

Isles of Scilly eelgrass bed voluntary monitoring programme

2017 Annual Survey

A report for Natural England, prepared by
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In association with Project Seagrass

<http://www.projectseagrass.org>

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In this report, we present novel data from an ongoing, spatially replicated, annual study of a comparatively un-impacted temperate eelgrass habitat, based around the Isles of Scilly, UK. Five sites were assessed: Broad Ledges Tresco, Higher Town Bay, Little Arthur, Old Grimsby Harbour, and West Broad Ledges. Metrics include eelgrass (*Zostera marina*) shoot density, number of leaves per shoot, maximum shoot length, as well as semi-quantitative recording of signs of wasting disease and epiphyte cover on a leaf-by-leaf basis. Findings from the 2017 survey, as well as their place in continuous time series from 1996, are presented and analysed. This represents twenty-two years of continuous annual monitoring around the Isles of Scilly.

Overall, eelgrass was present at all five survey sites around the Isles of Scilly. We did not find significant variation in shoot density between survey sites in 2017. However, longer-term trends reveal significant declines in average shoot density at four out of five surveyed sites since Special Area of Conservation designation in 2005, with Higher Town Bay declining by over 50%.

Canopy height was found to differ between sites but this may simply be a feature of environmental differences between sites, such as depth. No long-term changes in canopy height were found with the exception of Little Arthur, where a slight decrease is evident.

Shoot density and canopy height were combined into a measure of leaf area index (LAI), estimating total photosynthetic area per unit ground. Significant differences in LAI were observed between the five survey sites on the 2017 survey, with Little Arthur the most productive and Old Grimsby Harbour the least. Long-term declines in productivity are observed at Higher Town Bay, Little Arthur, and Old Grimsby Harbour.

The 2017 results also showed differences in eelgrass 'patchiness' between survey sites, with eelgrass being 80% absent at Higher Town Bay and 88% absent at Old Grimsby Harbour. Analysis of long-term trends showed that there have been significant declines in patch occupancy at Higher Town Bay (30%) and Old Grimsby Harbour (60%).

Long-term changes in wasting disease and epiphyte cover were observed but without any clear overall trend. Interestingly, both in 2017 and across the whole length of the survey, wasting disease prevalence differs significantly between survey sites, but epiphyte cover does not. This may indicate that the relative influence of local versus regional drivers is different for wasting disease and epiphytes but more research would be needed to explore this.

Finally, we continue to see *Sargassum muticum*, an invasive species of brown seaweed known as wireweed, at all surveyed sites in the Isles of Scilly. While this is not formally quantified, no obvious changes in abundance or distribution were evident.

The synthesis of these findings indicates concerning declines in eelgrass across the Isles of Scilly and, in particular, at Higher Town Bay and Old Grimsby Harbour, since SAC designation in 2005.

2.1 Seagrass

Seagrasses are globally dispersed along coastlines, covering approximately 0.3 to 0.6 million km² (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 stabilisation 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). 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 metapopulation processes spanning oceans (Rozenfeld 2008).

Seagrass population dynamics have typically been studied through measuring allometric relationships between specific life history components and shoot density or biomass, within a season (Olesen & Sand-Jensen 1994a, b). Whilst these studies are necessary to identify mechanisms contributing to seagrass turnover, it has been rare for investigators to look at natural populations across many years. By repeating annual surveys at the same point in each growing season, in order to control for within-season variation, the longer-term effects of biological or environmental drivers of population dynamics can be quantified.

2.2 Wasting disease

In the 1930s, a 'wasting disease' (*Labyrinthula zosterae*) substantially reduced populations of eelgrass, the predominant seagrass species of the north Atlantic. 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 monitoring reported in this study (Fowler 1992). We quantified signs of disease by its characteristic leaf lesions (den Hartog 1989; Burdick et al. 1993). We did not test for the presence of the causative agent directly (for example, by culturing or polymerase chain reaction). However, results from population dynamic modelling of this system are entirely consistent with these signs of disease being caused by an infectious agent (Bull et al. 2012).

2.3 Epiphytes

In this survey, we did not attempt to identify specific epiphytes as this would require a level of expertise and time that is beyond the scope of this project. Rather, we treated all visible epiphytes 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 *Zostera marina* is typical of many seagrasses, dominated by algae but comprising a range of invertebrate species as well

(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). This diversity in epiphytic species is likely to be structured by rich and, as yet, uncharted population dynamics.

2.4 Isles of Scilly

One of the main surviving seagrass 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 south west from Land's Ends, 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) sub-tidal sandbanks (eelgrass bed communities, sand and gravel communities, mixed sediment communities),
- 2) reefs (rocky shore communities, vertical rock, kelp forest communities, sub-tidal rock & boulder communities, sub-tidal faunal turf communities),
- 3) intertidal mudflats and sand flats (sand communities),
- 4) grey seals (*Halichoerus grypus*),
- 5) shore dock (*Rumex rupestris*).

Natural England has a duty to report on the condition of the eelgrass bed communities sub-feature every six years. This commitment, in part, motivated the support provided by Natural England for the current volunteer monitoring project.

In this report, we present novel data from an ongoing, spatially replicated, annual study of a comparatively un-impacted temperate seagrass habitat (Jones & Unsworth 2016, Jones et al. 2018). In this sub-tidal environment, there are no large grazing species, such as the geese that affect inter-tidal seagrass 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, our survey location is an archipelago with little industrial or agricultural impact or urbanisation (Figure 1b). Here, eelgrass grows substantially as a natural monoculture and we are able to make rare baseline observations of a seagrass ecosystem not previously thought to be in serious overall decline.

2.5 Survey site descriptions

The following section is included for completeness and is much as reported in previous Annual Reports (adapted from Cook 2011).

There have been no major developments close to any of the five eelgrass survey sites. However, there has been substantial work to extend the main quay in Hugh Town, St. Mary's. The amount of associated traffic and disturbance is unknown.

Broad Ledges Tresco Broad Ledge 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 small jetty that allows access to the island from the sea and is used by tourist boats when the tide permits. 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 weak tidal streams. The seabed here comprises coarse sand, mixed with small gravel, pebbles and some cobbles, as well as some *Sargassum muticum* plants and small macro algae, 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.

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 lies at the eastern end of the bay and runs from English Island along the edge 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, however, 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 30cm above the surrounding sea floor. The strong tidal streams bring large fronds of loose macro algae 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.

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. 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 macro algae. The eelgrass bed, however, lies in a small patch of medium sand and, despite the surrounding macro algae, the eelgrass bed is relatively free from any covering plants. 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.

Old Grimsby Harbour The bed lies along the southern edge 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 a large amount of chain lying on the sea floor

and over the eelgrass shoots. As the direction of the wind and current changes the moorings move round causing the chains to be dragged over the plants (Unsworth et al 2017). This can cause plants to be dislodged and even for the rhizomes to be damaged. The presence of exposed and dislodged rhizomes within the arc of the chains movement confirms this theory. The seabed is mainly medium sand overlaid with eelgrass, intermixed with some overlying loose macro algae. It should also be noted that during the 2010 survey, large quantities of green and brown algal masses were recorded across the site and no eelgrass was found. Time series presented in the current report show zero eelgrass for this site in 2010. However, a limited number of quadrat records were made that year at an adjacent site (c. 100m away), which could be used for comparisons.

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 macro algae 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.

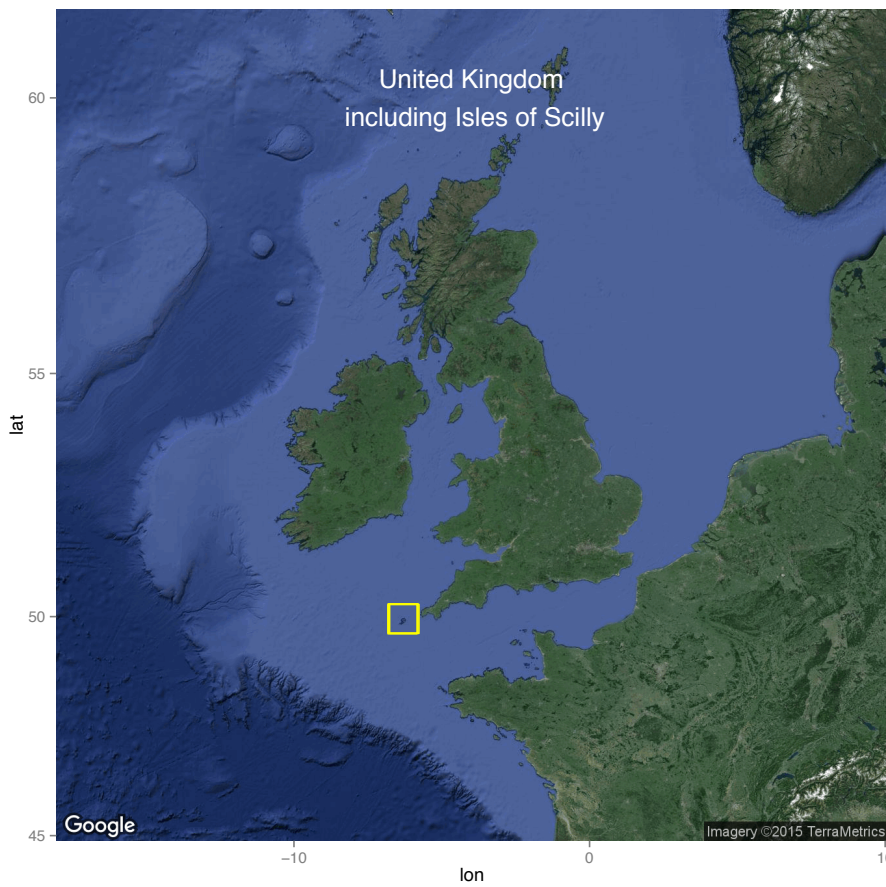


Figure 1a Location of the Isles of Scilly in relation to the rest of the United Kingdom. Yellow square surrounds the Isles of Scilly

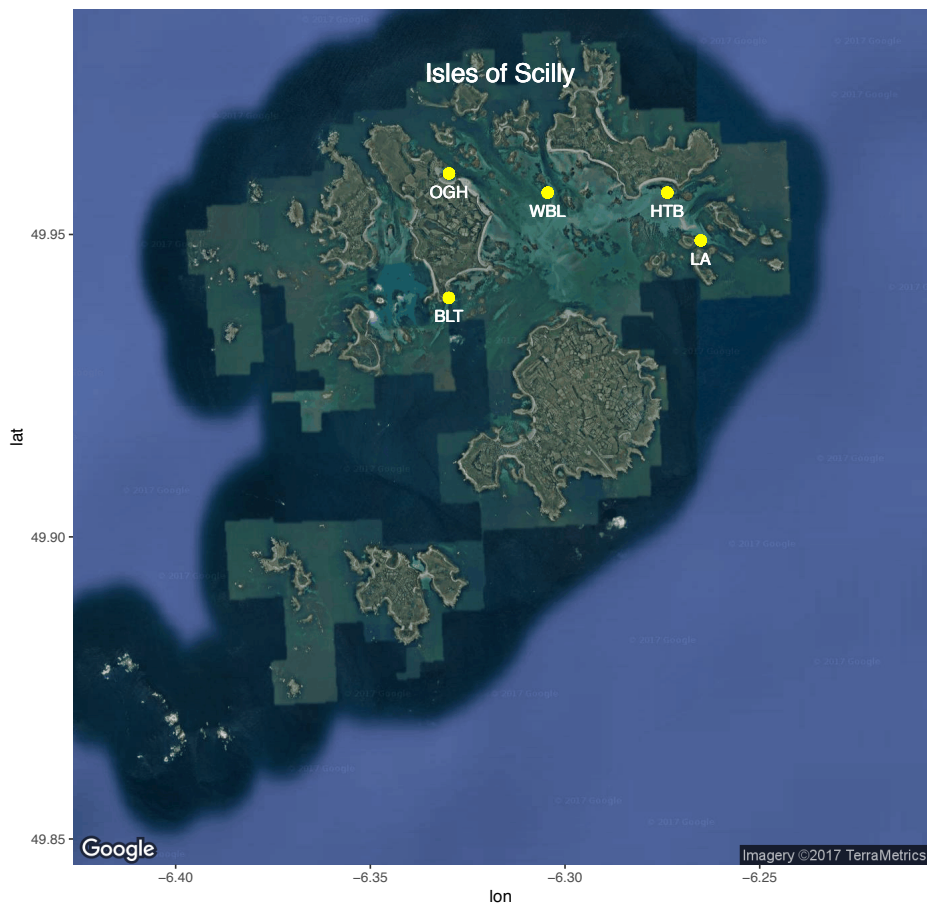


Figure 1b Locations of the five survey sites around the Isles of Scilly in 2017. Solid yellow circles indicate sites. Clockwise from bottom-left: Broad Ledges Tresco (blt), Old Grimsby Harbour (ogh), West Broad Ledges (wbl), Higher Town Bay (htb) and Little Arthur (la)

2.6 Survey aims

Some form of monitoring of the Isles of Scilly eelgrass beds has been undertaken since the 1980s. 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 current survey is a direct continuation of this process, with records that we regard as comparable beginning in 1996.

