<b>-0.906</b>	<b>0.166</b>	<b>-5.444</b>	<b>&lt; 0.001</b>
<b>blt - ogh</b>	<b>-1.451</b>	<b>0.180</b>	<b>-8.064</b>	<b>&lt; 0.001</b>
<b>blt - wbl</b>	<b>-1.263</b>	<b>0.172</b>	<b>-7.346</b>	<b>&lt; 0.001</b>
htb - la	-0.162	0.170	-0.955	0.875
<b>htb - ogh</b>	<b>-0.707</b>	<b>0.183</b>	<b>-3.870</b>	<b>0.001</b>
<b>htb - wbl</b>	<b>-0.519</b>	<b>0.175</b>	<b>-2.966</b>	<b>0.025</b>
<b>la - ogh</b>	<b>-0.546</b>	<b>0.176</b>	<b>-3.099</b>	<b>0.017</b>

Contrast	Estimate	SE	z-score	p-value
la - wbl	-0.357	0.168	-2.128	0.208
ogh - wbl	0.188	0.181	1.040	0.837

#### 4.1.6 Synthesis

- Broad scale coverage, as quantified through the proportion of quadrats with seagrass present, is generally stable at four out of five long-term monitoring sites. The substantial decline at Old Grimsby Harbour appears to have also stabilized, albeit currently at a much-reduced state compared to the start of the long-term monitoring period. Old Grimsby Harbour has experienced 68 % loss in quadrat occupancy since 1996 but a 4 % increase since the initial ReMEDIES survey in 2020.
- Where seagrass is present (occupied quadrats), shoot density is stable in the long term, with the exception of a decline at Higher Town Bay of 37 % since long-term monitoring began in 1996. This currently shows no sign of abating and has declined by 8 % during the life of the ReMEDIES project. Our analysis does not point to causes, and it could be that this change is entirely natural but is certainly a reason for concern and continued, regular monitoring. It should be noted that monitoring is located at the far end of the bay to where the majority of boats moor. Our findings do not suggest that boat activity is linked to observed eelgrass declines.
- Shoot morphology, quantified through maximum leaf lengths and number of leaves per shoot, are relatively stable over time. The median number of leaves per shoot is close to four in all years and across all survey sites. The median longest leaf length per shoot is c. 40-60 cm at all sites except Little Arthur, where this is > 80 cm.
- Leaf Area Index (LAI) follows the same trend as shoot density, remaining stable at four sites: Broad Ledges Tresco, Old Grimsby Harbour, and West Broad Ledges generate 5-9 m<sup>2</sup> photosynthetic leaf surface per m<sup>2</sup> ground, while Little Arthur produces 14 m<sup>2</sup> m<sup>-2</sup>. This higher level of productivity is underpinned by longer leaves without any reduction in shoot or leaf density, compared to other sites. Higher Town Bay began the long-term monitoring period with LAI values very similar to Little Arthur (LAI = 13.7 m<sup>2</sup> m<sup>-2</sup> at htb in 1996), as shorter leaves were offset by higher shoot density. However, the reduction in shoot density over the long-term monitoring period has not been compensated by an increase in leaf length, resulting in LAI values at Higher Town Bay now resembling those at the other three sites (LAI = 8.6 m<sup>2</sup> m<sup>-2</sup> at htb in 2023).
- Leaf lesions assumed to be caused by wasting disease remain clearly evident but at consistently low levels and with little variation between survey sites. It was these lesions that first appeared in the early 1990s and, in part, motivated the long-term monitoring that continues today. However, wasting disease now seems to be in an endemic state with little evidence of negative impacts on the eelgrass.

- Epiphyte cover can lead to serious impacts on eelgrass through shading but, as with wasting disease, seems consistent through time and across space on the eelgrass in the Isles of Scilly. While the percentage increase at Little Arthur seems high (75 % since 1996), this only represents a change from 3.3 % cover to 5.8 % cover in 28 years.
- Overall, the evidence from long-term monitoring through in-water sampling at five, localised survey sites, shows a relatively stable situation of high productivity and low disease and epiphyte cover.

## 4.2 Eelgrass spatial distribution and extent monitoring

In 2022, Natural England commissioned three projects aimed at developing capacity and capability in the areas of advance wave modelling, data acquisition using remotely operated vehicles (ROVs), and habitat suitability modelling (HSM). These were considered priorities for increasing understanding of seagrass extent and dynamics, as well as providing a robust evidence base for management and conservation. Each of these projects was delivered and reported to Natural England through a separate report. Here, we provide brief summaries of each, as well as integrating these with findings from the long-term annual monitoring.

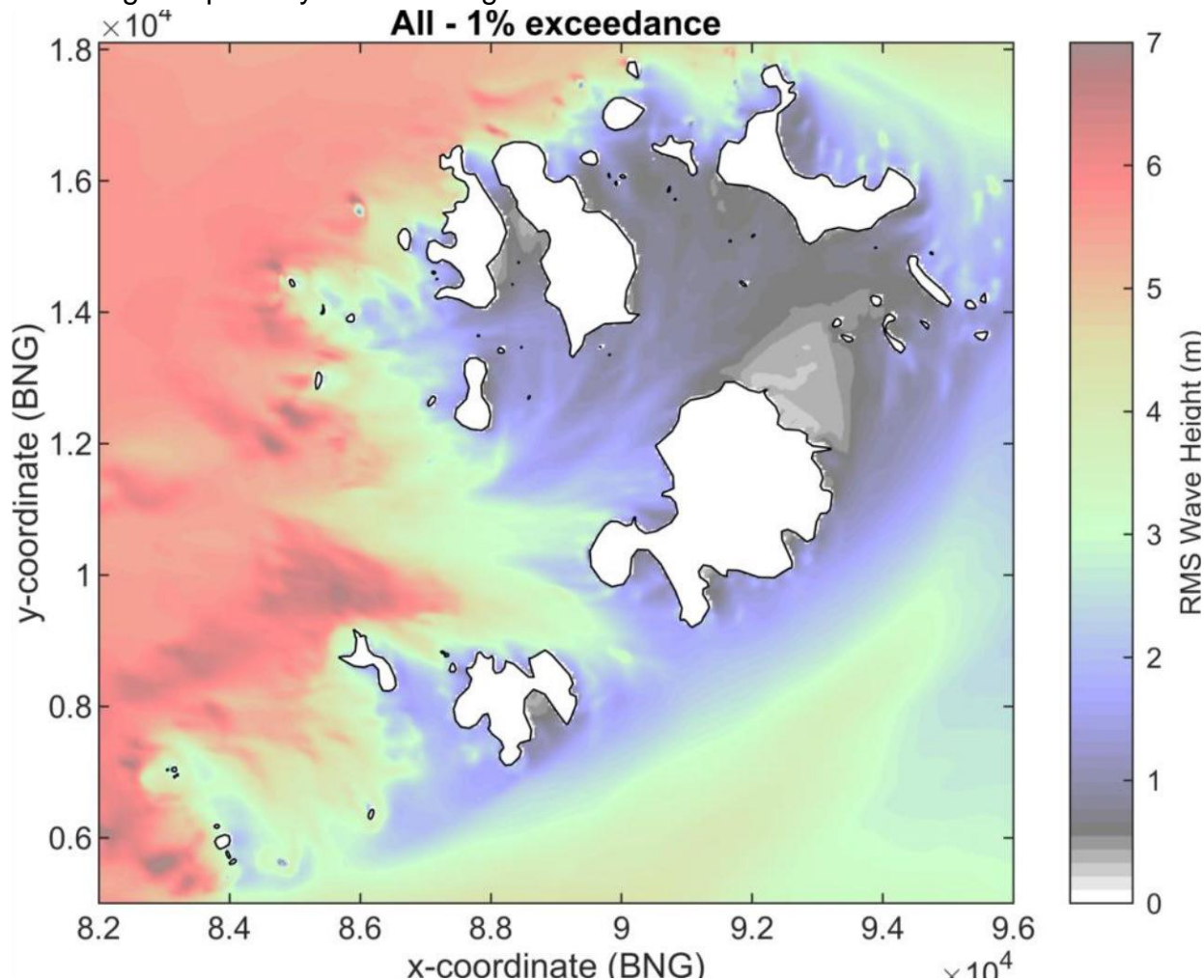
### 4.2.1 Wave and hydrodynamic modelling report

Coastal Marine Applied Research (CMAR) were contracted by Natural England to undertake hydrodynamic modelling of the Isles of Scilly archipelago (Conley et al., in press). The modelling exercise provided insights into the wave climate outside and within the interior of the archipelago, as well as a characterisation of hydrodynamics and bed shear stresses. We present a brief overview, closely based on that report.

Highly energetic waves occur off the coast off the Isles of Scilly. The predominant wave approach is from the west, with swell waves arriving from the Atlantic Ocean. On the eastern side of the islands, there is a degree of wave sheltering from the dominant westerly waves, provided by the islands themselves. A coupled wave-current hydrodynamic model was developed in Delft3D with the aim of reproducing wave and tidal conditions within the interior of the Isles of Scilly at a relatively high spatial resolution (40 m × 40 m). Validation against field measurements shows the model can reproduce wave heights within the interior of the islands with average Root Mean Square Error (RMSE) of +/- 0.16 m ( $R^2 = 0.81$ ) and flow velocity with RMSE +/- 0.07 m s<sup>-1</sup> ( $R^2 = 0.49$ ), representing close agreement with measured values for both waves and currents.