The aims of the annual Isles of Scilly eelgrass survey 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 shoot length,
- 4) the amount of infection on eelgrass leaves, thought to indicate wasting disease,
- 5) the amount of epiphyte cover on leaves.

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

3.1 Survey methods

Survey team The team for the 2017 Isles of Scilly eelgrass survey comprised, James Bull (Swansea University), Fiona Crouch (Marine Biological Association), Will Kay (Swansea University), Emma Kenyon (Sussex University), Keith Naylor (Swansea University), Sam Naylor, and Trudy Russell (Natural England). Whilst professional affiliations are given here, it must be stressed that all participants did so as volunteers and did not receive payment for their contributions to the survey (indeed in all cases, volunteers contributed to survey costs). The survey vessel was the RIB, 'Calypso', a 5.5m vessel with 90bhp four-stroke outboard engine, carrying VHF/DSC marine radio equipment, flares, 1st aid kit and emergency oxygen. Volunteers have appropriate training in these through approved agencies such as BSAC and RYA.

Survey location As far as possible, surveys 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 minimise the impact of the survey on the eelgrass. The resulting central datum for each survey was typically within 10-20m of the target coordinates and the actual coordinates were recorded.

Table 1 Survey site locations for Isles of Scilly eelgrass surveys, 2017

Site	Latitude	Longitude	Date surveyed
Broad Ledges Tresco (blt)	49°56.400'N	06°19.600'W	30 / 07 / 2017
Higher Town Bay (htb)	49°57.477'N	06°16.436'W	30 / 07 / 2017
Little Arthur (la)	49°56.924'N	06°15.911'W	01 / 08 / 2017
Old Grimsby Harbour (ogh)	49°57.607'N	06°19.773'W	31 / 07 / 2017
West Broad Ledges (wbl)	49°57.422'N	06°18.243'W	03 / 08 / 2017

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 distance components greater than 30m were discarded. This process continued until 25 sets of polar coordinates within the maximum survey radius of 30m 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.

Since the full survey includes measurements of eelgrass 'health' (disease and epiphytes), which is not possible *in situ*, shoots were removed at the level of the substrate, paying particular attention to not disturb or damage the rhizomes or roots, for further assessment *ex situ*. This is consistent with current Natural England seagrass survey methodology (Kevan Cook, pers. comm.).

Shoot counts Shoot counts were made in 25 x 25cm quadrats and shoot density was presented per quadrat. It would be tempting to extrapolate to 'per square metre', 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.

Shoot parameters 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 We define canopy height per quadrat as the median of the lengths of the longest leaf on each shoot in each quadrat.

Leaf area index We estimate 'leaf area index' (LAI) per quadrat 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 leaf widths are not measured, this metric is not strictly comparable to traditional LAI (the area of leaf per unit area of ground) but serves as a relevant proxy for making comparisons within this dataset.

Wasting disease Proportions of individual leaves showing signs of wasting disease (lesions characterised by black spots and streaks, den Hartog 1989) were scored for all leaves, based on an accepted categorisation: [a = 0%], [0% < b < 2%], [2% < c < 25%], [25% < d < 50%], [50% < e < 75%] and [75 < f < 100%] (Burdick et al. 1993 - see Figure 1 therein for a diagrammatic representation of the categories). Wasting disease is thought to spread primarily through direct contact by leaves (Burdick et al. 1993). Once the pathogen gains entry to the leaf, it spreads throughout the leaf, reducing photosynthetic potential and killing the tissue. Since older leaves tend to accumulate higher disease scores, we control for this within-leaf progression by analysing disease as either present or absent in each leaf, retaining the full quantification data for future use.

Epiphytes In this survey, we did not attempt to identify specific epiphytes, but rather treated all visible epiphytes as a functional group, likely to have a similar effect on eelgrass growth by restricting light reaching the photosynthetic surface of leaves. This is because identification of many epiphyte species, especially algae, is a highly specialised and time-consuming task, beyond the scope of this project. Here, we recorded the proportion of each eelgrass leaf covered in epiphytes of any type using the same percentage cover brackets as used for recording signs of wasting disease (Burdick et al. 1993), taking an average for each shoot for analysis.

3.2 Analytical methods

We present a brief set of initial analyses based on a series of questions about differences between the five survey sites in 2017, as well as on temporal trends through the whole period of the current Isles of Scilly eelgrass survey, 1996 - 2017. In all cases, we adopt the simple approach of:

- 1) identifying the quantitative question to be focused on,
- 2) graphically presenting the observation that answers the question,
- 3) presenting statistical analysis to assess the reproducibility of findings.

Throughout, the Generalised Linear Model (GLM) framework is ideal. This form of analysis is sufficiently flexible to model all the different types of data that we have recorded, rather than being limited by the assumption of 'Normally-distributed residuals' (here, we encounter 'count data', 'presence / absence data', 'continuous data with a lower boundary of zero' and 'proportion data'). Where nonlinear trends through time were assessed, we used the Generalised Additive Model (GAM), which is based on the GLM but with the facility to fit smoothed nonlinear trends.

Shoot counts Differences in shoot counts were assessed using either over-dispersed Poisson GLMs or negative binomial GLMs, as appropriate.

Presence / absence A number of quadrats at each site were found to include no eelgrass shoots. This information is important and was retained. As can be seen from satellite photos of the survey sites (Appendix 1), eelgrass meadows form remarkable patterns of vegetation, separated by bare sand (Irvine et al. 2016a, 2016b). Additionally, wasting disease was assessed as 'infected' or 'not infected' on a leaf-by-leaf basis. In the current study, this presence / absence data was modelled using binomial GLMs.

Mixture models Statistical models are underpinned by biological assumptions and statistical analysis is limited by the insight of the biologists conducting the analysis. We identify two reasons why individual quadrats might contain no eelgrass shoots: 1) rhizomes are present beneath the sand but no shoots have emerged within the quadrat area, and 2) no rhizomes are present, either through biological or environmental processes. A third possibility that shoots are missed through observer error seems unlikely to us but cannot be ruled out. Since we cannot be certain which process accounts for individual zero count records, we combine our 'shoot count' and 'presence / absence' data into 'mixture models' that simultaneously answer questions on counts and binomial outcomes without relying on explicit understanding, and partitioning, of the causes of zero counts.

Continuous data Leaf length data is 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 amongst sets of longer leaves). We model this type of bounded data using gamma GLMs.

Ordinal data Epiphyte scores are recorded as percentage cover brackets. Here we converted these (0-5) to 'proportion data' (0-1), first by averaging scores across quadrats, then dividing through by five. Here, we modelled 'proportion data' by logit-transforming (where, $\text{logit}[p] = \ln[p / (1-p)]$) the proportions with Gaussian (Normal) GLMs.

All statistical analyses were undertaken using R version 3.3.2 (R Core Team, 2016).

4.1 2017 Survey findings

Shoot counts Distributions of shoot counts across quadrats at each of the sampling sites, are presented in Figure 2 and Table 2. There are significant differences in quadrat occupancy between sites ($\chi^2_{df=4} = 32.04, p < 0.001$) but not shoot count ($\chi^2_{df=4} = 3.33, p = 0.504$).

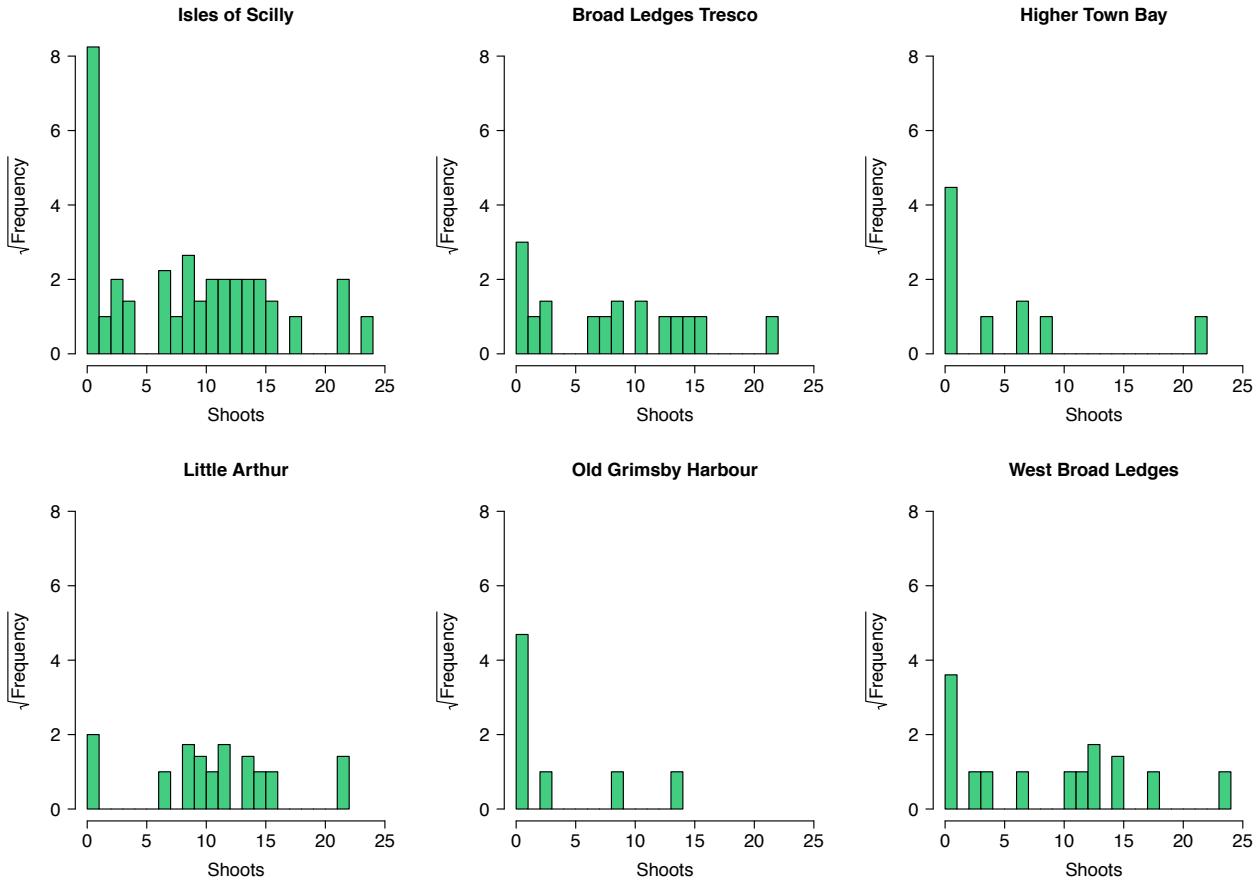


Figure 2 Frequency histogram of the number of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations (Note square root frequency scale)

Quadrat occupancy can be ranked (highest to lowest) as Little Arthur, Broad Ledges Tresco, West Broad Ledges, Higher Town Bay, and Old Grimsby Harbour. Estimates are given on a logit-transformed scale in Table 2a. Pairwise comparisons between sites shows that there are statistically significant differences between ogh and blt, la and htb, and between ogh and la (Table 2b).

Table 2a Quadrat occupancy summary (logit scale)

Site	blt	htb	la	ogh	wbl
Estimate	0.442	-1.386	1.386	-1.992	-0.080
Std. Error	0.437	0.511	0.571	0.629	0.409

Table 2b Pairwise comparisons between sites (Tukey *post hoc* tests, $p < 0.05$ in bold)

Sites	Estimate	Std. Error	z value	p value
htb - blt	-1.828	0.672	-2.720	0.050
la - blt	0.945	0.719	1.314	0.679
ogh - blt	-2.434	0.766	-3.180	0.013
wbl - blt	-0.522	0.598	-0.872	0.906
la - htb	2.773	0.766	3.618	0.003
ogh - htb	-0.606	0.810	-0.748	0.944
wbl - htb	1.306	0.655	1.996	0.265
ogh - la	-3.379	0.850	-3.977	< 0.001
wbl - la	-1.466	0.703	-2.087	0.223
wbl - ogh	1.912	0.750	2.549	0.079

Canopy height Distributions of canopy heights across quadrats, at each of the sampling locations, are presented in Figure 3 and Table 3. There is a significant difference in canopy height between survey sites ($\chi^2_{df=4} = 6.98, p < 0.001$).

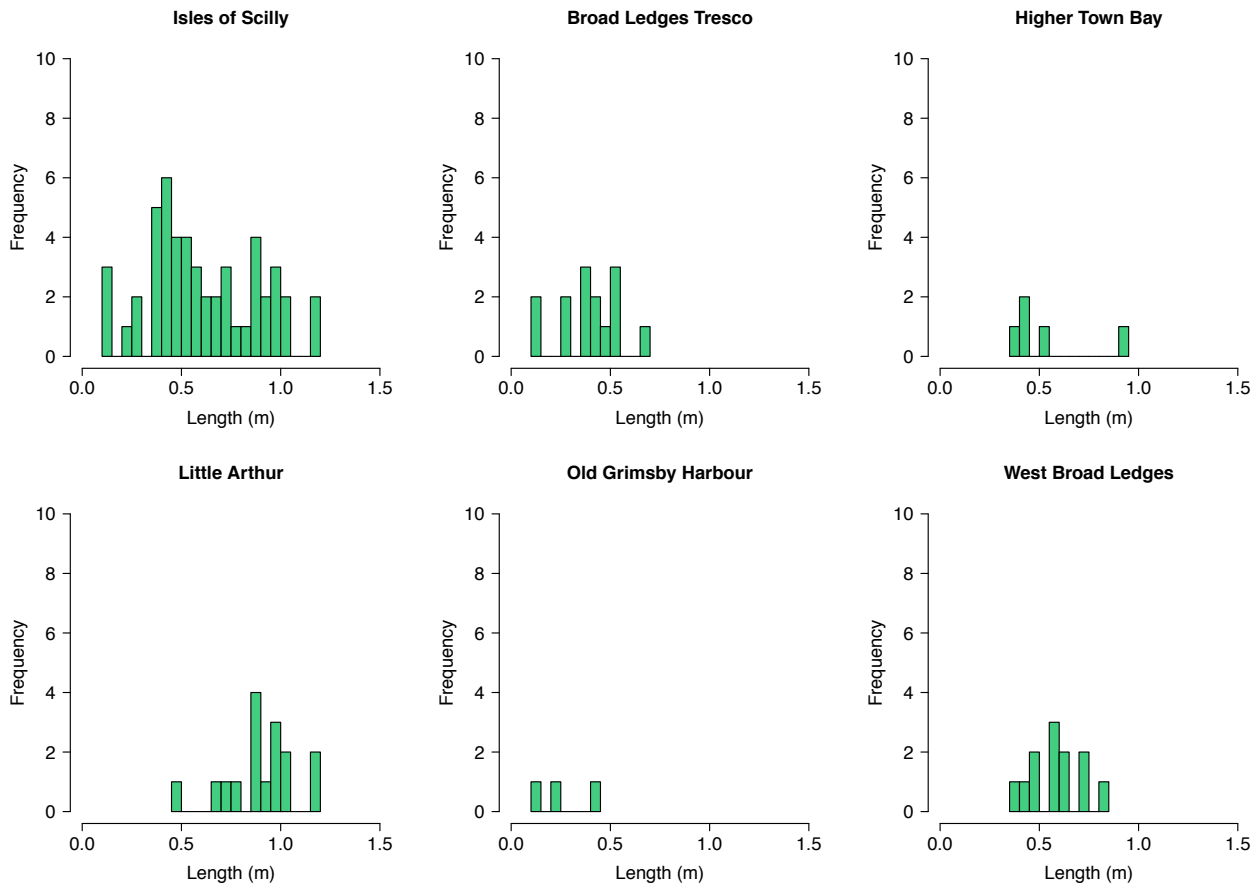


Figure 3 Frequency histogram of the ‘canopy height’ (m) of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations

Canopy height can be ranked (highest to lowest) as Little Arthur, West Broad Ledges, Higher Town Bay, Broad Ledges Tresco, and Old Grimsby Harbour. Estimates are given on a log-transformed scale in Table 3a. Pairwise comparisons between sites shows that there are statistically significant differences between all pairs except htb and blt, ogh and blt, and between wbl and htb (Table 3b).

Table 3a Canopy height summary (natural logarithm scale)

Site	blt	htb	la	ogh	wbl
Estimate	-0.940	-0.627	-0.104	-1.354	-0.525
Std. Error	0.084	0.141	0.079	0.182	0.091

Table 3b Pairwise comparisons between sites (Tukey *post hoc* tests, $p < 0.05$ in bold)

Sites	Estimate	Std. Error	z value	p value
htb - blt	0.312	0.164	1.904	0.302
la - blt	0.836	0.115	7.248	< 0.001
ogh - blt	-0.414	0.200	-2.065	0.224
wbl - blt	0.415	0.124	3.349	0.007
la - htb	0.523	0.161	3.241	0.001
ogh - htb	-0.726	0.230	-3.157	0.013
wbl - htb	0.103	0.168	0.612	0.972
ogh - la	-1.249	0.198	-6.304	< 0.001
wbl - la	-0.421	0.120	-3.496	0.004
wbl - ogh	0.829	0.203	4.076	< 0.001

Leaf analysis Distributions of leaf area index (LAI) across quadrats, at each of the sampling locations, are presented in Figure 4 and Table 4. There is a significant difference in LAI between sites ($\chi^2_{df=4} = 9.71, p < 0.001$).

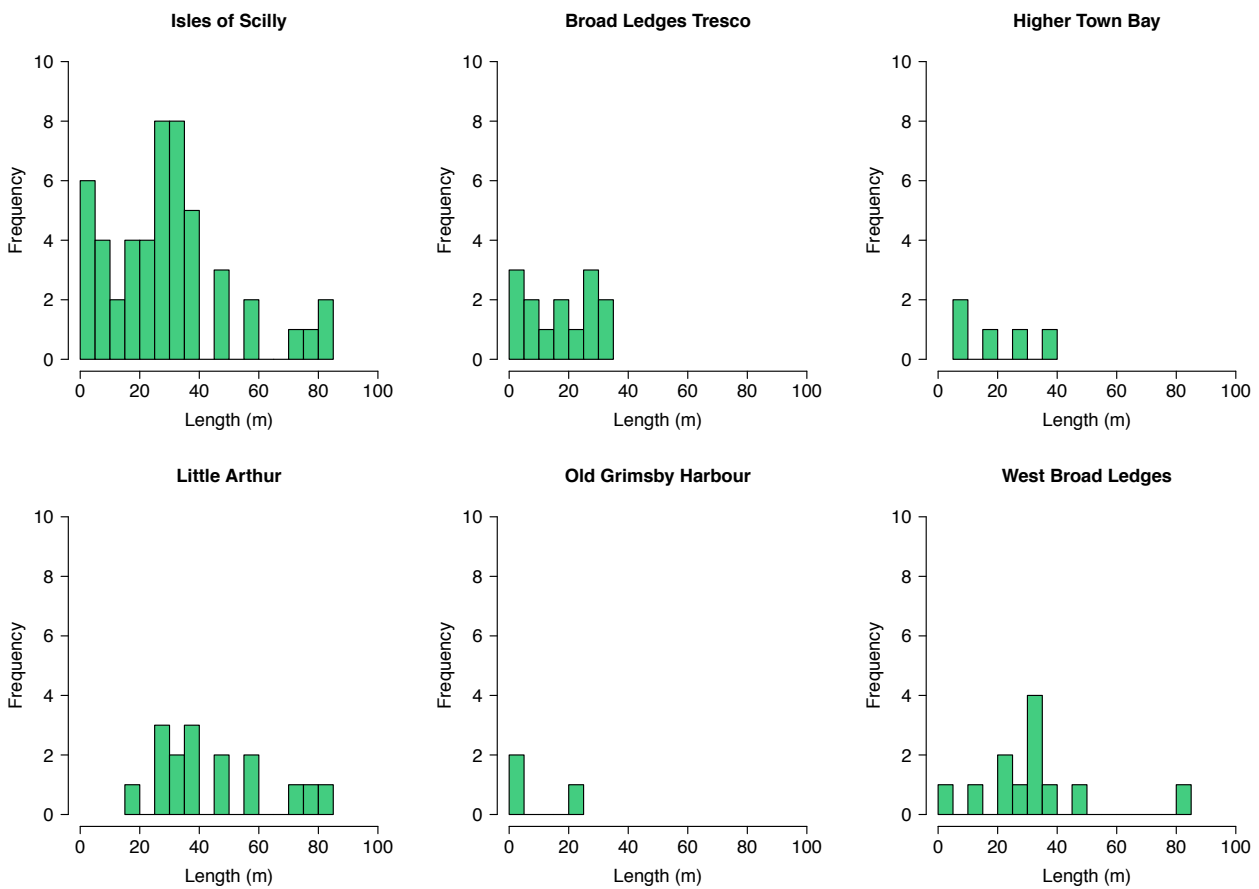


Figure 4 Frequency histogram of the ‘leaf area index’ (LAI) of eelgrass recorded per 25 x 25cm quadrat at each of the five survey locations

Leaf area index can be ranked (highest to lowest) as Little Arthur, West Broad Ledges, Higher Town Bay, Broad Ledges Tresco, and Old Grimsby Harbour. Estimates are given on a log-transformed scale in Table 4a. Pairwise comparisons between sites shows that there are statistically significant differences between la and blt, ogh and la, and between wbl and ogh (Table 4b).

Table 4a Leaf area index summary (natural logarithm scale)

Site	blt	htb	la	ogh	wbl
Estimate	2.859	2.973	3.800	2.314	3.443
Std. Error	0.163	0.273	0.153	0.353	0.176

Table 4b Pairwise comparisons between sites (Tukey *post hoc* tests, $p < 0.05$ in bold)

Sites	Estimate	Std. Error	z value	p value
htb - blt	0.113	0.3184	0.356	0.996
la - blt	0.941	0.224	4.206	< 0.001
ogh - blt	-0.545	0.389	-1.401	0.614
wbl - blt	0.584	0.241	2.429	0.101
la - htb	0.828	0.313	2.643	0.059
ogh - htb	-0.658	0.446	-1.474	0.566
wbl - htb	0.471	0.325	1.447	0.584
ogh - la	-1.486	0.385	-3.863	< 0.001
wbl - la	-0.357	0.233	-1.529	0.530
wbl - ogh	1.129	0.395	2.861	0.032

Wasting disease Distributions of disease prevalence across quadrats, at each of the sampling locations, are presented in Figure 5 and Table 5. There is no significant difference in the proportion of infected leaves per shoot between survey sites ($F_{df=4} = 1.292, p = 0.288$).

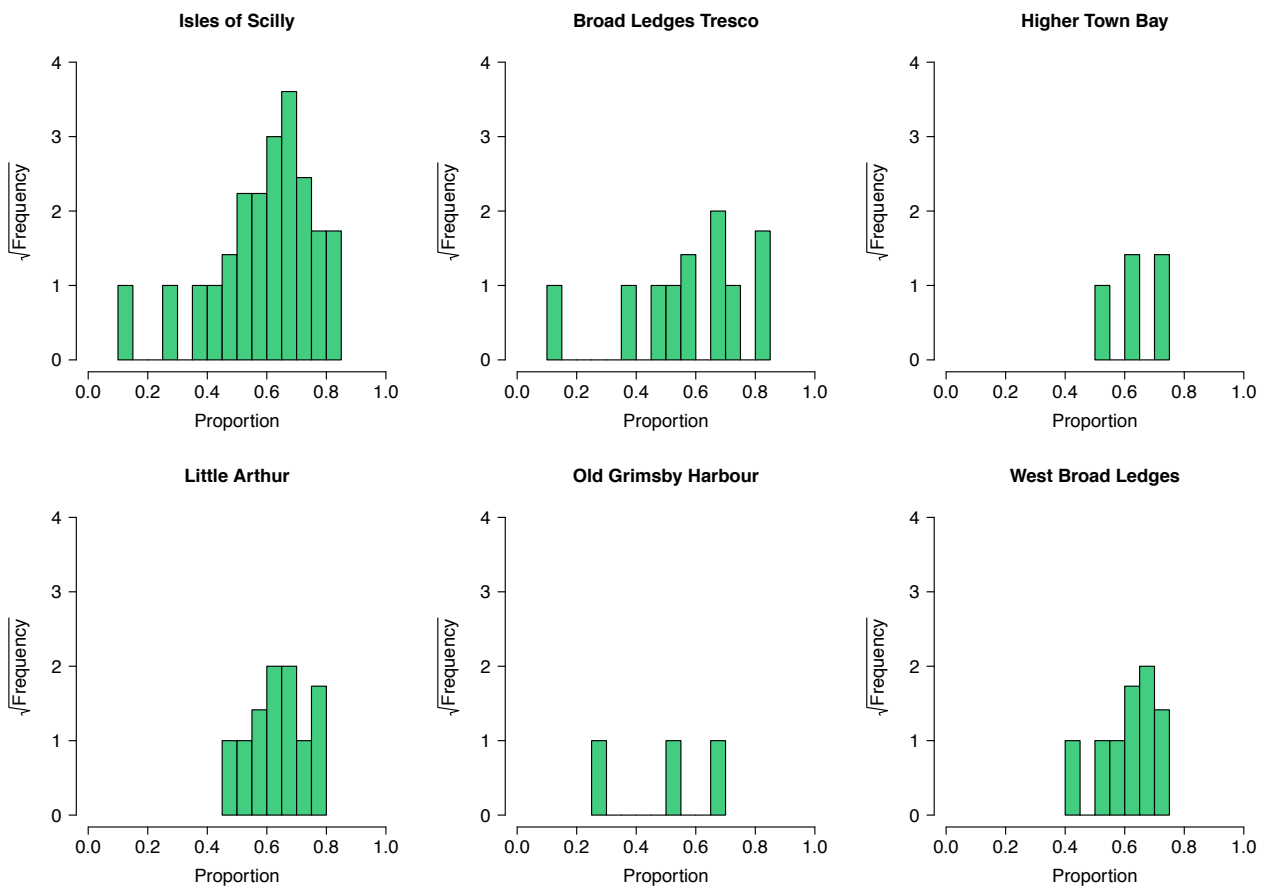


Figure 5 Frequency histogram of the proportion of infected eelgrass leaves recorded per 25 x 25cm quadrat at each of the five survey locations (Note square root frequency scale)

Disease prevalence can be ranked (highest to lowest) as Broad Ledges Tresco, Higher Town Bay (equal highest), West Broad Ledges, Little Arthur, and Old Grimsby Harbour. Estimates are given on a logit-transformed scale in Table 5a. Pairwise comparisons confirm the overall result that there are no statistically significant differences in disease prevalence between sites (Table 5b).