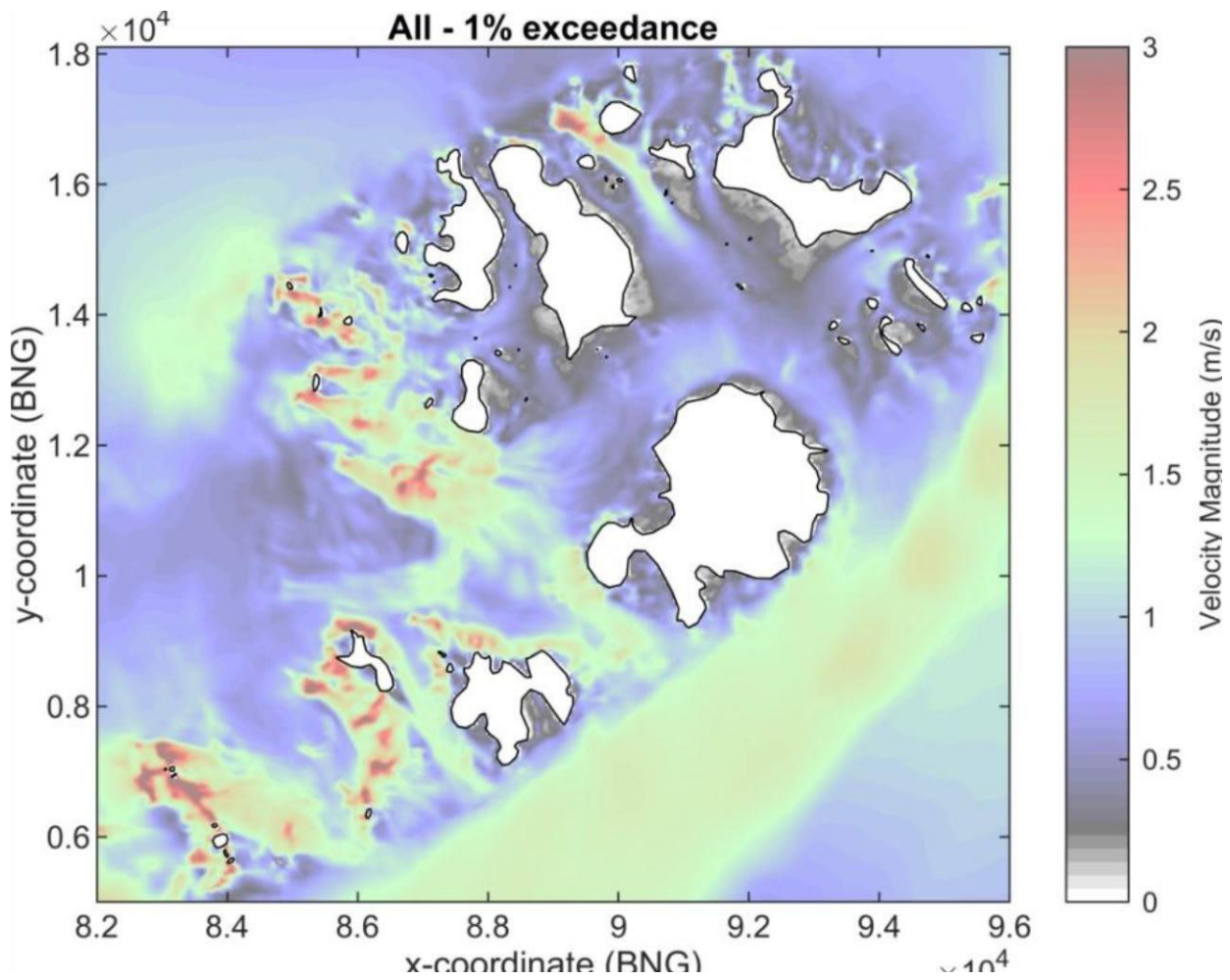
Wave and hydrodynamic conditions simulated by the Delft3D model reveal the spatial variation in hydrodynamics within the interior of the islands. Simulated wave heights are largest off the western side of the islands, with the western islands providing shelter to the interior areas (Figure 9). Peak current velocities are predicted to occur in the channels between the western islands, with much lower velocities across most of the interior of the

archipelago, typically ranging from 0.5-1 m s<sup>-1</sup> (Figure 10). Peak bed shear stresses are predicted to occur in the most exposed locations on the western flank of the islands, where the highest wave heights occur (Figure 11). Shear stress is associated with the point where sediment is lifted off the seabed, due to lateral water movement, and suspended in the water column. Resulting reductions in water quality then have negative consequences on eelgrass photosynthesis and growth.

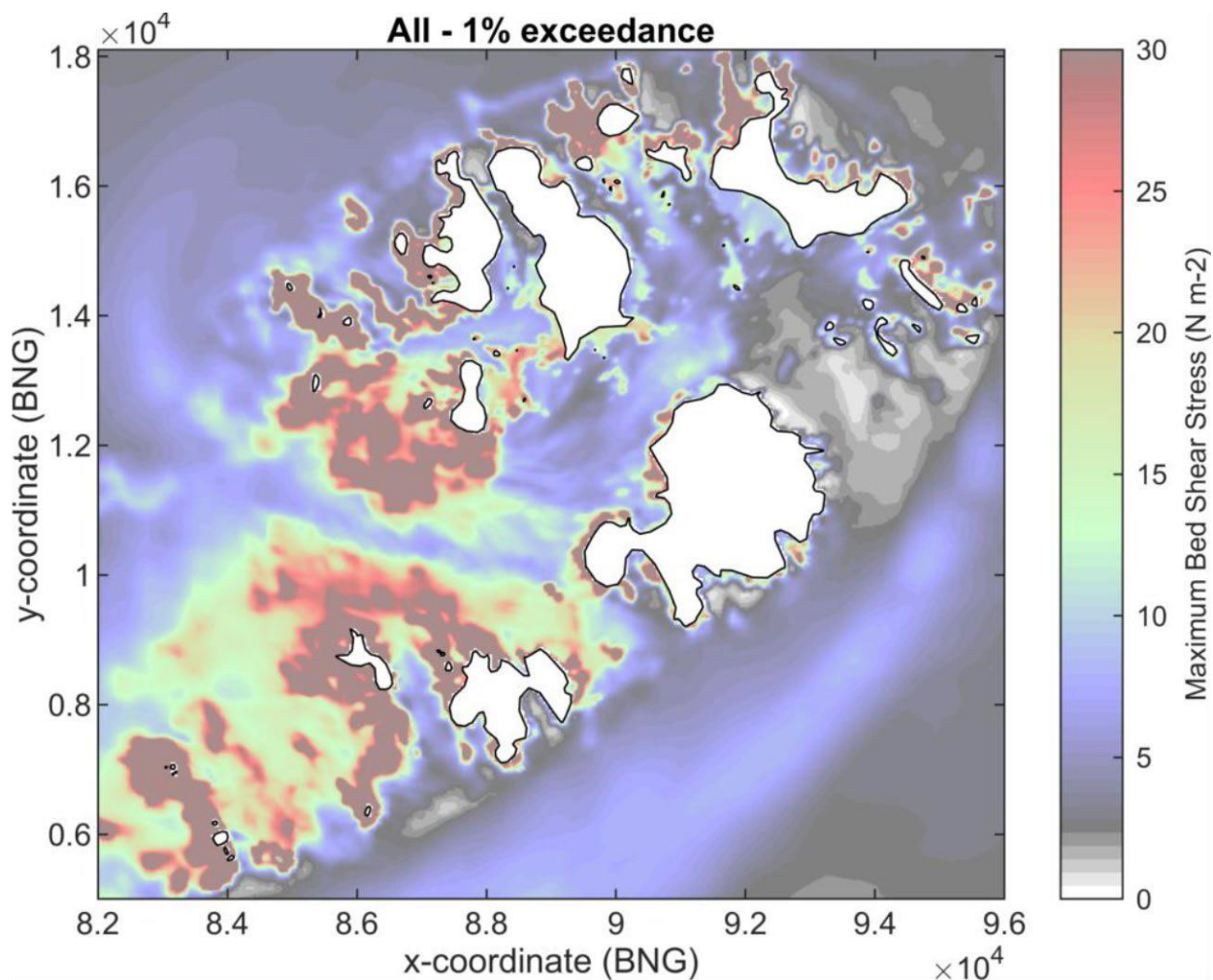


**Figure 9.** Peak Root Mean Square (RMS) wave height around the Isles of Scilly under 1 % exceedance wave conditions and a mean spring tide range (Figure 3-6 reproduced from Conley et al., in press).





**Figure 10.** Peak flow velocity magnitude around the Isles of Scilly under 1 % exceedance wave conditions and a mean spring tide range (Figure 3-5 reproduced from Conley et al., in press).



**Figure 11.** Peak bed shear stress around the Isles of Scilly under 1 % exceedance wave conditions and a mean spring tide range (Figure 3-7 reproduced from Conley et al., in press).

#### 4.2.2 Remotely operated vehicles for seagrass habitat monitoring

Data quality, in terms of resolution and accuracy, is identified as a key limiting factor to development of Habitat Suitability Models (HSMs) for many marine species, including eelgrass. Particularly in the case of sub-tidal marine species like *Z. marina*, obtaining data from the field to ground truth HSMs is particularly challenging, requiring time-consuming and costly in-water fieldwork involving often substantial teams. Remotely Operated Vehicles (ROVs) can potentially provide a much more cost-effective approach, with the added advantage of being able to collect accurately positioned and repeatable multivariate data in larger temporal and spatial quantities than in-water teams.

ROVs that are appropriate for ground truthing of *Z. marina* extent and condition include 1) Unmanned Aerial Vehicles (UAVs) and 2) Unmanned Surface Vehicles (USVs).

- 1) UAVs have proved successful in obtaining appropriate data, for example using multispectral cameras, for inter-tidal seagrass but there is a need to build capacity by extending this to sub-tidal seagrass.

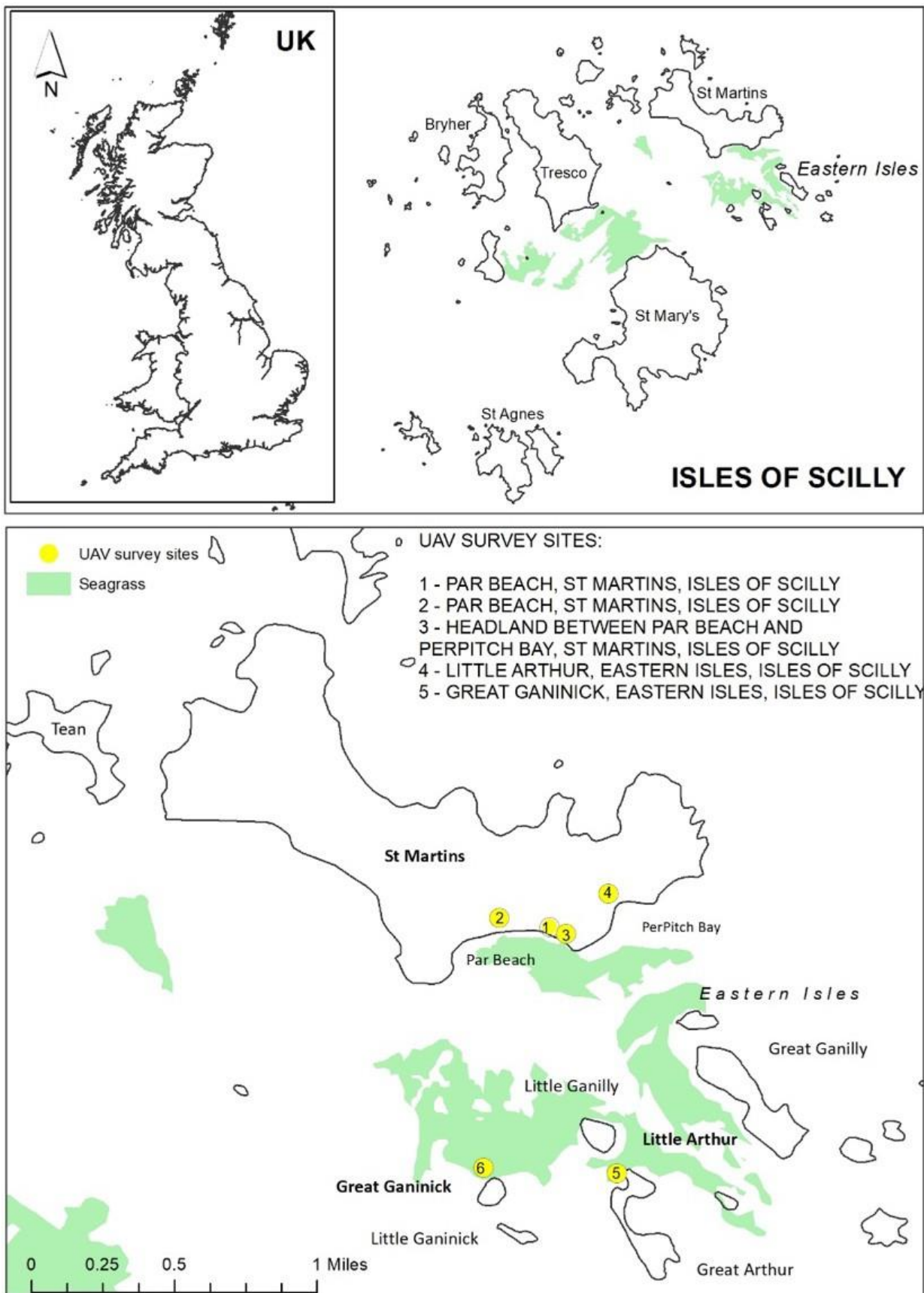


- 2) USVs in combination with active acoustic sensors (echosounders) have been trialed to a limited extent for sub-tidal vegetation but considerable capacity building is still needed to be able to reliably use this approach for *Z. marina* extent and condition monitoring.