Table 5a Wasting disease prevalence summary (logit scale)

Site	blt	htb	la	ogh	wbl
Estimate	0.741	0.741	0.528	0.110	0.535
Std. Error	0.128	0.216	0.100	0.291	0.115

Table 5b Pairwise comparisons between sites (Tukey *post hoc* tests, $p < 0.05$ in bold)

Sites	Estimate	Std. Error	z value	p value
htb - blt	-0.000	0.251	-0.001	1.000
la - blt	-0.214	0.163	-1.313	0.666
ogh - blt	-0.631	0.318	-1.986	0.256
wbl - blt	-0.206	0.173	-1.196	0.739
la - htb	-0.213	0.238	-0.898	0.890
ogh - htb	-0.631	0.362	-1.743	0.388
wbl - htb	-0.206	0.245	-0.843	0.911
ogh - la	-0.418	0.308	-1.358	0.637
wbl - la	0.007	0.153	0.048	1.000
wbl - ogh	0.425	0.313	1.358	0.637

Epiphytes Distributions of average epiphyte scores across quadrats, at each of the sampling locations, are presented in Figure 6 and Table 6. There is a significant difference in the average epiphyte score per quadrat between survey sites ($F_{df=4} = 10.13, p < 0.001$).

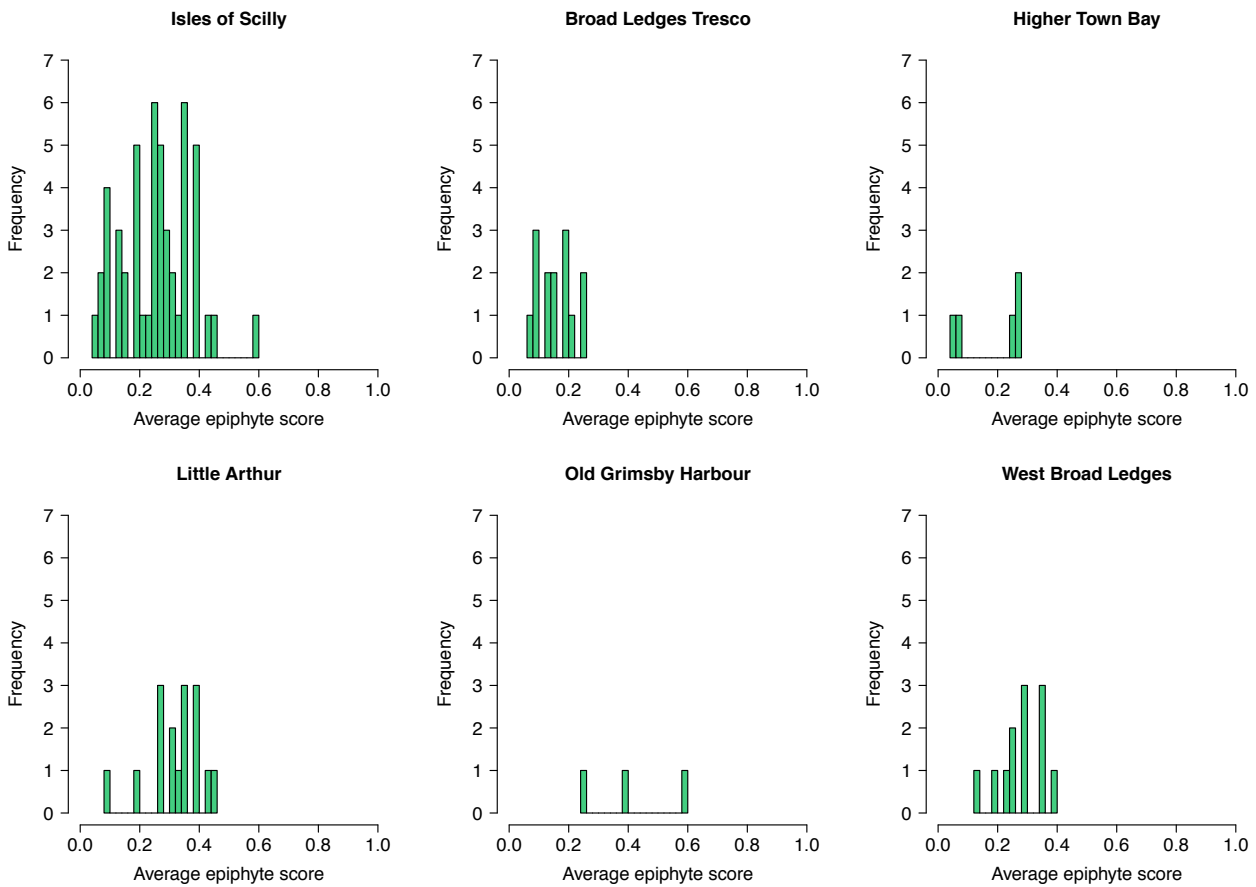


Figure 6 Frequency histogram of the average epiphyte score recorded per 25 x 25cm quadrat at each of the five survey locations

Epiphyte cover can be ranked (highest to lowest) as Old Grimsby Harbour, Little Arthur, West Broad Ledges, Higher Town Bay, and Broad Ledges Tresco. Estimates are given on a logit-transformed scale in Table 6a. Pairwise comparisons between sites shows that there are statistically significant differences between la and blt, ogh and blt, wbl and blt, la and htb, and between ogh ad htb (Table 6b).

Table 5a Epiphyte score summary (logit scale)

Site	blt	htb	la	ogh	wbl
Estimate	-1.816	-1.702	-1.224	-0.875	-1.256
Std. Error	0.094	0.157	0.088	0.202	0.101

Table 5b Pairwise comparisons between sites (Tukey *post hoc* tests, p < 0.05 in bold)

Sites	Estimate	Std. Error	z value	p value
htb - blt	0.139	0.315	0.440	0.992
la - blt	0.910	0.199	4.568	< 0.001
ogh - blt	1.302	0.271	4.813	< 0.001
wbl - blt	0.719	0.213	3.380	0.006
la - htb	0.772	0.282	2.739	0.045
ogh - htb	1.164	0.336	3.464	0.005
wbl - htb	0.580	0.291	1.991	0.257
ogh - la	0.392	0.231	1.695	0.421
wbl - la-	0.192	0.160	-1.200	0.740
wbl - ogh	-0.584	0.243	-2.403	0.107

4.2 Time series analysis, 1996 - 2017

Shoot counts Time series of shoot counts throughout the monitoring period, at each of the sampling locations, are presented in Figure 7 and Table 7. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.94,2.00} = 12.31, p < 0.001$) and specifically at Higher Town Bay, where shoot density has declined over about the last ten years, as well as Little Arthur, and Old Grimsby Harbour, where there is variation through time but with no overall trend (Figure 7).

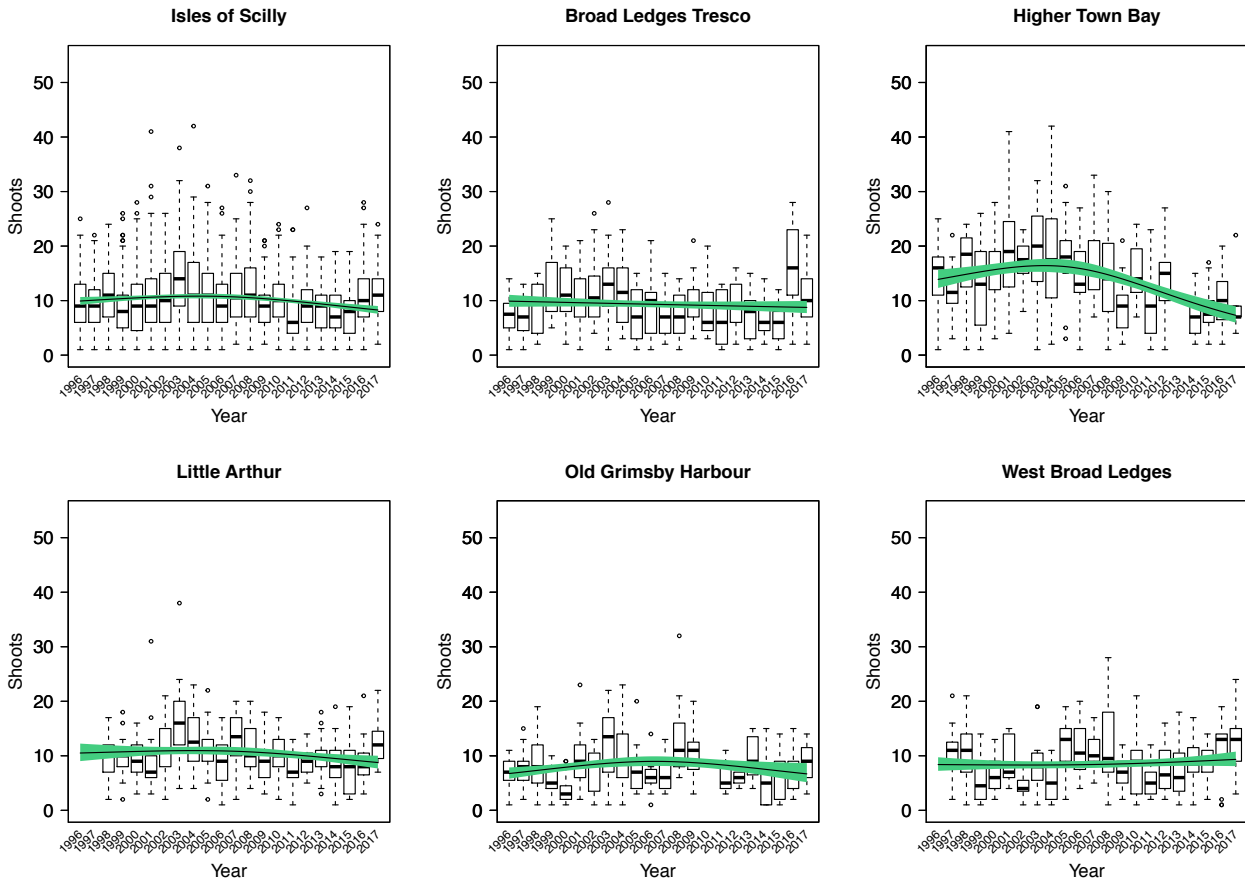


Figure 7 Time series of eelgrass shoot densities for all quadrats at each of the five survey sites, from 1996 to 2017. Box-whisker plots show median (centre line), interquartile range (box) and an additional 1.5 x interquartile range (whiskers), with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in green. Quadrats in which no eelgrass was recorded are excluded here.

Table 7 Shoot count time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{df=degrees\ of\ freedom}$	p-value
blt	$F_{df=1.004, 1.008} = 1.183$	0.275
htb	$F_{df=1.977, 1.999} = 40.08$	< 0.001
la	$F_{df=1.800, 1.960} = 2.923$	0.039
ogh	$F_{df=1.755, 1.940} = 5.456$	0.013
wbl	$F_{df=1.383, 1.620} = 0.196$	0.723

Canopy height Time series of canopy heights throughout the monitoring period, at each of the sampling locations, are presented in Figure 8 and Table 8. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.88, 1.99} = 7.46$, $p = 0.0013$) and specifically at Little Arthur, where canopy height has declined on average (Figure 8).