Bertelli et al. (in press) reported a field campaign conducted by researchers from the Universities of Plymouth and Swansea during April 2022 that compared and contrasted extent and condition of sub-tidal *Z. marina* around the Isles of Scilly. The collected data:

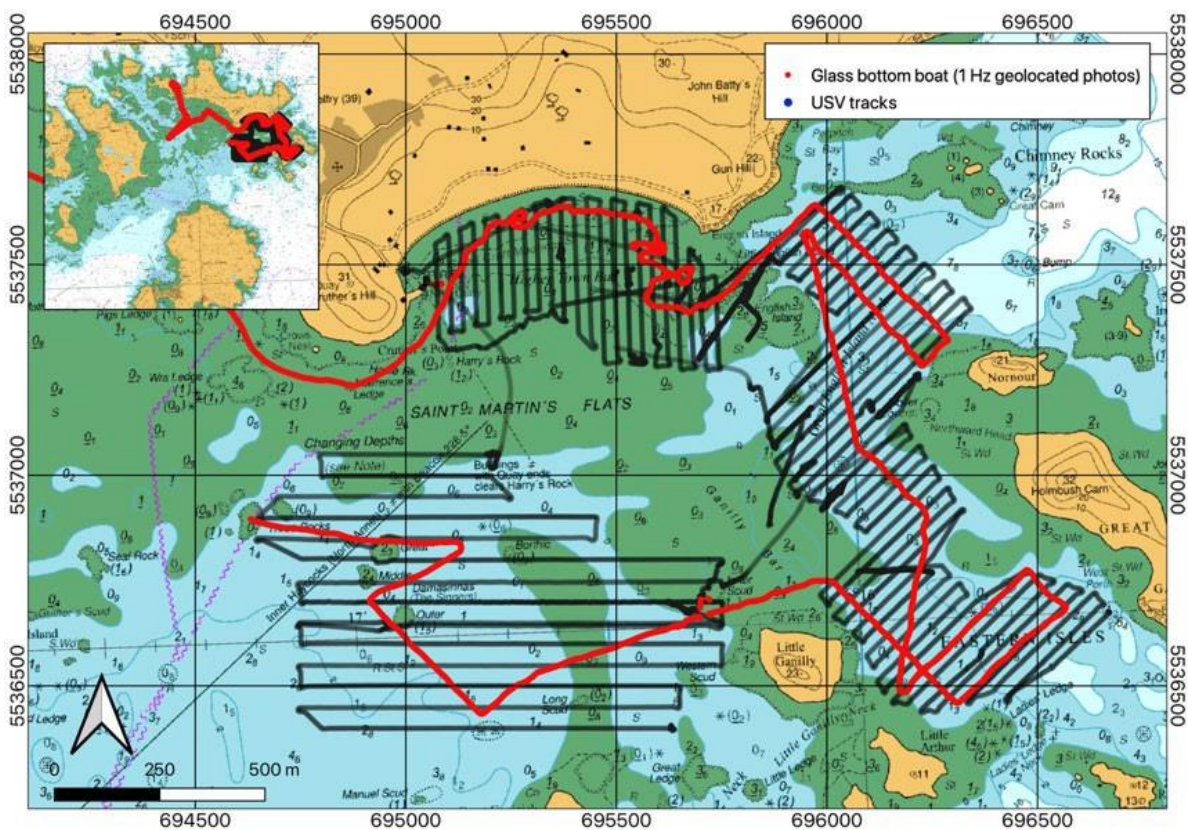
- 1) support validation of HSMs through assessment of sensitivity and specificity;
- 2) support the identification of optimal threshold probability levels that will be critical in the development of binary decision-support tools for *Z. marina* in the Isles of Scilly SAC; and
- 3) establish the quality and value of the ROV collected datasets.

In addition, to assess the efficacy of the ROV-based datasets, more traditional boat-based observations were made, validating the collected ROV-based data. Approximately 10,000 geo-located images were acquired.



**Figure 12.** Location map of UAV flight take-off and landing sites on St Martin's and Eastern Isles, in context of UK and Isles of Scillies. Seagrass presence layer (green) taken from EMODNet – EOV\_seagrass cover (Figure 5 reproduced from Bertelli et al., in press).

The UAV flights conducted on the Isles of Scilly show that small fixed-wing UAVs can successfully capture high-resolution aerial imagery of seagrass meadow extent (Figure 12). This alternative monitoring method demonstrates how seagrass meadow extent and presence can be simply mapped to assess overall seagrass health.



**Figure 13.** Map of USV coverage (black lines). Boat-based seabed validation coverage shown in red (Figure 19 reproduced from Bertelli et al., in press).

The USV platform demonstrated a lower resource footprint than traditional crewed vessels both in terms of personnel and vessel/fuel costs (Figure 13). It was also able to operate in restricted environments due to the shallow draft (< 0.4 m) and increased manoeuvrability of the USV. In addition, repeatable surveys are made possible through precise auto pilot, able to run pre-planned lines (< 1 m accuracy) allowing the same seabed to be resurveyed repeatedly.

#### 4.2.3 Use of fine scale modelled hydrodynamic data for habitat suitability modelling of *Zostera marina* around the Isles of Scilly

Habitat suitability modelling (HSM), sometimes used interchangeably with Species Distribution Modelling (SDM), has become a popular tool for determining and predicting species distributions within spatial and temporal timeframes. This tool can be used for a number of ecological objectives, for example, predicting the extent of vulnerable species in relation to changing environmental conditions such as climate change, the distribution and potential spread of invasive species, and for informing suitable locations for restoration.

These models predict species distribution by identifying areas where environmental conditions are conducive to the species in question. To carry out HSM, good quality species presence data is needed as well as the predictor variables (environmental variables) that have been identified as important in determining or affecting the distribution of the species.

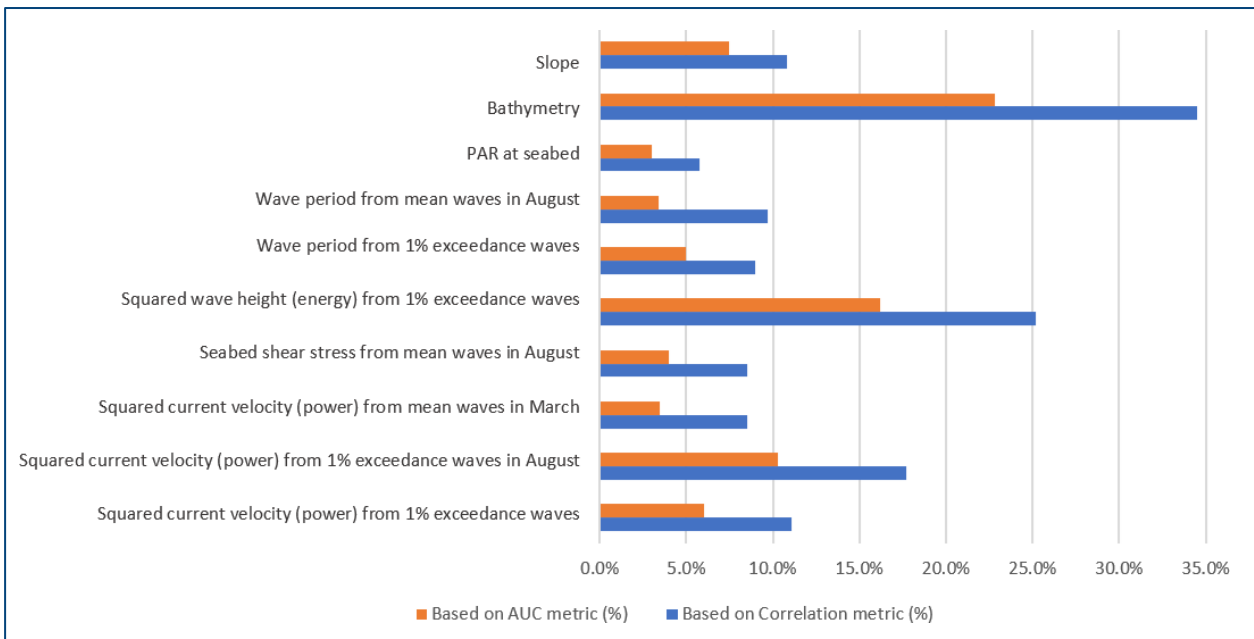
Both accurate species occurrence data and environmental data are severely limited for eelgrass; principally in terms of the spatial resolution needed for effective modelling. In particular, Bertelli et al. (2023) demonstrated that high resolution wave modelling could substantially improve our ability to model habitat suitability for eelgrass. In the last of three reports to Natural England, Bertelli et al. (in press) develop an eelgrass HSM for the Isles of Scilly that incorporates advanced wave and current modelling (the wave modelling study reported above) and vastly improved mapping of eelgrass at sub-metre scale (the ROV study reported above).

A hierarchical series of similar HSMs were run to assess the contributions of advanced wave modelling algorithms (3<sup>rd</sup> gen. vs. 1<sup>st</sup> gen.), tidal flow (currents), and offshore waves (swell) on predictions.

To summarise the wave data assessed, improved representation of underlying physics in 3<sup>rd</sup> generation models led to an increase of 29 % predicted wave heights over 1<sup>st</sup> generation wave model predictions, inclusion of currents actually reduced this disparity to 23 % but demonstrates that there is an important interaction (in this case antagonistic, on average) between wave and current processes, and inclusion of swell (even taking into account the shelter provided by the islands) increased predicted wave height by an average of 391 % compared to 1<sup>st</sup> generation wave models.