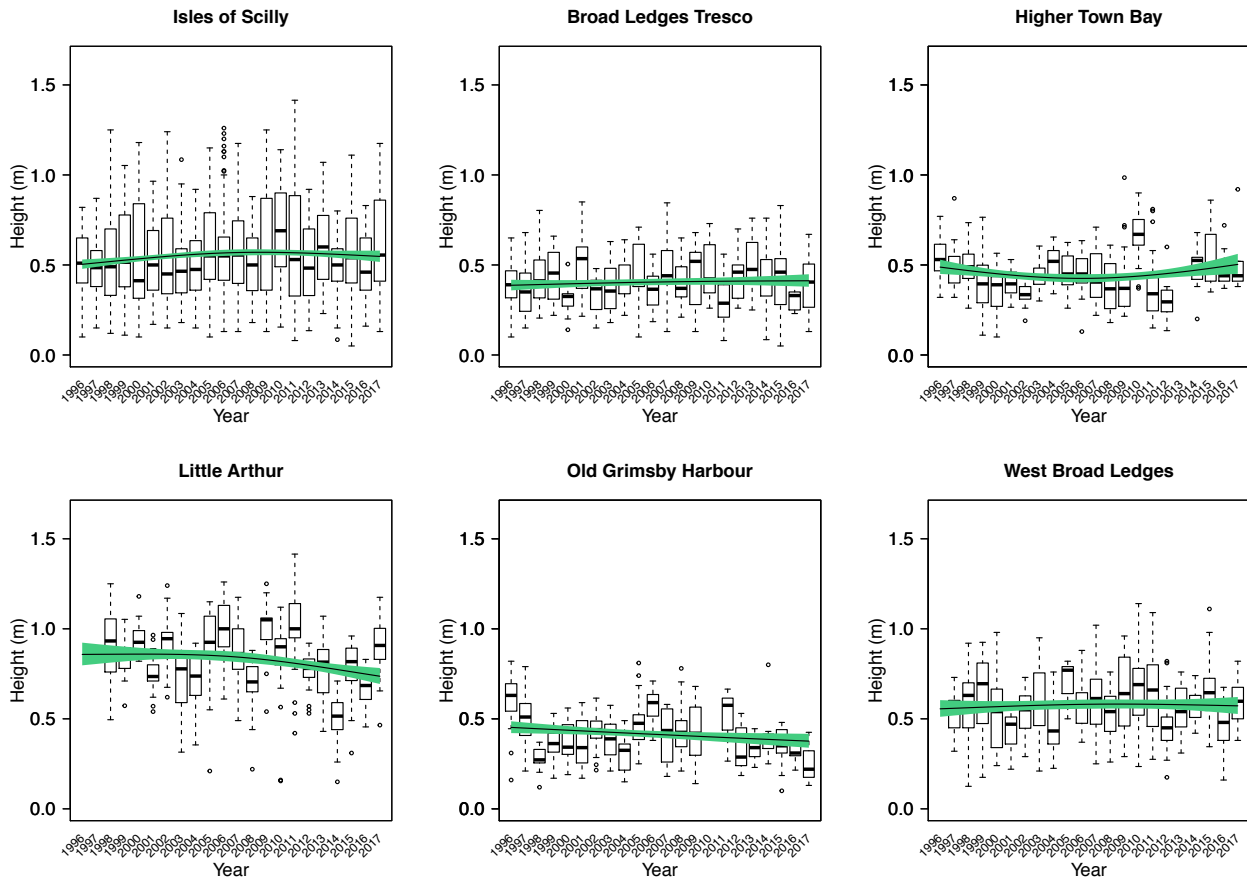


Figure 8 Time series of eelgrass ‘canopy heights’ for all quadrats at each of the five survey sites, from 1996 to 2017. Box-whisker plots show median (centre line), interquartile range (box) and an additional 1.5 x interquartile range (whiskers), with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in green. Quadrats in which no eelgrass was recorded are excluded here.

Table 8 Canopy height time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{df=degrees\ of\ freedom}$	p -value
blt	$F_{df=1.817, 1.967} = 3.181$	0.064
htb	$F_{df=1.806, 1.962} = 2.054$	0.107
la	$F_{df=1.913, 1.992} = 9.548$	< 0.001
ogh	$F_{df=1.001, 1.001} = 2.430$	0.119
wbl	$F_{df=1.082, 1.158} = 0.497$	0.559

Leaf analysis Time series of leaf area index (LAI) throughout the monitoring period, at each of the sampling locations, are presented in Figure 9 and Table 9. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.88, 1.99} = 7.46$, $p = 0.0013$) and specifically at Higher Town Bay and Little Arthur, where LAI has declined through time, as well as Old Grimsby Harbour, where there is variation through time but with no overall trend (Figure 9).

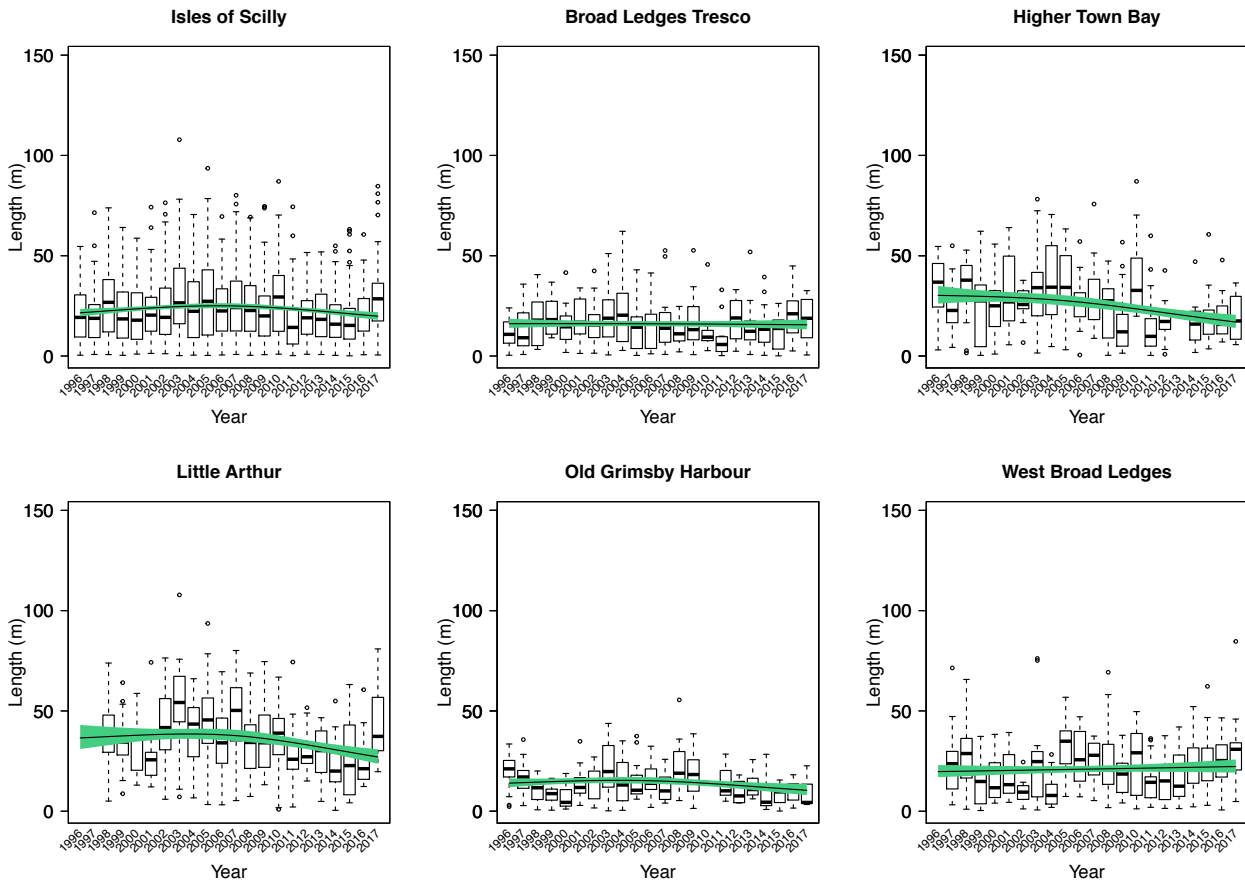


Figure 9 Time series of the ‘leaf area index’ (LAI) of eelgrass for all quadrats at each of the five survey sites, from 1996 to 2017. Box-whisker plots show median (centre line), interquartile range (box) and an additional 1.5 x interquartile range (whiskers), with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in green. Quadrats in which no eelgrass was recorded are excluded here.

Table 9 Leaf area index (LAI) time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{\text{degrees of freedom}}$	p-value
blt	$F_{df=1.764, 1.944} = 1.752$	0.189
htb	$F_{df=1.627, 1.861} = 9.852$	< 0.001
la	$F_{df=1.882, 1.986} = 7.881$	< 0.001
ogh	$F_{df=1.000, 1.001} = 12.25$	< 0.001
wbl	$F_{df=1.001, 1.002} = 0.306$	0.580

Eelgrass ‘patchiness’ Time series of quadrat occupancies throughout the monitoring period, at each of the sampling locations, are presented in Figure 10 and Table 10. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.00,1.00} = 13.77, p < 0.001$) and specifically at Higher Town Bay and Old Grimsby Harbour, where quadrat occupancy has declined through time (Figure 10).

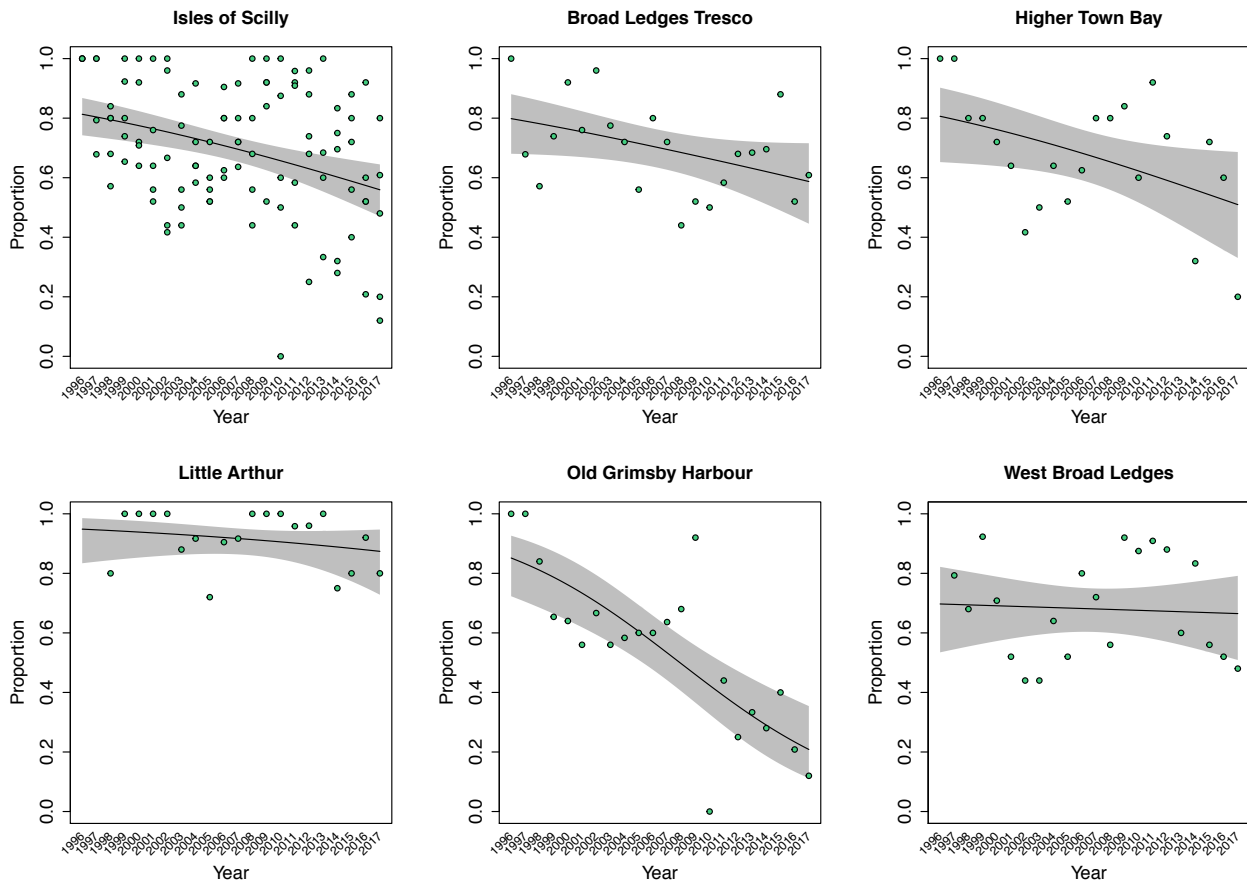


Figure 10 Time series of the proportion of occupied quadrats at each of the five survey sites, from 1996 to 2017. Green points indicate proportions of quadrats occupied at each site. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in grey.

Table 10 Quadrat occupancy time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{df=degrees\ of\ freedom}$	p-value
blt	$F_{df=1.035, 1.069} = 3.966$	0.062
htb	$F_{df=1.000, 1.000} = 4.368$	0.049
la	$F_{df=1.000, 1.000} = 0.984$	0.333
ogh	$F_{df=1.000, 1.000} = 21.52$	< 0.001
wbl	$F_{df=1.000, 1.000} = 0.066$	0.800

Wasting disease Time series of the number of infected leaves per quadrat throughout the monitoring period, at each of the sampling locations, are presented in Figure 11 and Table 11. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.97,2.00} = 43.44$, $p < 0.001$) and specifically at Old Grimsby Harbour, where disease prevalence has increased through time, as well as Higher Town Bay and West Broad Ledges where there is variation through time but with no overall trend (Figure 11).

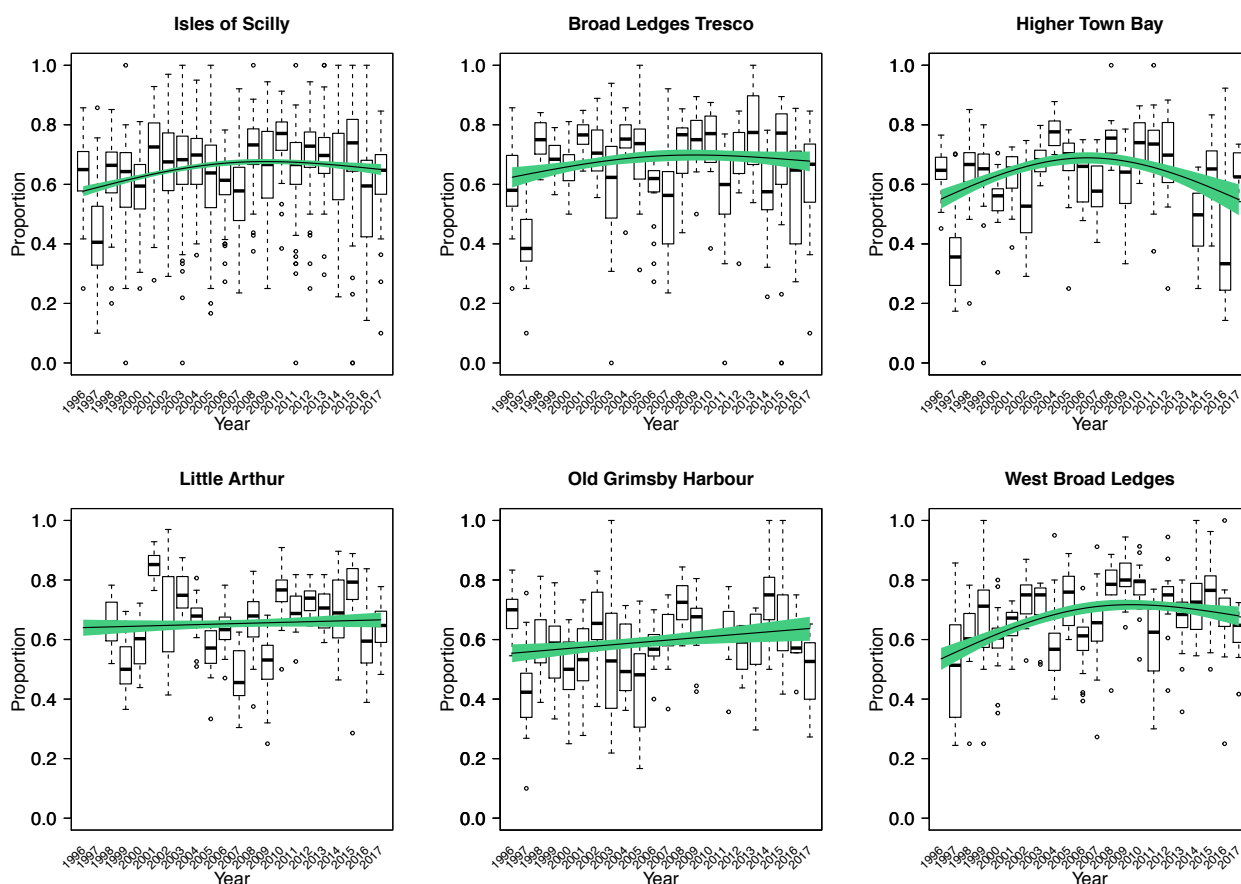


Figure 11 Time series of the disease prevalence per quadrat at each of the five survey sites, from 1996 to 2017. Box-whisker plots show median (centre line), interquartile range (box) and an additional 1.5 x interquartile range (whiskers), with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in green. Quadrats in which no eelgrass was recorded are excluded here.

Table 11 Disease prevalence time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{\text{degrees of freedom}}$	p-value
blt	$F_{df=1.780, 1.952} = 4.105$	0.035
htb	$F_{df=1.980, 2.000} = 31.16$	< 0.001
la	$F_{df=1.000, 1.001} = 1.554$	0.213
ogh	$F_{df=1.711, 1.917} = 11.16$	< 0.001
wbl	$F_{df=1.947, 1.997} = 27.92$	< 0.001

Epiphytes Time series of the average epiphyte score per quadrat throughout the monitoring period, at each of the sampling locations, are presented in Figure 12 and Table 12. There is a significant nonlinear trend overall across the Isles of Scilly ($F_{df=1.97,2.00} = 43.44$, $p < 0.001$) which is evident at all sites (Table 12) and shows an increase through approximately the first half of the survey period, followed by a decline (Figure 12).

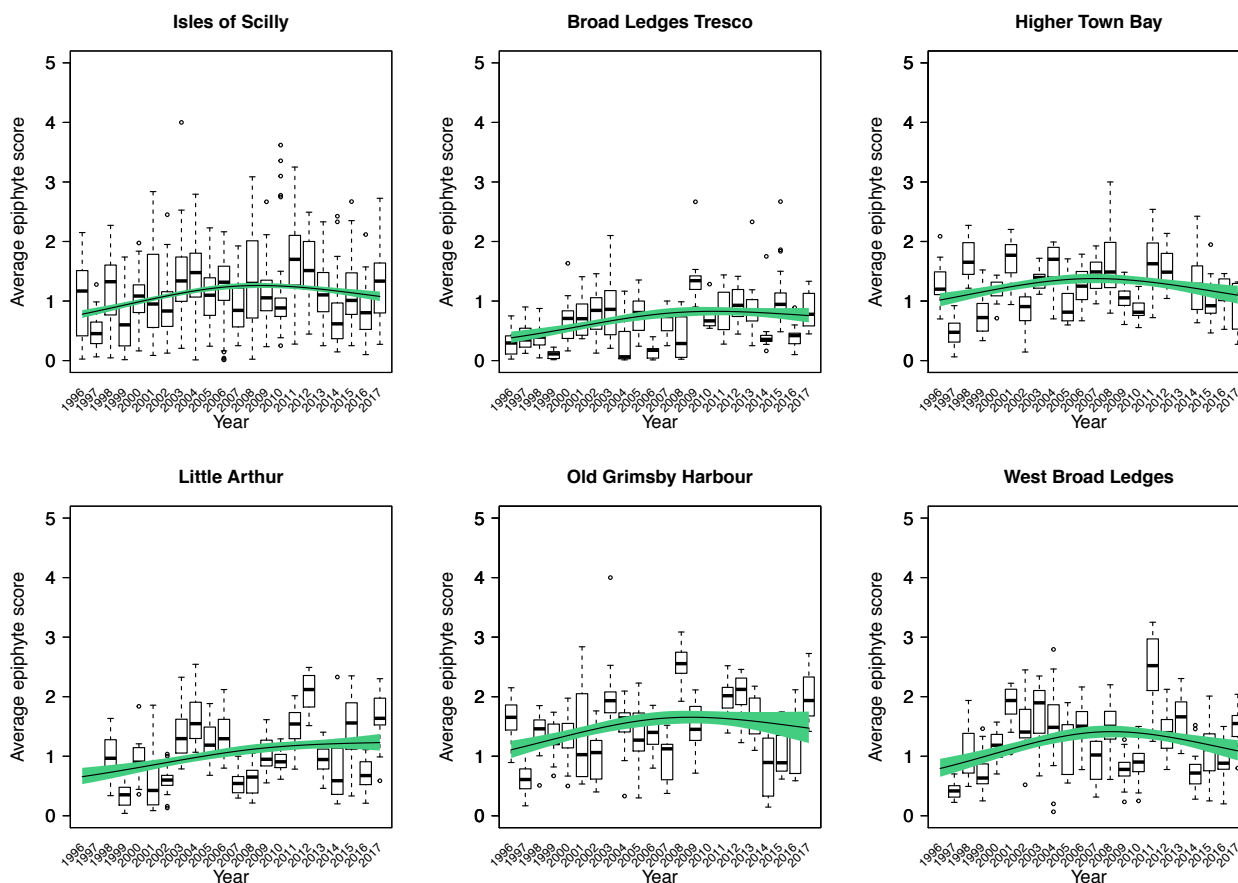


Figure 12 Time series of the average epiphyte scores per quadrat at each of the five survey sites, from 1996 to 2017. Box-whisker plots show median (centre line), interquartile range (box) and an additional 1.5 x interquartile range (whiskers), with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model smooth, using cubic splines). Trend lines are surrounded by 95% confidence envelopes in green. Quadrats in which no eelgrass was recorded are excluded here.

Table 12 Epiphyte score time series (1996-2017) summary ($p < 0.05$ in bold)

Site	$F_{df=degrees\ of\ freedom}$	p-value
blt	$F_{df=1.877, 1.985} = 10.13$	< 0.001
htb	$F_{df=1.937, 1.996} = 7.482$	0.001
la	$F_{df=1.466, 1.715} = 15.50$	< 0.001
ogh	$F_{df=1.977, 1.999} = 16.81$	< 0.001
wbl	$F_{df=1.966, 1.999} = 20.11$	< 0.001

5.1 Key findings

The core metric recorded in this survey is **shoot density**, which is by far the most common measurement of density (as opposed to extent) used worldwide. Observed trends show shoot density peaking around 2005, then declining at a constant proportional rate thereafter (Figure 7). Therefore, we quantified annual change through log-linear regression from 2005 onwards, estimating average annual changes as: blt = +1.9%, htb = -6.0%, la = -1.4%, ogh = -1.7%, wbl = -1.2%. The change since a given number of years in the past can be calculated using the formula $N = N_0(1 + r)^t$, where N is the shoot density today, N_0 is the shoot density in the starting year, r is the annual change estimate, and t is the number of years elapsed (here, $t = 12$). Based on this estimation, overall percentage changes at each of the monitoring sites **since 2005** are:

Broad Ledges Tresco: 25.9% increase, **Higher Town Bay: 52.5% decline**, Little Arthur: 15.5% decline, Old Grimsby Harbour: 18.1% decline, West Broad Ledges: 13.3% decline. (Declines greater than 20% in bold.)

The other key estimator of eelgrass abundance is '**patch occupancy**', measured as the proportion of sampled quadrats with eelgrass, as opposed to bare sand. Unlike shoot density, patch occupancy probability trends have remained constant since the beginning of our monitoring. (Figure 10). Overall percentage changes at each of the site monitoring sites **since monitoring began in 1996** are:

Broad Ledges Tresco: 21.2% decline, **Higher Town Bay: 29.9% decline**, Little Arthur: 7.2% decline, **Old Grimsby Harbour: 60.3% decline**, West Broad Ledges: 3.2% decline. (Declines greater than 20% in bold.)

These overall findings are extremely concerning on two counts. First, precipitous declines have been observed across several sites using both the shoot density and patch occupancy metrics. Second, trends in shoot density and patch occupancy differ substantially. This suggests dynamics at these two spatial scales are decoupled, with different drivers likely causing the declines in each metric. While it is becoming increasingly urgent to identify the causes of these declines, it seems likely that multiple threats operate between survey sites and across spatial scales.

In some sense, this is not surprising: trends are likely to differ between survey sites as they experience differential impacts from human and natural stressors. Also, trends are likely to differ when measured through shoot density or patch occupancy as the relative influence of flowering versus rhizome extension operate at different spatial scales. We suggest that a multi-faceted approach to understanding multi-scale dynamics will be needed to disentangle the causes of eelgrass decline. A combination of spatiotemporal analysis, predictive risk modelling, and population genetics will be needed to provide effective evidence-based habitat management within the Isles of Scilly SAC.

5.2 Individual site summaries

Broad Ledges Tresco We previously reported that 2016 was a highly unusual one at this site (Bull & Kenyon 2017). Exceptionally high shoot density was only partially offset by lower than typical canopy height, resulting in a reprieve from the substantial drop in productivity (as measured

by leaf area index). Although not as great as the previous year, 2017 was again an above average year for Broad Ledges Tresco. It is important to continue to closely monitor this site to see if this is transient, especially as no obvious cause for recent high shoot density is apparent.

Higher Town Bay This site continues to show a serious decline in shoot density, now having **exceeded 50% reduction** since SAC designation in 2005. Higher Town Bay typically has shorter plants than other sites, which is consistent with it being the shallowest site and is not, in itself, a cause for concern. As a result, a significant decrease in shoot density over the years underpins a decrease in productivity (leaf area index). The decline in patch occupancy is even more worrying. While there has been a 30% drop in the long term average occupancy since 2005, in fact 2017 was itself an outlier in this trend, with **80% absence** of eelgrass (Figure 10). This site is one of two that is particularly in trouble (the other being Old Grimsby Harbour).

Little Arthur Whilst 'patch occupancy' was relatively low in 2017 by the standards expected for this site, Little Arthur remains the site with the most continuous expanse of eelgrass on our survey. In addition, both shoot density and canopy height were above average this year. Overall, recent declines in leaf area index have been overturned this year and the Little Arthur site is of least concern in our monitoring programme. However, we caution that one good year, against a backdrop of long term decline should not lull us into complacency.

Old Grimsby Harbour Trends at Old Grimsby Harbour are strikingly different to all other monitored locations around the Isles of Scilly. This site has shown a significant decrease in shoot density, canopy height or leaf area index much in line with other sites. However, where eelgrass is present, declines are not as great as at some other sites. The observation that sets Old Grimsby Harbour apart is the **60% decline in patch occupancy** since our monitoring began in 1996 (Figure 10), with no signs of this abating.

West Broad Ledges This site shows the lowest levels of long term decline in both shoot density and patch occupancy (Figures 7 and 10). However, we note that the last three years (2015-2017) show consistent decreases in patch occupancy, taking 2017 to the third lowest level since our monitoring began in 1996.

5.3 Wasting disease

It is interesting that wasting disease has remained evident at relatively low but persistent levels, suggesting an endemic state. Across the north Atlantic, wasting disease is notable for periodic large scale epidemic outbreak. To understand this conflicting situation, further research beyond the remit of this study would be needed. In this year's report, for the first, time we have analysed the long term trends in wasting disease prevalence. Statistically significant nonlinear trends in disease prevalence are seen at Higher Town Bay, Little Arthur, and Old Grimsby Harbour. Interestingly, trends differ between sites (Figure 11), suggesting local influences have a substantial role to play in disease dynamics.