The eelgrass presence data came from a novel synthesis of point data from EMODNet, NBN, and Seagrass Spotter (<https://seagrassspotter.org>). The HSM including 3<sup>rd</sup> generation + current + swell predictions generated an AUC score of 0.86, representing a very good overall level of sensitivity and specificity against the data.

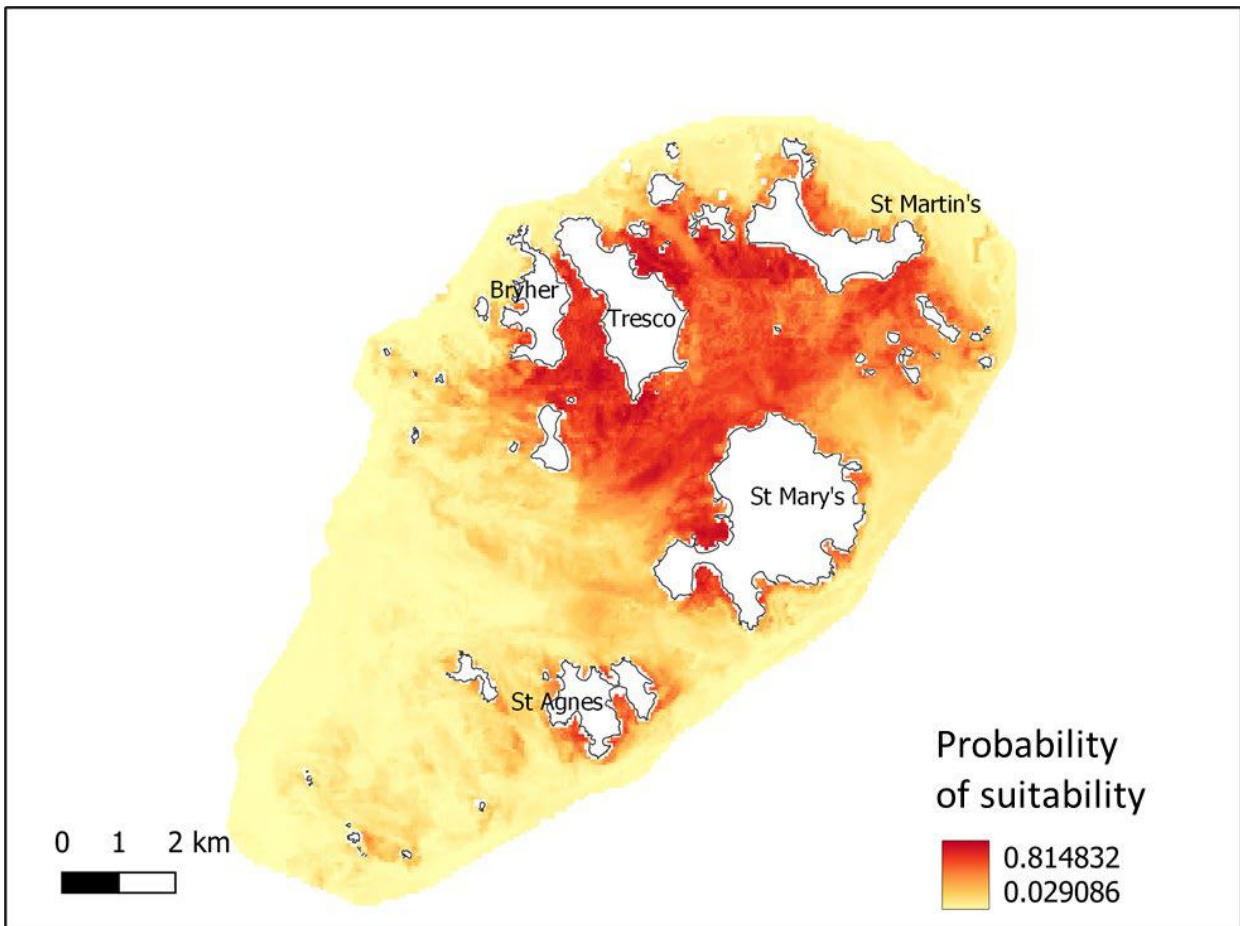
When 3<sup>rd</sup> generation + current + swell predictions were included in the final HSM, wave height and current velocity were found to be the second and third most influential factors, after bathymetry, in predicting eelgrass distribution (Figure 14). Light levels (photosynthetically active radiation, PAR) at the seabed were found to be the least influential, but this may, in part, be down to a relative high level of correlation between bathymetry and light. This raises an important caveat when interpreting HSM predictions – since these are pattern- rather than process-based models, it may be that while depth was found to be the most influential factor, that's not to say it wasn't actually caused by light levels (the effects of which are masked by correlation with depth).



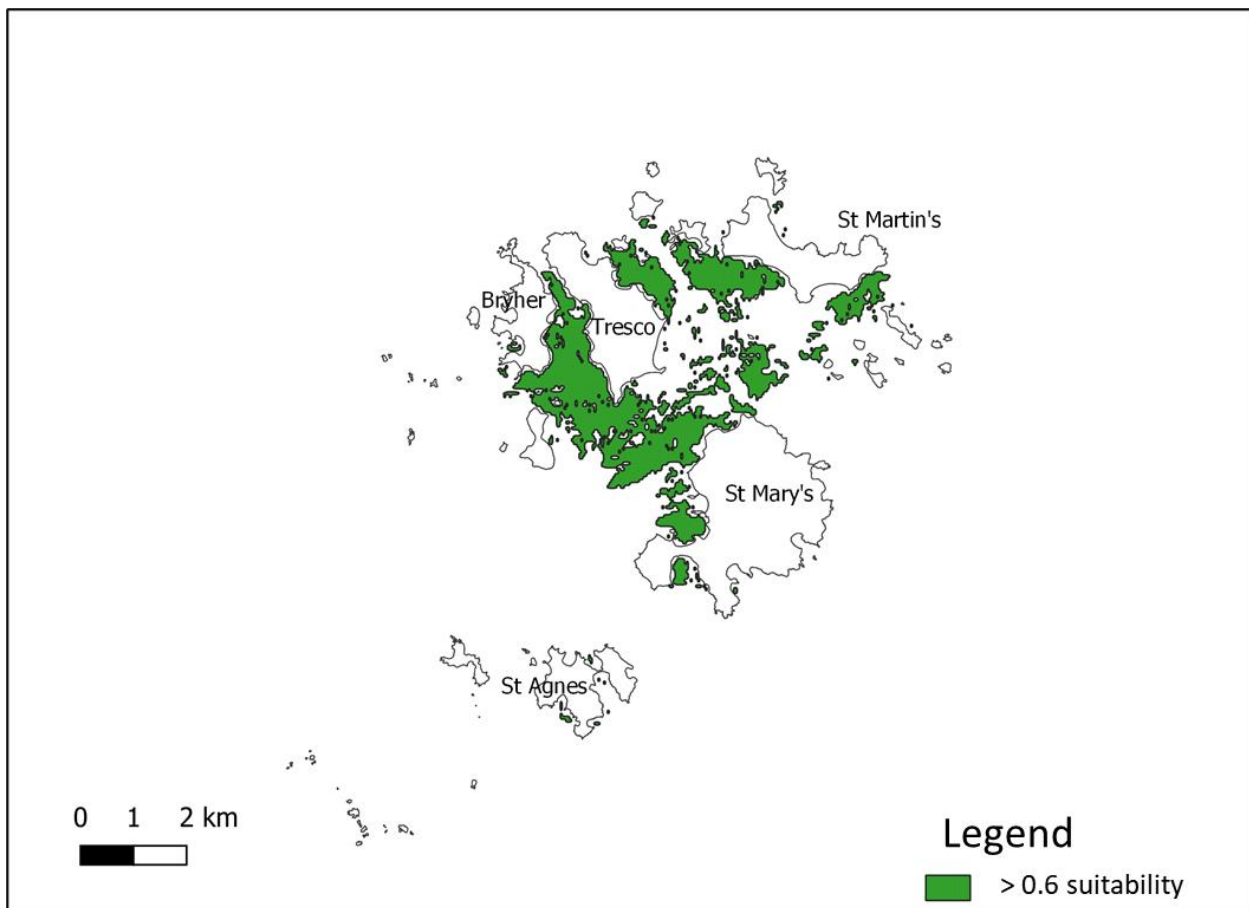
**Figure 14.** Summary of relative variable importance for predicting seagrass presence around the Isles of Scilly (Figure 3 reproduced from Bertelli et al., in press).

Finally, a heatmap of eelgrass habitat suitability was generated (Figure 15) and converted to a binary output for decision making (Figure 16). This was based on a suitability threshold of 0.6 but was relatively insensitive to actual level. Thresholds balance between over- and under-predicting and should be established according to the aims of the study.





**Figure 15.** Predicted habitat suitability for *Zostera marina*, based on ensemble model results for Isles of Scilly. The legend shows the colour scale for the probability of habitat suitability (Figure 4 reproduced from Bertelli et al., in press).



**Figure 16.** Predicted habitat suitability for *Zostera marina*, based on ensemble model results for Isles of Scilly clipped to a 0.6 threshold of probable suitability. (Figure 5 reproduced from Bertelli et al., in press).

Overall, predictions are considered to be good in the eastern areas of water between the Isles of Scilly, when compared to ground truthing data acquired in the ROV exercise reported above. However, the HSM is substantially over-predicting in waters around Bryher and Treasco in the west, when compared to ground-truthing. It is unknown to what extent this is inaccuracy in model predictions vs. eelgrass not fully realizing suitable habitat towards the western half of the archipelago. This disparity, and the potential for directing management efforts if the predictions are validated through further mapping and analysis, should be seen as a priority for focusing future efforts.

Since the reports summarized here were produced, Castle et al. (2022) have presented a UK-wide HSM exercise for *Z. marina*. Direct comparisons between their predictions and those summarized here are virtually impossible, as Castle et al. (2022) worked at 300 m resolution – far too coarse to be of use over a restricted area such as the Isles of Scilly but useful and necessary to cover the whole UK. However, a key recommendation from Castle et al. (2022) was to develop HSM modelling at higher resolution at a case study site. The Isles of Scilly HSM work reported here provides an excellent candidate for that, and work is ongoing at Swansea University to make detailed comparisons addressing the critical issues of transferability across scales and locations (Bertelli et al., in prep.).

## 4.2.4 Synthesis

- Advanced, 3<sup>rd</sup> generation, wave modelling provides a substantial improvement over earlier approaches. This comes about primarily through more sophisticated physics in the algorithm (for example, inclusion of wave-wave interactions) but also through incorporation of currents and long-range swell. The work undertaken in Scilly provides a cutting-edge resource for all benthic applications within the Isles of Scilly SAC. Additionally, the work undertaken provides a template and justification for the adoption of advanced wave modelling elsewhere.
- The use of unmanned aerial and surface vehicles has been developed during a process of capacity building for mapping and ground-truthing in the Isles of Scilly. Knowledge and expertise gained through that exercise will be transferable to other locations. Additionally, acquisition of c. 10,000 geo-located images across the SAC provides a lasting resource for benthic studies in the Isles of Scilly.
- Improved wave modelling and eelgrass extent mapping through the above two exercises has been incorporated into habitat suitability modelling. By comparing HSM performance and predictions across the Isles of Scilly, the inclusion of targeted, local data acquisition, over low-resolution national database sources, has been demonstrated.

# 5 Conclusions and recommendations

## 5.1 Conclusions

While most metrics at most sites show very little change over the course of long-term monitoring, the 37 % reduction in shoot density at Higher Town Bay and 68 % reduction in extent at the study location towards the centre of Old Grimsby Harbour exceed the 30 % threshold suggested as appropriate to initiate investigative monitoring (Foden et al., 2010). This is all the more so since changes reported here are measured in terms of long-term, smoothed trends that remove the effects of one-off outliers, analogous to the five-year rolling mean assessed by Foden et al. (2010).

It should also be noted that the decline at Old Grimsby Harbour has apparently stabilized. However, without identifying the cause of these localized changes, it is hard to make recommendations about potential interventions. Furthermore, the welcome change of trajectory at Old Grimsby Harbour has only been evident for around four years, and Duarte & Kirkman (2001) found that the time frame needed to confirm changes to be persistent rather than simply transient is 5-10 years.

Informal interactions with various stakeholders have indicated the prospect of attempting restoration of the eelgrass in Old Grimsby Harbour. A golden rule of restoration is that it is likely to be ineffective until the source of the original loss has been removed (Gamble et al., 2021). While the long-term monitoring in Scilly does not investigate causes of



observed trajectories, there is now some statistical support for the negative trajectory in eelgrass patchiness having stabilized recently (although with the caveat, above). Additionally, while patchiness, as measured through quadrat occupancy, is lower than a decade ago, within-patch shoot density, morphology, disease, and epiphyte measures have remained comparable to other sites throughout – where there is eelgrass in Old Grimsby Harbour, it seems to be doing fine. Finally, HSM predictions based on recent ground-truthing indicate this area provides a highly suitable environment for eelgrass.

Another, more substantial site that has been identified with respect to restoration is St. Mary's Harbour. The HSM modelling reported here indicates that this area is highly suitable, but local factors, the most obvious being boat traffic, make such an assessment very unreliable. Furthermore, without robust documentation of changes over time, this report can have little to directly contribute to that discussion, except noting that few data have been published on eelgrass in St. Mary's Harbour (but see Unsworth et al., 2017).

In addition to localized, long-term monitoring, it also seems clear that the wider context of the state of eelgrass across the Isles of Scilly is needed, to determine how representative such focal studies are. Due to the recent investment in remotely operated data acquisition and habitat suitability modelling, this is now possible for the Isles of Scilly. However, neither documenting trajectories through time using long-term monitoring, nor quantifying changes across space with correlative habitat suitability modelling, are sufficient to understand resilience to environmental change.

With some substantial, albeit localized, changes recorded through long-term eelgrass monitoring, maybe the most important development needed is to build on observation of patterns in time and space with approaches that identify processes underpinning changes. The considerable investment in multi-faceted eelgrass monitoring across the Isles of Scilly presents a rare opportunity to bridge the gap between theory and application.

Considerable ecological research has been done to understand resilience in populations and ecological communities. Frequently, however, the application of advances in conceptual ecology are limited by data deficiencies. Another highly informative approach would be Before-After Control-Impact (BACI), 'Beyond BACI', and related trials to make targeted manipulations, for example to wave exposure, aimed at understanding cause and effect. With few anthropogenic factors impacting eelgrass around the Isles of Scilly, this area should be considered a prime candidate, although extensive engagement with local stakeholders, as well as permissions, would be needed first.

Looking ahead, and more widely, a key issue with the development of predictive modelling of this type is one of 'transferability'. Can relationships between species distribution and environment quantified in one location be applied to another? Due to its time consuming and relatively costly nature, the detailed nature of species and environment data acquired in Scilly may not be available in other areas of high importance.

## 5.2 Recommendations

- It is clear that, at minimum, continued in-water monitoring of Isles of Scilly eelgrass is highly recommended. Changes in trajectory take many years to confirm, and the dataset assembled here is world-leading in terms of length and detail.
- To advance understanding of changes in eelgrass state and predict responses to environmental change within the Isles of Scilly, we need to combine spatial and temporal data to develop and inform ecological models. Priorities for data and modelling, beyond the current long-term monitoring of eelgrass condition are:
  1. establishing a time series of high-resolution aerial images (UAV, manned aircraft, and/or satellite) to document changes in extent over time;
  2. development of HSMs to incorporate changes in biotic and abiotic factors over time; and
  3. development of a new generation of HSMs, based on process-oriented ecological parameters (e.g., fitness), rather than first-generation, correlative models, based on presence alone.
- Finally, while the Isles of Scilly eelgrass is amongst the best studied in the UK, comparisons with other UK (or international) sites is needed to manage and conserve this ecosystem at the national level. We recommend recognising a set of National Seagrass Reference Sites. These should be particularly well-studied sites across the range of geographic and environmental gradients in which eelgrass is found (for example, islands, estuaries, sheltered open coastline). Focussing limited resources into a small number of carefully chosen references sites would allow:
  1. collection of the multi-faceted data types needed to combine spatial and temporal bio-indicators of state and condition, moving us from simple surveillance to understanding and predictive ability;
  2. change the task of predicting responses to change from one of extrapolation beyond known environmental boundaries to one of interpolation, or filling in the gaps, between much expanded environmental condition boundaries; and
  3. allow proper cross-validation of local and national habitat suitability models across spatial scales and locations.

## 6 References

- Alotaibi NM, Kenyon EJ, Cook KJ, Börger L, Bull JC (2019) Low genotypic diversity and long-term ecological decline in a spatially structured seagrass population. *Scientific Reports* 9: 18387.
- Bertelli CM, Bull JC, Cullen-Unsworth LC, Unsworth RK (2021). Unravelling the spatial and temporal plasticity of eelgrass meadows. *Frontiers in Plant Science* 12: 664523.
- Bertelli CM, Bennett WG, Karunarathna H, Reeve DE, Unsworth RK, Bull JC (2023) High-resolution wave data for improving marine habitat suitability models. *Frontiers in Marine Science* 9: 1004829.
- Borowitzka MA, Lavery P, van Keulen M (2007) Epiphytes of seagrasses. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 441-461.
- Bowden DA, Rowden AA, Attrill MJ. (2001) Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of experimental marine biology and ecology* 259: 133-154.
- Bull JC, Kenyon EJ, Cook KJ (2012) Wasting disease regulates long-term population dynamics in a threatened seagrass. *Oecologia* 169: 135-142.
- Bull JC & Kenyon EJ (2021) LIFE Recreation ReMEDIES – Isles of Scilly seagrass survey (2020). Natural England Report NECR358.
- Burdick DM, Short FT, Wolf J (1993) An index to assess and monitor the progression of wasting disease in eelgrass *Zostera marina*. *Mar. Ecol. Progress. Ser.* 94: 83-90.
- Castle L, Pinder J, Lillis H & Manca E (2022) Using an ensemble modelling approach to predict suitable habitat for *Zostera marina* beds, *Modiolus modiolus* beds and *Sabellaria spinulosa* reefs in UK water. JNCC Report No. 718, JNCC, Peterborough.
- Cook KJ (2011) Isles of Scilly *Zostera marina* monitoring: 2011 Expedition Report. Report to Natural England.
- Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. (1997) The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.
- Cullinane JJ, Mahoney O, Whelan P (1985) Algal epiphytes of subtidal *Zostera marina* L. on the south coast of Ireland. *Cryptogam Algal* 6: 239-251.
- den Hartog C (1987) Wasting disease and other dynamics phenomena in *Zostera* beds. *Aquat. Bot.* 27: 3-14.
- den Hartog C (1989) Early records of wasting disease-like damage patterns in eelgrass *Zostera marina*. *Dis. Aquat. Organ.* 7: 223-226.

- Duarte CM (2002) The future of seagrass meadows. *Envir. Cons.* 29: 192-206.
- Duarte CM, Chiscano CL (1999) Seagrass biomass and production: A reassessment. *Aquat. Bot.* 65: 159-174.
- Duarte CM, Kirkman H (2001) Methods for the measurement of seagrass abundance and depth distribution. In: Short FT, Coles RG (Eds), *Global Seagrass Research Methods*. Elsevier Sciences BV, Amsterdam, pp. 141-153.
- Foden J, Brazier DP (2007) Angiosperms (seagrass) within the EU water framework directive: a UK perspective. *Marine Pollution Bulletin* 55: 181-195.
- Foden J, Brazier P, Best M, Scanlan C (2010) Water Framework Directive development of classification tools for ecological assessment: Intertidal Seagrass (Marine Angiosperms). UK TAG Report for Marine Plants Task Team, Publishing UK TAG.
- Fowler SL (1992) Marine monitoring in the Isles of Scilly: Report to Natural England.
- Fourqurean JW, Manuel S, Coates KA, Kenworthy WJ, Smith SR (2010) Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to a loss of seagrass meadows in Bermuda. *Mar. Ecol. Progr. Ser.* 419: 223-232.
- Gamble C, Glover A, Debney A, Bertelli C, Green B, Hendy I, ..., Preston J (2021) *Seagrass Restoration Handbook: UK and Ireland*. Zoological Society of London.
- Gillanders BM (2007) Seagrasses, fish and fisheries. In: Larkum AWD, Orth RJ, Duarte CM, editors. *Seagrasses: Biology, ecology and conservation*. Dordrecht: Springer, pp. 503-536.
- Green AE, Unsworth RK, Chadwick MA, Jones PJ (2021) Historical analysis exposes catastrophic seagrass loss for the United Kingdom. *Frontiers in plant science*, 12: 629962.
- Irvine MA, Bull JC, Keeling MJ (2018). Conservation of pattern as a tool for inference on spatial snapshots in ecological data. *Scientific reports* 8(1): p.132.
- Jackson EL, Higgs S, Allsop T, Cawthray A, Evans J, Langmead O (2011) Isles of Scilly seagrass mapping. Natural England Commissioned Reports, Number 087.
- Johnson MP, Edwards M, Bunker F, Maggs CA (2005) Variation in assemblage structure from individual leaves to regional scale. *Aquat. Bot.* 82: 12-26.
- Jones BL, Unsworth RK (2016). The perilous state of seagrass in the British Isles. *Roy. Soc. Open Sci.* 3(1), 150596.
- Kendrick GA, Duarte CM, Mårba N (2005) Clonality in seagrasses, emergent properties and seagrass landscapes. *Mar. Ecol. Progr. Ser.* 290: 291-296.