5.4 Epiphyte cover

This is also the first annual report where we analyse long term trends in epiphyte cover. In contrast to wasting disease, epiphyte cover has shown a very similar nonlinear trend at all sites in our survey, increasing through approximately half of our monitoring period, and declining thereafter

(Figure 12). This pattern is very similar to long term changes in eelgrass shoot density but further in-depth research would be needed to understand the relationship between eelgrass and epiphytes in the Isles of Scilly.

5.5 *Sargassum muticum*

This invasive species has spread along the south and west coasts of the UK and has been a regular feature of the Isles of Scilly eelgrass survey for several years. We do not formally quantify distributions of *S. muticum* as part of this project but can report that the species was present at all surveyed sites but was not strikingly more prevalent than in previous years. It is debatable how much of an impact this invasive is likely to have on eelgrass: while shading might negatively impact on eelgrass, direct competition for space between the two species seems unlikely as *S. muticum* requires a hard substrate to establish.

5.6 Synthesis

Twenty-two years of continuous monitoring represents a globally important long-term dataset. This length and intensity of monitoring is necessary to uncover sustained trends in abundance and distribution of populations and biological communities. Worryingly, the picture for eelgrass around the Isles of Scilly is one of decline across the archipelago. Despite its envious position far from sources of pollution and many other direct human impacts, there is serious cause for concern about the status of *Zostera marina* in the Isles of Scilly Special Area of Conservation.

We are very grateful to Natural England for their major contribution to essential survey costs this year. More than ever, we are indebted to Lisa at The Bylet for putting us up and putting up with us. As usual, Island Carriers went the extra mile in helping us move kit and launch (and recover!) our rib. We are also grateful to Dave McBride of Dive Scilly and Jolene Williams of Moonshadow Diving for their assistance with air fills and allowing us to leave cylinders at their air station. Every year financial and logistical constraints present serious challenges to the continuation of this survey and we are always indebted to the many residents of the Isles of Scilly who help us overcome these issues and make the survey a success.

- 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.
- 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 (2017) Isles of Scilly eelgrass voluntary monitoring programme: 2016 annual report. Natural England Evidence Project Report, RP02939.
- 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.
- 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 Algol* 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.
- 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.
- 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.
- Irvine MA, Bull JC, Keeling MJ (2016a) Aggregation dynamics explain vegetation patch-size distributions. *Theoretical Population Biology* 108: 70-74.

7 REFERENCES

Irvine MA, Jackson EL, Kenyon EJ, Cook KJ, Keeling MJ, Bull JC (2016b) Fractal measures of spatial pattern as a heuristic for return rate in vegetative systems. *Royal Society Open Science* 3(3): 150519.

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.

Jones BLJ, Cullen-Unsworth, LC, Unsworth RK (2018) Tracking nitrogen source using $\delta^{15}\text{N}$ reveals human and agricultural drivers of seagrass degradation across the British Isles. *Frontiers in Plant Science* 9, 133.

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.

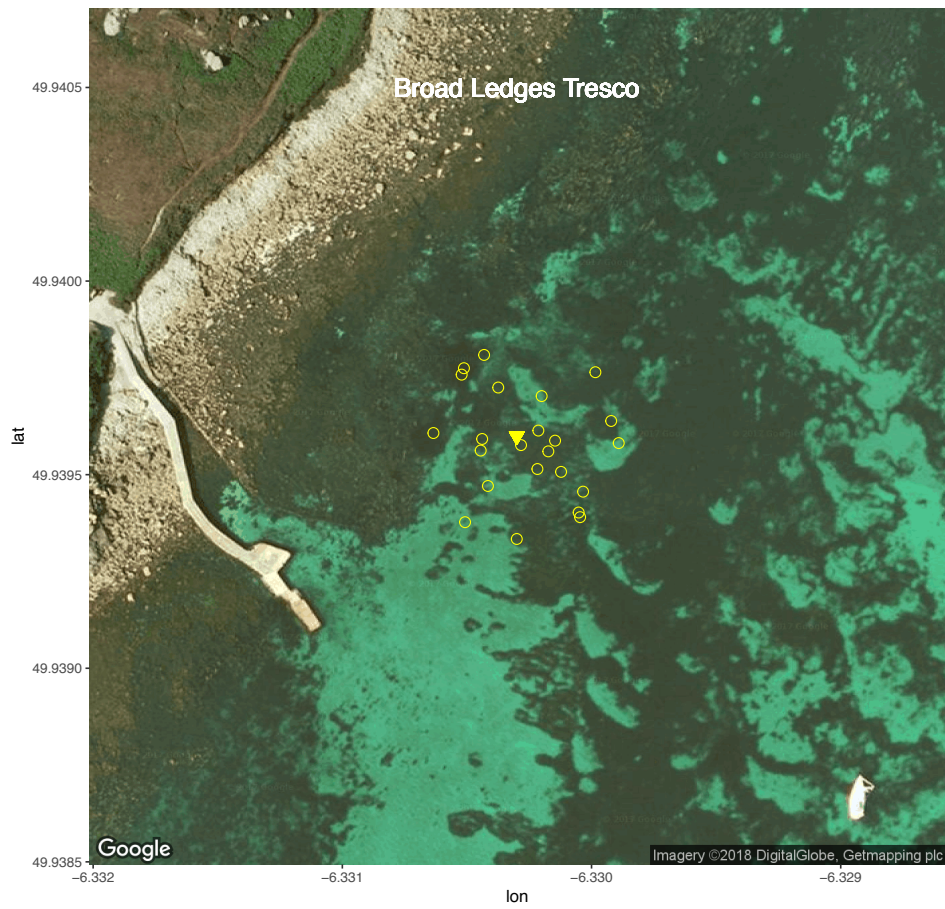
Piazzi L, Cinelli F (2000) Effects of the spread of the introduced Rhodophyceae *Antithamnion preissii* and *Womersleyella setacea* on the macroalgal community of *Posidonia oceanica* rhizomes in the western Mediterranean Sea. *Cryptogam. Algol.* 21: 291-300.

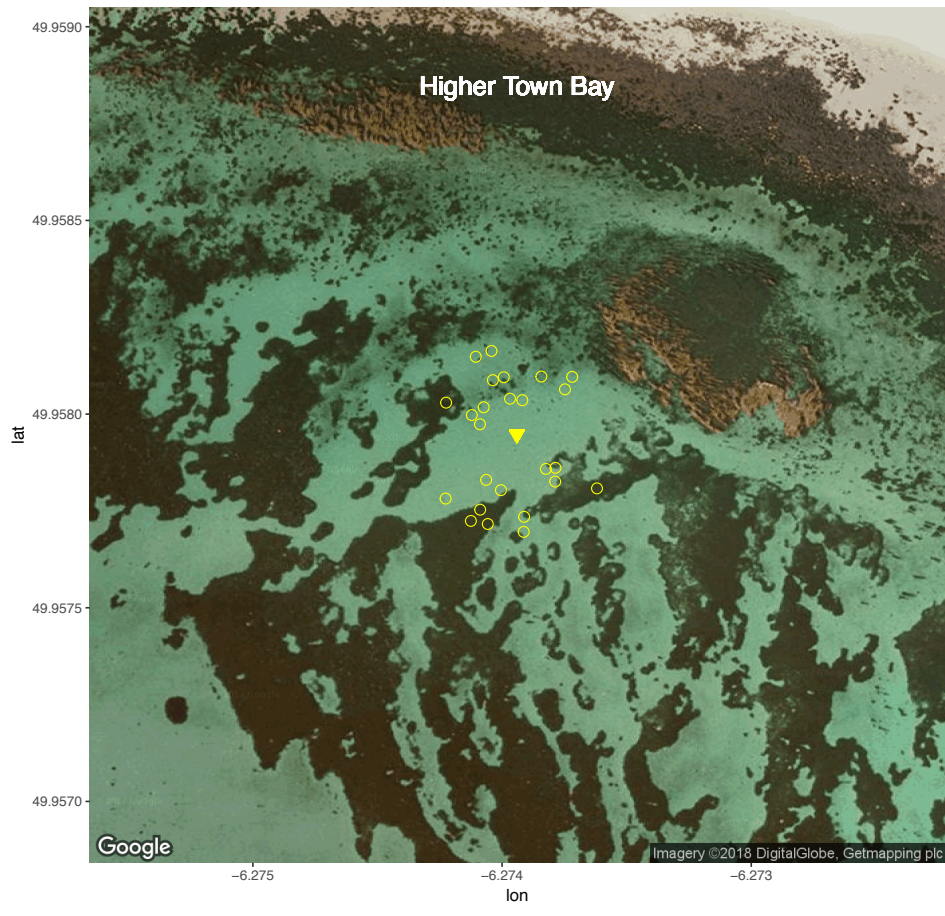
Potouroglou M, Kenyon EJ, Gall A, Cook KJ, Bull JC (2014) The roles of flowering, overwinter survival and sea surface temperature in the long-term population dynamics of *Zostera marina* around the Isles of Scilly, UK. *Marine Pollution Bulletin* 83: 500-507.

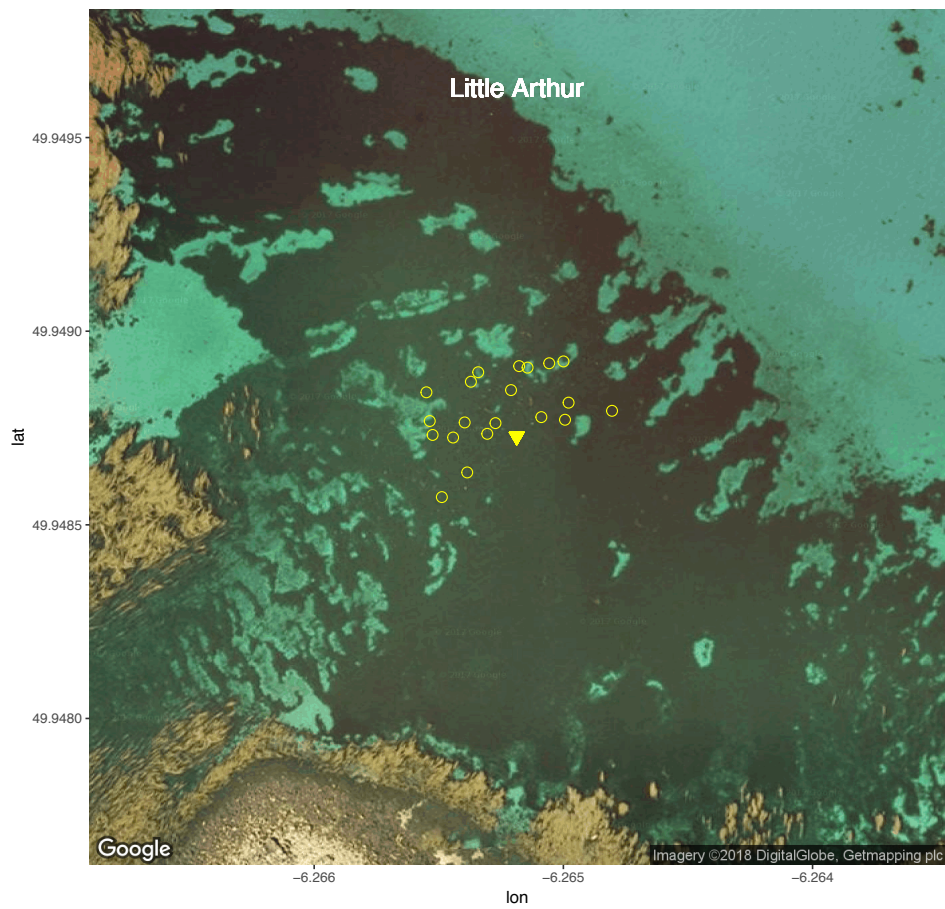
7 REFERENCES

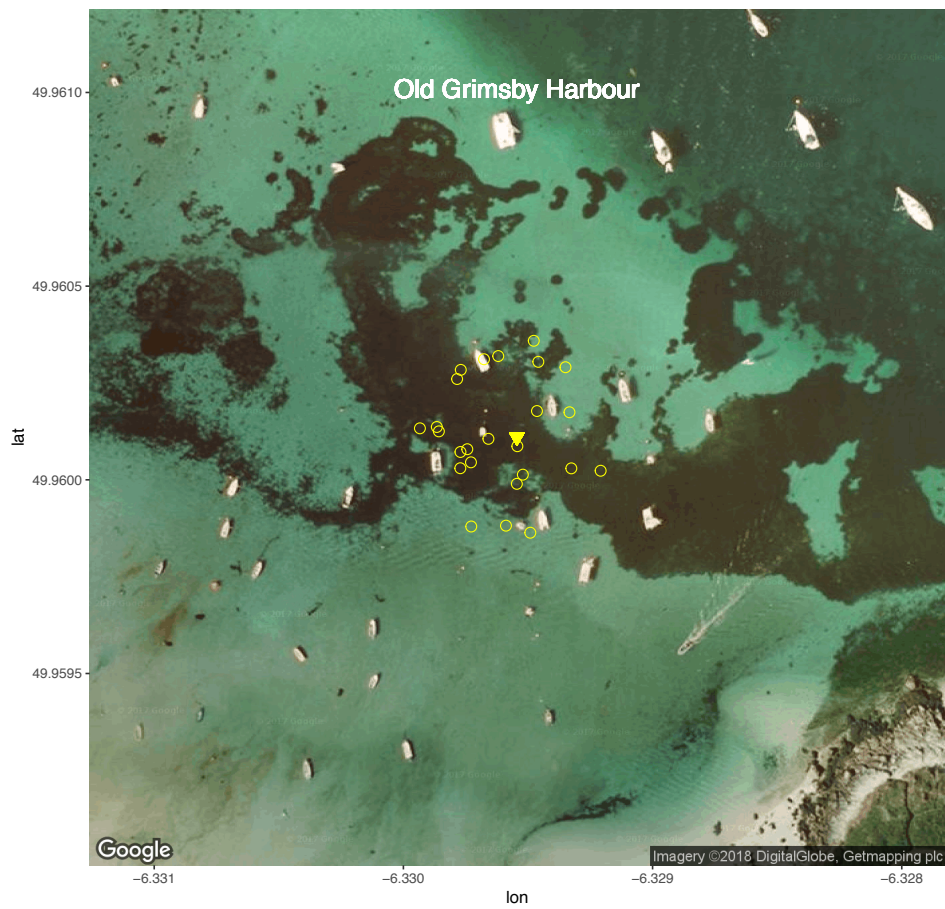
- Potouroglou M, Bull JC, Krauss KW, Kennedy HA, Fusi M, Daffonchio D, Mangora MM, Githaiga MN, Diele K, Huxham M, (2017) Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports* 7: 11917.
- R Core Team (2016) R: A language and environment for statistical computing. 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.
- 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 Sci.* 8: 1309.
- van der Heide T, Eklöf JS, van Nes EH, van der Zee EM, Donadi S, et al. (2012) Ecosystem engineering by seagrasses interacts with grazing to shape an intertidal landscape. *PLoS ONE* 7: e42060.
- 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.