- Lethbridge RC, Borowitzka MA, Benjamin K (1988) The development of an artificial *Amphibolis*-like seagrass of complex morphology and preliminary data on its colonization by epiphytes. *Aquat. Bot.* 31: 153-168.
- Lobelle D, Kenyon EJ, Cook KJ, Bull JC (2013) Local and metapopulation processes drive seagrass-epiphyte population dynamics. *PLoS ONE* 8: e57072.
- Muehlstein LK (1989) Perspectives on the wasting disease of eelgrass *Zostera marina*. *Dis. Aqua. Organ.* 7: 211-221.
- Olesen B, Sand-Jensen K (1994a) Biomass-density patterns in the temperate seagrass *Zostera marina*. *Mar. Ecol. Progr. Ser.* 109: 283-291.
- Olesen B, Sand-Jensen K (1994b) Demography of shallow eelgrass (*Zostera marina*) populations: shoot dynamics and biomass development. *J. Ecol.* 82: 379-390.
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW (2006) A global crisis for seagrass ecosystems. *Biosci.* 56: 987-996.
- Piazzini L, Cinelli F (2000) Effects of the spread of the introduced Rhodophyceae *Antithamnion preissii* and *Womersleyella setacea* on the macroalgal community of *Posidonia oceanica* rhizomes in the western Mediterranean Sea. *Cryptogam. Algal.* 21: 291-300.
- Potouroglou M, Kenyon EJ, Gall A, Cook KJ, Bull JC (2014) The roles of flowering, overwinter survival and sea surface temperature in the long-term population dynamics of *Zostera marina* around the Isles of Scilly, UK. *Marine Pollution Bulletin* 83: 500-507.
- Potouroglou M, Bull JC, Krauss KW, Kennedy HA, Fusi M, Daffonchio D, Mangora MM, Githaiga MN, Diele K, Huxham M, (2017) Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports* 7: 11917.
- R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rasmussen E (1977) The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy CP, Helfferich C (eds) *Seagrass Ecosystems, a Scientific Perspective*. Marcel Dekker. New York. pp1-51.
- Reusch TBH, Stam WT, Olsen JL (1999) Microsatellite loci in eelgrass *Zostera marina* reveal marked polymorphism within and among populations. *Mol. Ecol.* 8: 317-322.
- Rozenfeld AF, Arnaud-Haond S, Hernández-García E, Eguíluz VM, Serrão EA, & Duarte CM. (2008) Network analysis identifies weak and strong links in a metapopulation system. *Proceedings of the National Academy of Sciences* 105: 18824-18829.
- Short FT, Ibelings BW, den Hartog C (1988) Comparison of a current eelgrass disease to the wasting disease of the 1930s. *Aquat. Bot.* 30: 295-304.

Thayer GW, Bjorndal KA, Ogden JC, Williams SL, Zieman JC (1984) Role of larger herbivores in seagrass communities. *Estuaries* 7: 351-376.

Unsworth RK, Williams B, Jones BL & Cullen-Unsworth LC (2017) Rocking the boat: damage to eelgrass by swinging boat moorings. *Frontiers in Plant Science* 8:262774.

Waycott M, Duarte C, Carruthers T, Orth R, Dennison W, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. USA* 106: 12377-12381.

Zipperle AM, Coyer JA, Reise K, Stam WT, Olsen JL (2011) An evaluation of small-scale genetic diversity and the mating system in *Zostera noltii* on an intertidal sandflat in the Wadden Sea. *Ann. Bot.* 107: 127-133.

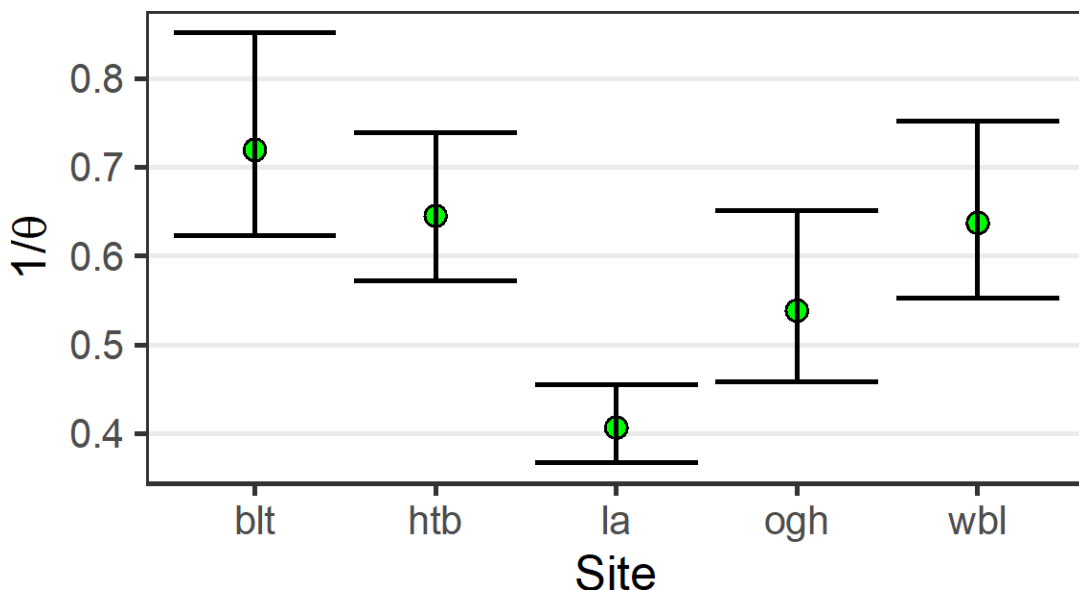
## 7 Appendices

### 7.1 Appendix 1 – Spatial and temporal heterogeneity

#### 7.1.1 Shoot counts

There was a relatively small, positive correlation between shoot counts across consecutive years ( $r = 0.07$ ). This first-order autoregression was strongly supported ( $\Delta\text{AICc} = 97.9$ ). This is expected, particularly as eelgrass is perennial. It does suggest that multi-year analyses which do not incorporate temporal correlation may be statistically flawed. However, there was no support for spatial correlation between survey sites ( $\Delta\text{AICc} = -57.2$ ).

Spatial heterogeneity between sites was evident through different levels of dispersion (random variation in non-zero shoot counts) through time at each site. Little Arthur has the lowest variation through time, while the other sites are broadly comparable (Supplementary Figure S1). This was quantified as the reciprocal of the dispersion parameter,  $1/\theta$ , of a negative binomial distribution, where a larger value indicates greater variability:  $1/\theta_{\text{blt}} = 0.72$  (95 % c.i. = 0.62, 0.85),  $1/\theta_{\text{htb}} = 0.65$  (95 % c.i. = 0.57, 0.74),  $1/\theta_{\text{la}} = 0.41$  (95 % c.i. = 0.37, 0.46),  $1/\theta_{\text{ogh}} = 0.54$  (95 % c.i. = 0.46, 0.65),  $1/\theta_{\text{wbl}} = 0.64$  (95 % c.i. = 0.55, 0.75). This spatial heterogeneity was strongly supported ( $\Delta\text{AICc} = 43.7$ ).



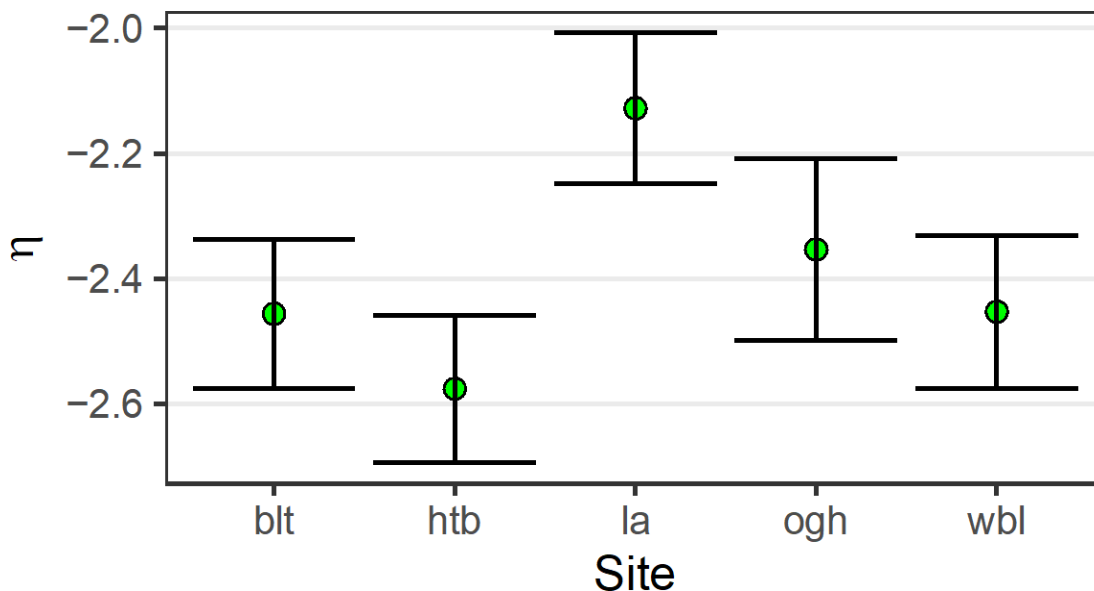
**Figure S1.** Heteroscedacity in shoot counts recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show reciprocals of estimated dispersion parameters,  $1/\theta$ , from a negative binomial GLM (where a larger value indicates greater variability over time). Error bars show 95 % confidence intervals.



### 7.1.2 Leaf counts

Spatial heterogeneity in leaf counts between sites was evident through different levels of dispersion through time at each site. Little Arthur has the highest variation through time, while the other sites are broadly comparable (Supplementary Figure S2). This was quantified as the dispersion parameter,  $\eta$ , of a generalized Poisson distribution, where a larger value indicates greater dispersion:  $\eta_{\text{blt}} = -2.45$  (95 % c.i. = -2.57, -2.34),  $\eta_{\text{htb}} = -2.58$  (95 % c.i. = -2.69, -2.46),  $\eta_{\text{la}} = -2.13$  (95 % c.i. = -2.25, -2.01),  $\eta_{\text{ogh}} = -2.35$  (95 % c.i. = -2.50, -2.21),  $\eta_{\text{wbl}} = -2.45$  (95 % c.i. = -2.57, -2.33). This spatial heterogeneity was strongly supported ( $\Delta\text{AICc} = 23.1$ ).

In this case, negative dispersion values represent under-dispersion (less variability than would be expected by chance). This is not surprising as, presumably, a natural balance between the rate at which old leaves are lost and new leaves grow maintains a relatively constant leaf count for a given time in the growing season each year.

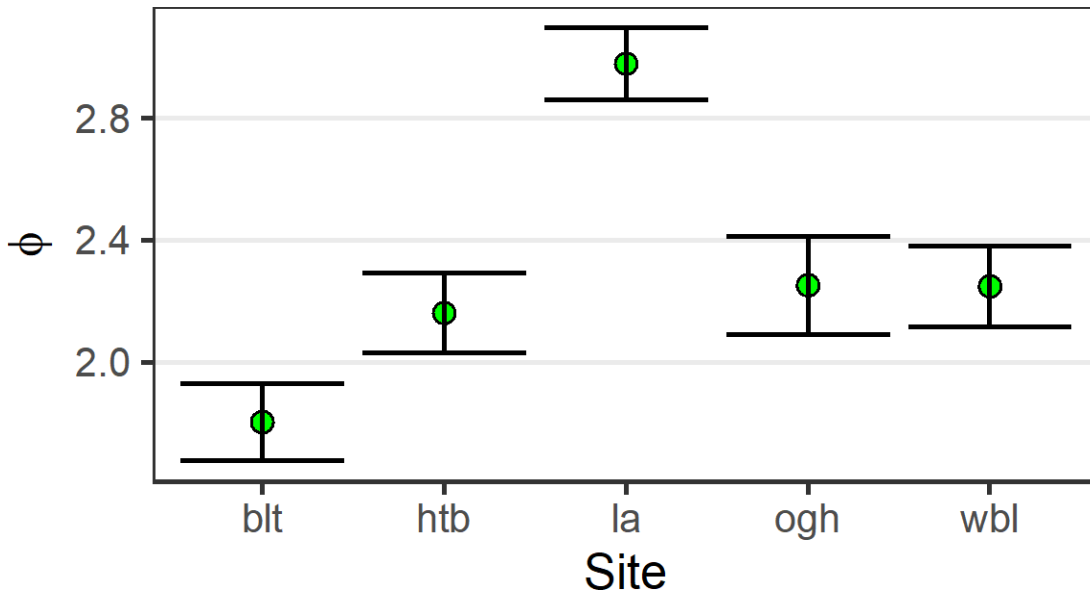


**Figure S2.** Spatial heterogeneity in median leaf counts per 25 cm  $\times$  25 cm quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show estimated dispersion parameters,  $\eta$ , from a generalized Poisson GLM (where a larger value indicates greater variation over time). Error bars show 95 % confidence intervals.

### 7.1.3 Leaf lengths

Spatial heterogeneity in median longest leaf lengths between sites was evident through different levels of dispersion through time at each site. Little Arthur has the highest variation through time, while the other sites are broadly comparable (Supplementary Figure S3). This was quantified as the dispersion parameter,  $\phi$ , of a gamma distribution, where a larger value indicates greater dispersion:  $\phi_{\text{blt}} = 1.80$  (95 % c.i. = 1.68, 1.93),  $\phi_{\text{htb}}$

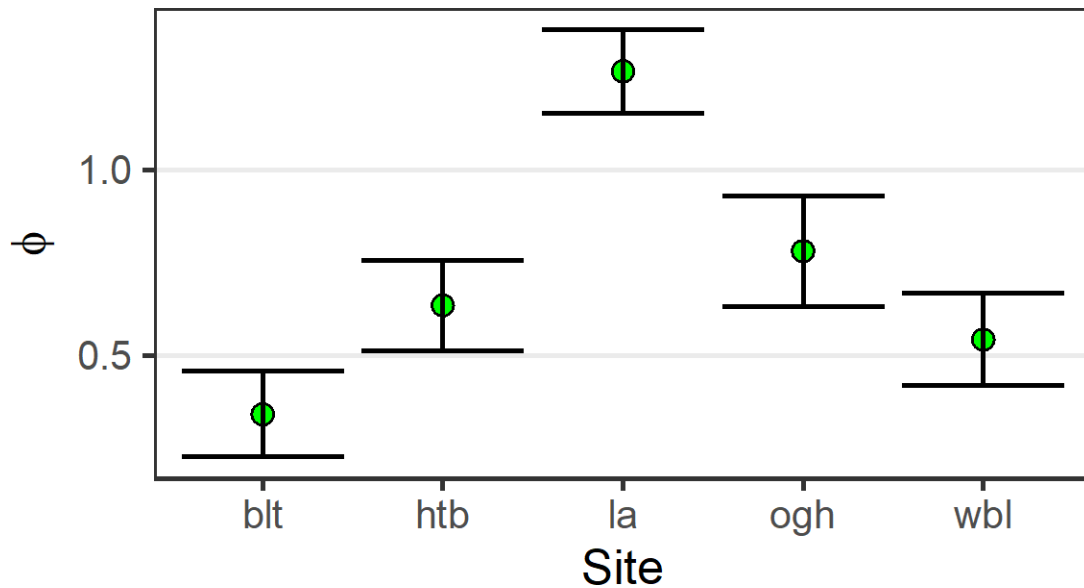
= 2.16 (95 % c.i. = 2.03, 2.29),  $\varphi_{la} = 2.98$  (95 % c.i. = 2.86, 3.10),  $\varphi_{ogh} = 2.25$  (95 % c.i. = 2.09, 2.41),  $\varphi_{wbl} = 2.25$  (95 % c.i. = 2.12, 2.38). This spatial heterogeneity was strongly supported ( $\Delta AICc = 169$ ).



**Figure S3.** Spatial heterogeneity in median longest leaf per shoot, per 25 cm  $\times$  25 cm quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show estimated dispersion parameters,  $\varphi$ , from a gamma GLM (where a larger value indicates greater dispersion). Error bars show 95 % confidence intervals.

#### 7.1.4 Leaf area index

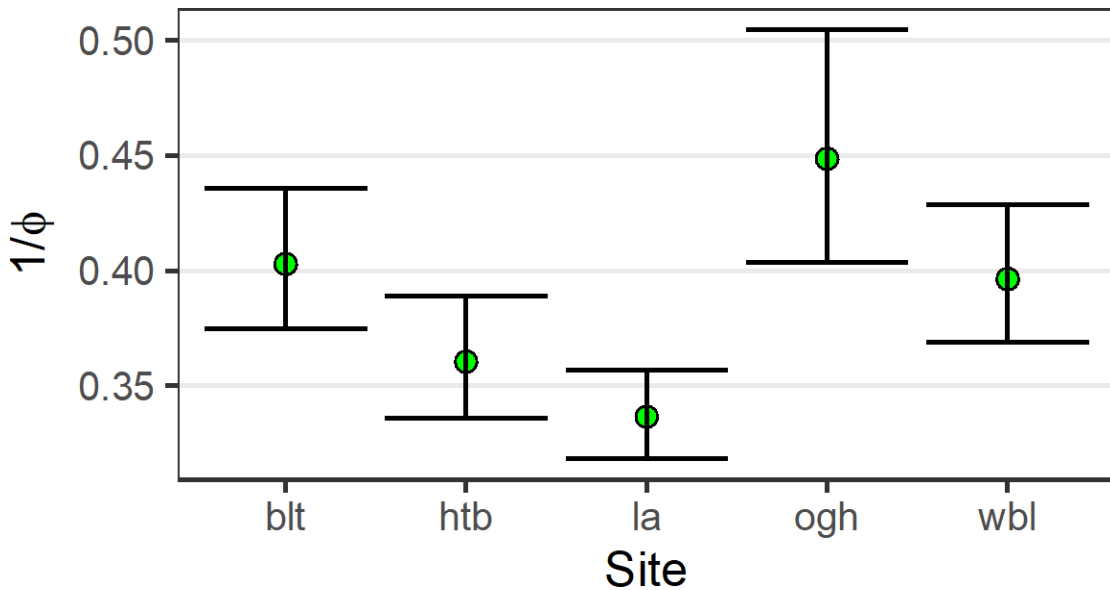
Spatial heterogeneity in LAI between sites was evident through different levels of dispersion through time at each site. Little Arthur has the highest variation through time and Broad Ledges Tresco has the least random variation over time, while the other sites are broadly comparable (Supplementary Figure S4). This was quantified as the dispersion parameter,  $\varphi$ , of a gamma distribution, where a larger value indicates greater dispersion:  $\varphi_{blt} = 0.34$  (95 % c.i. = 0.23, 0.46),  $\varphi_{htb} = 0.64$  (95 % c.i. = 0.51, 0.76),  $\varphi_{la} = 1.27$  (95 % c.i. = 1.15, 1.38),  $\varphi_{ogh} = 0.78$  (95 % c.i. = 0.63, 0.93),  $\varphi_{wbl} = 0.54$  (95 % c.i. = 0.42, 0.67). This spatial heterogeneity was strongly supported ( $\Delta AICc = 123$ ).



**Figure S4.** Spatial heterogeneity in LAI at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show estimated dispersion parameters,  $\phi$ , from a gamma GLM (where a larger value indicates greater dispersion). Error bars show 95 % confidence intervals.

### 7.1.5 Wasting disease

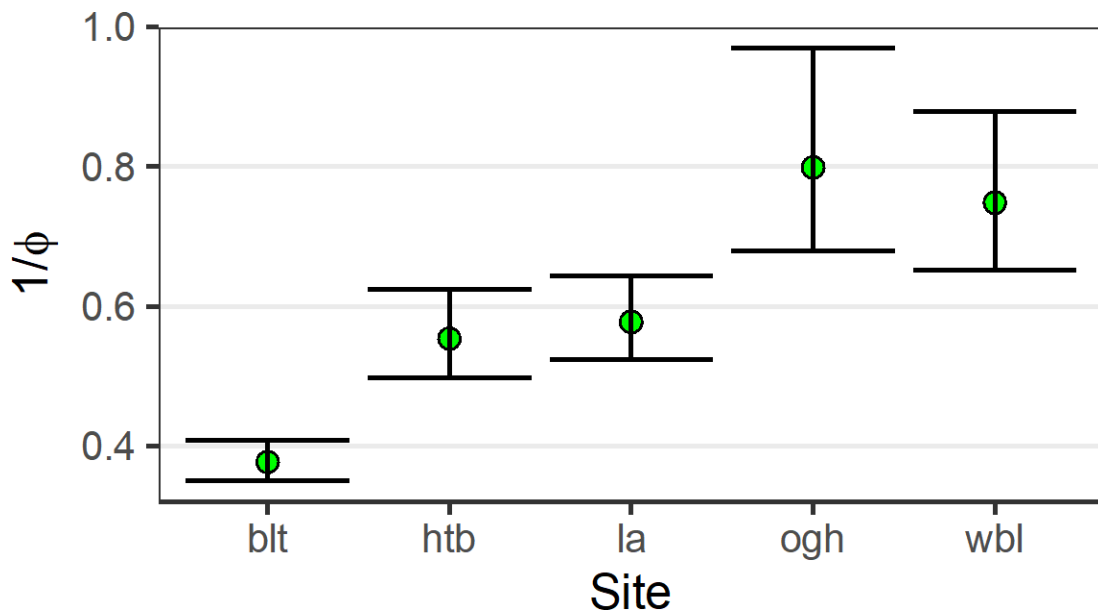
Spatial heterogeneity in wasting disease between sites was evident through different levels of dispersion through time at each site. Little Arthur has the lowest variation through time and Old Grimsby Harbour has the greatest random variation over time, while the other sites are intermediate (Supplementary Figure S5). This was quantified as the reciprocal of the dispersion parameter,  $1/\phi$ , of a beta distribution, where a larger value indicates greater dispersion:  $1/\phi_{\text{blt}} = 0.40$  (95 % c.i. = 0.37, 0.44),  $1/\phi_{\text{htb}} = 0.36$  (95 % c.i. = 0.34, 0.39),  $1/\phi_{\text{la}} = 0.34$  (95 % c.i. = 0.32, 0.36),  $1/\phi_{\text{ogh}} = 0.45$  (95 % c.i. = 0.40, 0.50),  $1/\phi_{\text{wbl}} = 0.40$  (95 % c.i. = 0.37, 0.43). This spatial heterogeneity was strongly supported ( $\Delta\text{AICc} = 23.1$ ).