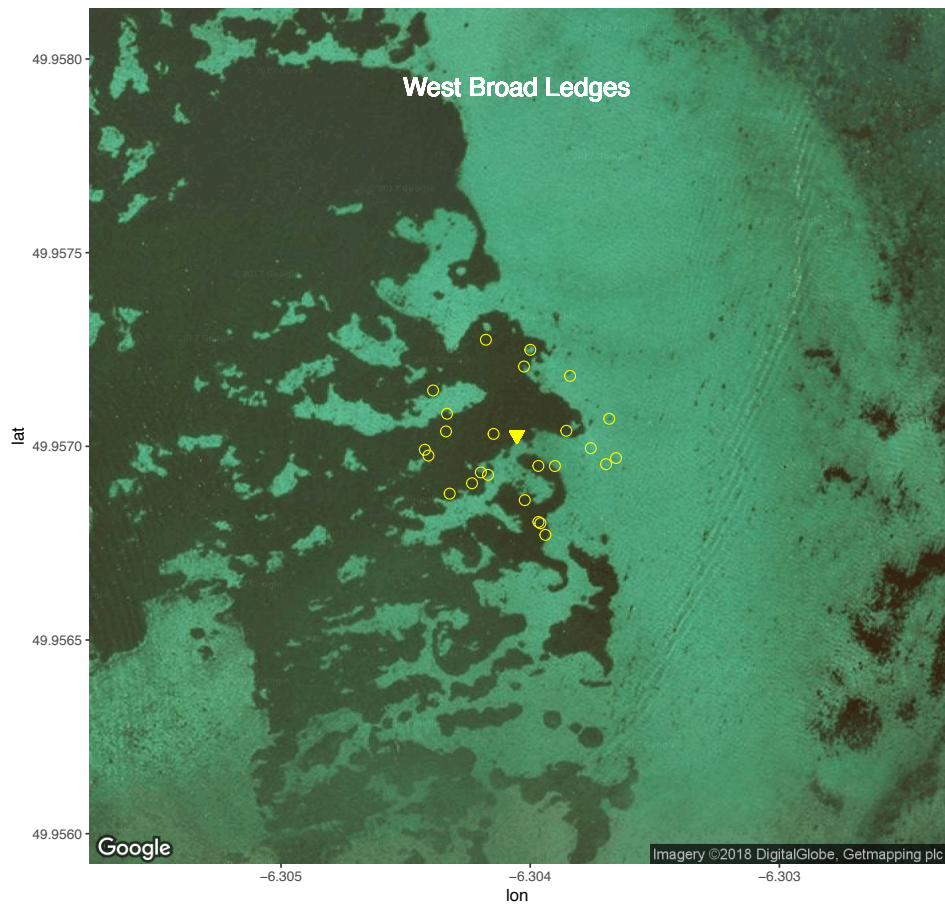
Appendix 1 - Locations of quadrats used in the 2017 survey. Yellow triangles show the central datum (anchor) for each survey. Yellow circles show individual quadrats (not to scale, quadrats do not overlap). Google Earth images are from 2005 so these are primarily illustrative to give an indication of the spatial scale of seagrass patchiness in relation to our survey and care should be taken over interpretation. It should also be noted that not all the 'dark' patches in the photos necessarily represent seagrass. Kelp is also present at these locations and, to a lesser extent, submerged rocks.











Appendix 2 - Summary data

Broad Ledges Tresco

quadrant	distance / m	bearing / deg	number of shoots	median canopy height / cm	lower quartile canopy height	upper quartile canopy height	median leaves per shoot	lower quartile leaves per shoot	upper quartile leaves per shoot	median infected leaves per shoot	lower quartile infected leaves per shoot	upper quartile infected leaves per shoot	median average epiphyte score	lower quartile average epiphyte score	upper quartile average epiphyte score
1	25.1	338	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	29.6	142	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	23.7	318	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	24	272	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	29.6	180	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	24.9	130	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	27.5	81	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	29.4	94	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	28.3	141	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	10.1	116	15	51	18	80	3	1	5	3	0	3	0.8	0	1.77
11	24.7	322	2	13	11	14	2	2	2	1	0	1	1.25	0.54	1.96
12	16.6	210	16	53	10	72	4	1	4	2	0	3	0.5	0	1
13	10	265	9	43	22	63	4	3	5	2	1	3	1	0.69	1.95
14	11.2	148	13	38	21	54	4	3	5	3	2	4	0.67	0.15	1.57
15	11.2	248	7	41	21	45	4	3	4	3	2	4	1	0.29	1.28
16	14.9	339	22	37	16	48	4	2	5	3	1	4	1.29	0.88	1.87
17	28.9	211	8	26	13	37	4	3	5	3	0	4	1.1	0.38	1.71
18	2.9	155	3	26	22	45	4	3	4	2	0	2	0.5	0.5	0.66
19	13.5	32	11	40	14	62	4	1	5	3	0	3	0.33	0	1.31
20	29.1	51	3	13	8	13	3	3	3	0	0	0	1	1	1
21	6.4	76	9	48	36	71	4	3	5	2	1	4	0.67	0.12	0.96
22	11.1	97	14	50	25	75	4	2	5	2	1	4	0.78	0.08	1.42
23	16.4	129	11	67	44	79	5	4	5	2	2	3	0.5	0.29	1.14

Higher Town Bay

quadrant	distance / m	bearing / deg	number of shoots	median canopy height / cm	lower quartile canopy height	upper quartile canopy height	median leaves per shoot	lower quartile leaves per shoot	upper quartile leaves per shoot	median infected leaves per shoot	lower quartile infected leaves per shoot	upper quartile infected leaves per shoot	median average epiphyte score	lower quartile average epiphyte score	upper quartile average epiphyte score
1	28.2	208	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	11	285	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	22.9	44	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	28.1	176	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	12.3	309	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	25.2	332	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	27.6	228	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	17	336	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	27.1	198	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	14.7	131	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	16.8	347	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	18	23	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
13	14.1	293	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
14	25	343	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
15	10.4	349	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
16	18.9	47	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
17	9.9	9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
18	27.8	124	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	17.5	141	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
20	13	140	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
21	22.3	294	7	41	14	43	4	2	4	2	0	3	0.25	0.04	0.47
22	23.8	175	9	92	40	102	4	2	5	3	1	4	1.33	0.6	2.11
23	16.7	196	22	44	28	55	4	3	5	3	2	4	1.33	0.42	2.12
24	24.1	206	4	38	21	45	4	4	4	2	1	3	1.25	0.07	1.96
25	15.8	214	7	52	38	70	5	4	5	3	2	3	0.4	0.25	0.97

Little Arthur

quadrant	distance / m	bearing / deg	number of shoots	median canopy height / cm	lower quartile canopy height	upper quartile canopy height	median leaves per shoot	lower quartile leaves per shoot	upper quartile leaves per shoot	median infected leaves per shoot	lower quartile infected leaves per shoot	upper quartile infected leaves per shoot	median average epiphyte score	lower quartile average epiphyte score	upper quartile average epiphyte score
1	21.5	329	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	20.2	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	20	9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	28.4	75	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	25.4	280	14	77	64	96	4	3	18	3	2	11	2	1.7	2.84
6	13.4	353	11	118	43	128	4	2	21	2	1	3	1.33	0.62	2.67
7	20.5	320	15	86	52	100	4	2	5	2	0	3	1.4	0.56	1.72
8	8.5	275	22	93	30	112	4	3	5	2	0	3	1.62	0.84	2.12
9	14.7	71	16	99	24	117	4	2	5	2	0	3	2	0.69	2.81
10	7.2	302	9	88	29	99	4	3	5	3	1	3	1.6	1.05	1.95
11	15.5	285	14	117	76	131	4	3	5	3	1	4	0.45	0.06	1.2
12	23	24	27	104	45	135	4	2	38	3	1	24	1.75	0.91	3.83
13	18.3	269	14	96	69	109	4	3	5	2	0	3	2	0.78	2.64
14	17.8	57	10	104	83	121	4	3	15	3	2	6	2.27	1.69	3.19
15	25.4	32	14	102	57	128	4	3	33	3	2	12	1.8	1.33	3.31
16	28.9	296	11	80	48	105	5	2	5	3	1	4	1	0.47	1.36
17	17.6	234	12	46	17	56	3	2	5	2	1	4	1.73	0.64	2.31
18	27.7	231	9	88	44	102	4	3	5	3	2	4	1.6	0.78	2
19	24.2	271	10	65	46	68	4	3	5	3	1	3	1.32	1	2.69
20	9	52	7	86	28	94	5	3	6	3	2	4	2.25	0.66	2.74

Old Grimsby Harbour

quadrant	distance / m	bearing / deg	number of shoots	median canopy height / cm	lower quartile canopy height	upper quartile canopy height	median leaves per shoot	lower quartile leaves per shoot	upper quartile leaves per shoot	median infected leaves per shoot	lower quartile infected leaves per shoot	upper quartile infected leaves per shoot	median average epiphyte score	lower quartile average epiphyte score	upper quartile average epiphyte score
1	25.7	187	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	14.7	256	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	25.1	320	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	18.6	241	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	23.9	314	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	24.4	35	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	16.8	255	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	27.8	172	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	24.2	337	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	26	112	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	28	275	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	28	10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
13	23.2	277	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
14	8.2	266	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
15	18.1	120	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
16	15.1	241	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
17	9.4	38	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
18	22.5	274	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	28.9	207	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
20	13.5	180	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
21	23.8	347	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
22	11	171	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
23	2.7	177	3	22	16	41	4	2	4	0	0	2	1.25	1.01	1.96
24	22.4	16	9	13	9	26	2	1	4	2	0	3	2	0.8	3
25	16.7	65	14	42	18	51	4	3	5	2	0	3	3	1.33	4.06

West Broad Ledges

quadrant	distance / m	bearing / deg	number of shoots	median canopy height / cm	lower quartile canopy height	upper quartile canopy height	median leaves per shoot	lower quartile leaves per shoot	upper quartile leaves per shoot	median infected leaves per shoot	lower quartile infected leaves per shoot	upper quartile infected leaves per shoot	median average epiphyte score	lower quartile average epiphyte score	upper quartile average epiphyte score
1	6.7	273	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	27.3	298	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	27	108	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	22.9	42	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	28.8	342	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	19.8	6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	14.1	216	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	29.8	164	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	25.7	166	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	26.1	257	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	26.2	165	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	24.8	9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
13	25.6	229	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
14	10.8	145	18	61	17	76	5	2	6	3	0	4	1.8	0.43	2.12
15	27	80	13	50	28	63	4	4	5	3	2	3	1	0.64	2
16	14.1	129	15	60	35	75	4	3	5	2	1	3	1.75	1.2	2.28
17	14.3	85	24	82	44	93	4	3	5	3	1	4	2	1.43	2.5
18	18.8	173	3	38	36	46	4	4	4	2	1	2	1.5	1.02	2.21
19	21	287	14	63	26	88	4	3	24	3	1	15	1.32	0.22	2.66
20	18.9	223	7	72	54	87	4	3	5	3	2	4	1.5	1	2.42
21	21.6	100	11	72	43	92	4	3	5	2	2	3	1.75	1.27	2.42
22	29.3	103	14	59	30	71	4	3	26	3	2	18	1.5	1.08	2.82
23	14.9	224	15	50	19	72	4	3	5	3	1	4	1.25	0.18	2.13
24	20.4	273	5	60	52	73	4	4	29	3	2	13	1.25	1	2.18
25	26.8	261	12	44	22	59	3	2	5	2	1	4	0.67	0.33	1.36