**Figure S5.** Spatial heterogeneity in wasting disease at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show estimated dispersion parameters,  $1/\phi$ , from a beta GLM (where a larger value indicates greater dispersion). Error bars show 95 % confidence intervals.

### 7.1.6 Epiphytes

Spatial heterogeneity in epiphyte cover between sites was evident through different levels of dispersion through time at each site. Broad Ledges Tresco has the lowest variation through time, with Higher Town Bay and Little Arthur intermediate, and Old Grimsby Harbour and West Broad Ledges showing the greatest variability through time (Supplementary Figure S6). This was quantified as the reciprocal of the dispersion parameter,  $1/\phi$ , of a beta distribution, where a larger value indicates greater dispersion:  $1/\phi_{\text{blt}} = 0.38$  (95 % c.i. = 0.35, 0.41),  $1/\phi_{\text{htb}} = 0.$  (95 % c.i. = 0.),  $1/\phi_{\text{la}} = 0.55$  (95 % c.i. = 0.50, 0.62),  $1/\phi_{\text{ogh}} = 0.80$  (95 % c.i. = 0.68, 0.97),  $1/\phi_{\text{wbl}} = 0.75$  (95 % c.i. = 0.65, 0.88). This spatial heterogeneity was strongly supported ( $\Delta\text{AICc} = 88.6$ ).



**Figure S6.** Spatial heterogeneity in epiphyte cover at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). Green points show estimated dispersion parameters,  $1/\phi$ , from a beta GLM (where a larger value indicates greater dispersion). Error bars show 95 % confidence intervals.

### 7.1.7 Synthesis

Temporal variability in all metrics was quantified as a necessary component of statistical modelling to assess longer-term trends at each survey site. However, these shorter timescale, apparently random fluctuations through time also provide information on eelgrass resilience. The natural spread of values that a population or ecological community exists in is known as its ‘resistance’ to disturbance, an important element of ecological resilience.

Little Arthur is the site with greatest random fluctuation in LAI. However, decomposing LAI, we see that Little Arthur has the least fluctuation in shoot density but that this is outweighed by the site having the greatest fluctuation in canopy height. Therefore, Little Arthur shows substantially greater resistance to disturbance in terms of annual reproduction (shoot density) but greater fluctuation in total above-ground productivity.

Interpretation of this finding is far from straightforward, not least because large natural fluctuations may not translate into risk unless the population is already relatively close to a threshold of ecological collapse. Once such a threshold has been identified, it is often too late. Seagrass is particularly prone to this type of collapse due to its nature as an ‘ecosystem engineer’. Put simply, as seagrass increases it slows up water movement, causing suspended sediment to fall out of the water column, increasing light levels necessary for photosynthesis, and so further increasing the seagrass. If this positive feedback cycle is pushed into reverse and seagrass decreases, the population can pass a

threshold below which it no longer promotes water quality, ambient light levels drop, and the seagrass declines to extinction.

## 7.2 Appendix 2 – Summary data for the current year

### 7.2.1 Broad Ledges Tresco

bearing	distance	shoot	length	leaf	wasting	epiphyte
32.00	26.90	1.00	5.00	4.00	0.01	0.01
220.00	17.40	9.00	59.00	4.00	0.08	0.00
242.00	16.30	5.00	51.00	4.00	0.11	0.00
244.00	28.00	9.00	35.00	4.00	0.01	0.00
225.00	27.20	1.00	25.00	4.00	0.14	0.01
126.00	16.00	7.00	41.00	4.00	0.03	0.00
175.00	15.50	7.00	57.00	5.00	0.03	0.00
69.00	25.10	5.00	30.50	4.00	0.06	0.00
43.00	26.40	8.00	43.50	4.00	0.04	0.00
28.00	10.10	1.00	46.00	4.00	0.01	0.01
291.00	19.10	8.00	64.00	4.00	0.06	0.01
297.00	10.00	8.00	65.50	4.00	0.03	0.03
161.00	23.70	8.00	33.00	4.00	0.02	0.00
328.00	13.10	4.00	74.00	3.50	0.02	0.02
252.00	17.00	9.00	66.00	4.50	0.10	0.10
275.00	21.00	6.00	51.50	4.00	0.09	0.35
141.00	10.50	7.00	31.00	4.00	0.00	0.09
289.00	10.60	5.00	72.00	4.00	0.07	0.12
224.00	9.70	10.00	49.00	3.50	0.04	0.09
55.00	20.90	2.00	50.00	4.00	0.01	0.01
266.00	15.30	13.00	58.00	4.00	0.05	0.08
122.00	24.00	3.00	36.00	4.00	0.00	0.02



## 7.2.2 Higher Town Bay

bearing	distance	shoot	length	leaf	wasting	epiphyte
112.00	21.80	12.00	100.50	4.00	0.00	0.01
150.00	29.60	20.00	37.00	4.00	0.00	0.04
246.00	14.20	18.00	38.50	4.00	0.00	0.01
311.00	22.10	9.00	20.00	4.00	0.00	0.00
130.00	22.10	3.00	27.00	4.00	0.00	0.01
127.00	29.60	28.00	42.00	4.00	0.00	0.00
180.00	6.40	10.00	27.00	4.50	0.06	0.02
130.00	4.10	11.00	23.00	4.00	0.00	0.00
115.00	28.70	8.00	63.50	4.50	0.02	0.00
261.00	24.70	14.00	52.50	4.00	0.03	0.00
68.00	12.40	7.00	42.00	4.00	0.00	0.00
45.00	26.80	17.00	49.00	4.00	0.00	0.00
41.00	24.70	10.00	63.00	4.00	0.02	0.00
20.00	13.70	8.00	34.00	3.50	0.06	0.02
228.00	27.70	2.00	23.00	5.50	0.04	0.04
87.00	22.60	8.00	68.00	4.00	0.06	0.00
302.00	27.10	10.00	53.50	4.00	0.03	0.00
269.00	24.50	6.00	64.00	4.00	0.01	0.00
251.00	14.10	23.00	46.00	4.00	0.06	0.00
188.00	13.80	9.00	33.00	4.00	0.05	0.00
272.00	21.70	2.00	52.50	4.00	0.04	0.00

### 7.2.3 Little Arthur

bearing	distance	shoot	length	leaf	wasting	epiphyte
252.00	26.80	6.00	81.00	4.00	0.01	0.00
308.00	12.70	13.00	90.00	4.00	0.01	0.00
13.00	29.70	12.00	70.50	4.00	0.00	0.00
350.00	27.80	9.00	91.00	4.00	0.01	0.00
218.00	22.50	12.00	69.00	4.00	0.00	0.00
272.00	26.10	12.00	72.00	4.00	0.01	0.00
127.00	27.50	12.00	78.50	3.00	0.03	0.01
323.00	12.70	11.00	75.00	4.00	0.02	0.06
281.00	18.50	10.00	76.00	4.00	0.00	0.06
47.00	11.10	7.00	52.00	4.00	0.00	0.03
164.00	11.80	9.00	75.00	4.00	0.02	0.03
26.00	25.40	5.00	87.00	4.00	0.03	0.07
166.00	22.30	7.00	86.00	4.00	0.02	0.04
11.00	28.60	19.00	52.00	4.00	0.00	0.00
118.00	19.50	7.00	62.00	4.00	0.00	0.00
339.00	15.90	13.00	69.50	4.00	0.00	0.00
306.00	29.00	11.00	83.00	4.00	0.00	0.02
199.00	29.40	4.00	76.50	4.00	0.00	0.01
130.00	20.30	5.00	67.00	4.00	0.03	0.00
68.00	13.20	5.00	58.00	4.00	0.03	0.00
49.00	13.80	1.00	52.00	8.00	0.01	0.01
340.00	26.00	8.00	71.00	4.00	0.04	0.00
280.00	10.10	8.00	79.50	4.00	0.15	0.00
327.00	29.60	8.00	81.50	4.50	0.00	0.11

## 7.2.4 Old Grimsby Harbour

bearing	distance	shoot	length	leaf	wasting	epiphyte
79.00	29.50	8.00	55.00	4.00	0.05	0.23
350.00	26.30	4.00	64.00	4.00	0.06	0.21
6.00	23.50	7.00	53.00	5.00	0.04	0.08
331.00	12.30	8.00	66.50	4.00	0.02	0.09
346.00	27.10	7.00	51.00	4.00	0.00	0.11
45.00	19.10	10.00	69.50	4.00	0.03	0.00
15.00	18.80	11.00	45.00	4.00	0.03	0.07
36.00	25.80	15.00	56.00	4.00	0.05	0.21
12.00	21.40	11.00	61.00	4.00	0.00	0.12
38.00	27.00	7.00	46.00	4.00	0.00	0.13
349.00	24.30	5.00	73.00	4.00	0.00	0.12

## 7.2.5 West Broad Ledges

bearing	distance	shoot	length	leaf	wasting	epiphyte
133.00	20.40	14.00	51.50	4.00	0.01	0.00
166.00	10.70	24.00	87.00	4.00	0.01	0.00
190.00	26.40	12.00	68.50	4.00	0.02	0.00
123.00	15.80	2.00	36.50	4.50	0.04	0.00
146.00	27.10	2.00	35.50	4.00	0.14	0.00
30.00	10.20	1.00	35.00	5.00	0.01	0.00
306.00	24.00	1.00	44.00	4.00	0.07	0.00
31.00	12.20	3.00	41.00	4.00	0.39	0.00
8.00	16.10	7.00	35.00	4.00	0.08	0.00
236.00	23.90	9.00	44.00	5.00	0.00	0.00
127.00	25.10	9.00	24.00	4.00	0.00	0.00
295.00	14.80	10.00	37.00	3.50	0.00	0.00
256.00	26.10	10.00	36.50	4.00	0.00	0.00
248.00	28.70	16.00	31.00	4.00	0.07	0.00

bearing	distance	shoot	length	leaf	wasting	epiphyte
334.00	27.40	2.00	24.50	3.00	0.06	0.00
335.00	27.30	18.00	67.00	4.00	0.03	0.00
353.00	21.40	15.00	70.00	4.00	0.03	0.00
69.00	23.80	14.00	65.50	4.00	0.03	0.00

