Isles of Scilly eelgrass bed voluntary monitoring programme

2019 Annual Survey

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In association with Project Seagrass

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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 this year's survey, as well as their place in continuous time series from 1996, are presented and analysed. This represents twenty-four years of continuous annual monitoring around the Isles of Scilly.

Overall, eelgrass was present at all five survey sites around the Isles of Scilly but we found significant variation in shoot density between survey sites this year. Longer-term trends reveal that considerable annual fluctuations in shoot density show no consistent changes through time across the Isles of Scilly.

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 linear trends in canopy height were found at three sites. At Little Arthur a slight decrease is evident; whereas at Broad Ledges Tresco a slight increase is observed.

Shoot density, number of leaves per shoot, 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, with Little Arthur the most productive and Broad Ledges Tresco the least (per occupied quadrat). Long-term declines in productivity are observed at Higher Town Bay, with the other sites remaining relatively stationary.

The proportion of pre-determined quadrats located on eelgrass versus bare sand is used as a measure of patchiness. Analysis of long-term trends showed that there have been significant declines in patch occupancy at Old Grimsby Harbour (66% loss) and concerning losses at Higher Town Bay (22% decline).

Long-term changes in wasting disease and epiphyte cover have been observed but without any clear, linear trend. Interestingly, across the whole length of the survey, wasting disease prevalence and epiphyte cover both differ significantly between survey sites. However, trends in disease and epiphyte community are not the same more research would be needed to explore the drivers of these dynamics.

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 again 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. However, analysis of long-term trends at different scales point to patch creation and loss, rather than within-patch dynamics, as the key processes to focus on to identify causes of decline.

2.1 Seagrass

Seagrasses are globally dispersed along coastlines, covering approximately 0.3 to 0.6 million km^2 (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-Jenson 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 the 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 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, including algae as well as 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 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) 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 in the last year. However, there was substantial work to extend the main quay in Hugh Town, St. Mary's in recent few years. 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 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 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. This site is accessible for sampling at most states of the tide although currents present a challenge at certain times.

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 seagrass shoots have been observed growing to within c.50m the harbour at the western end of the bay (pers. obs. 2019). 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. This site is only accessible for sampling during a narrow window of slack water, with low water being preferable.

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 seagrass lies to the west of Little Arthur but this is not accessible for sampling 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) 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. This site is best sampled at either lower or high water slack.

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 is consistent with 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 in our randomly allocated quadrats. 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 by targeting observed eelgrass patches, which could be used for comparisons. This site is accessible for sampling at any state of the tide, although care needs to be taken to avoid other water users.

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. This site is only accessible for sampling at slack water, with high water being preferable.

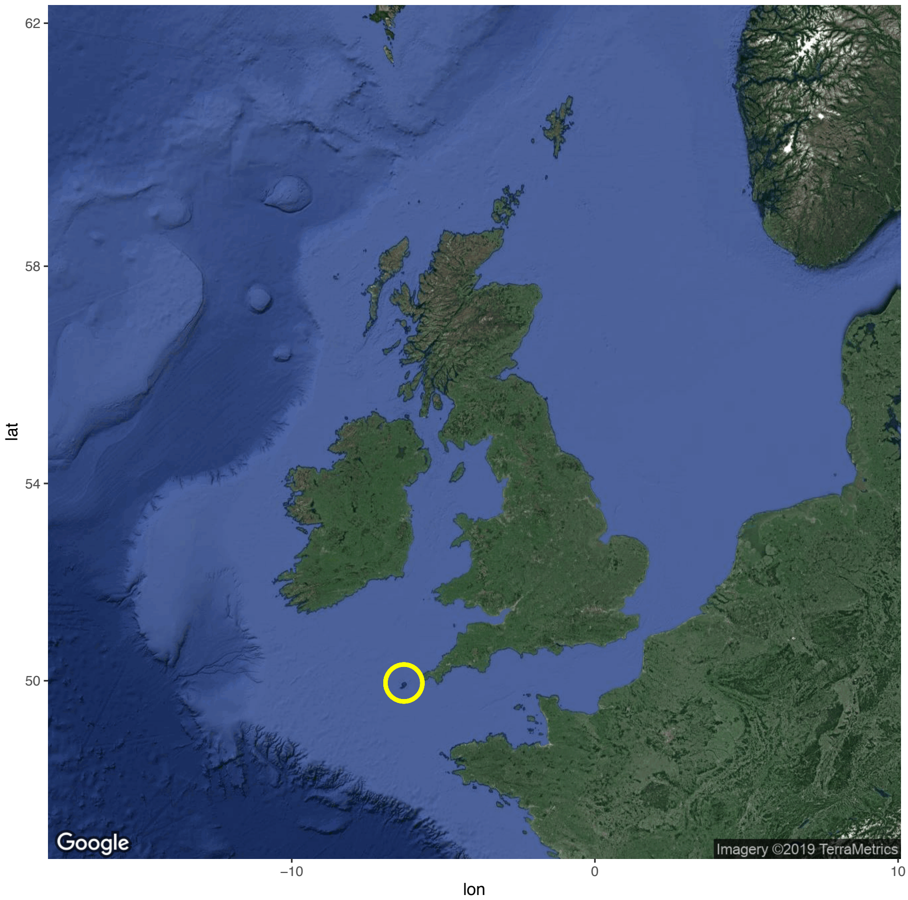

Figure 1a Location of the Isles of Scilly in relation to the rest of the United Kingdom. Yellow circle surrounds the Isles of Scilly

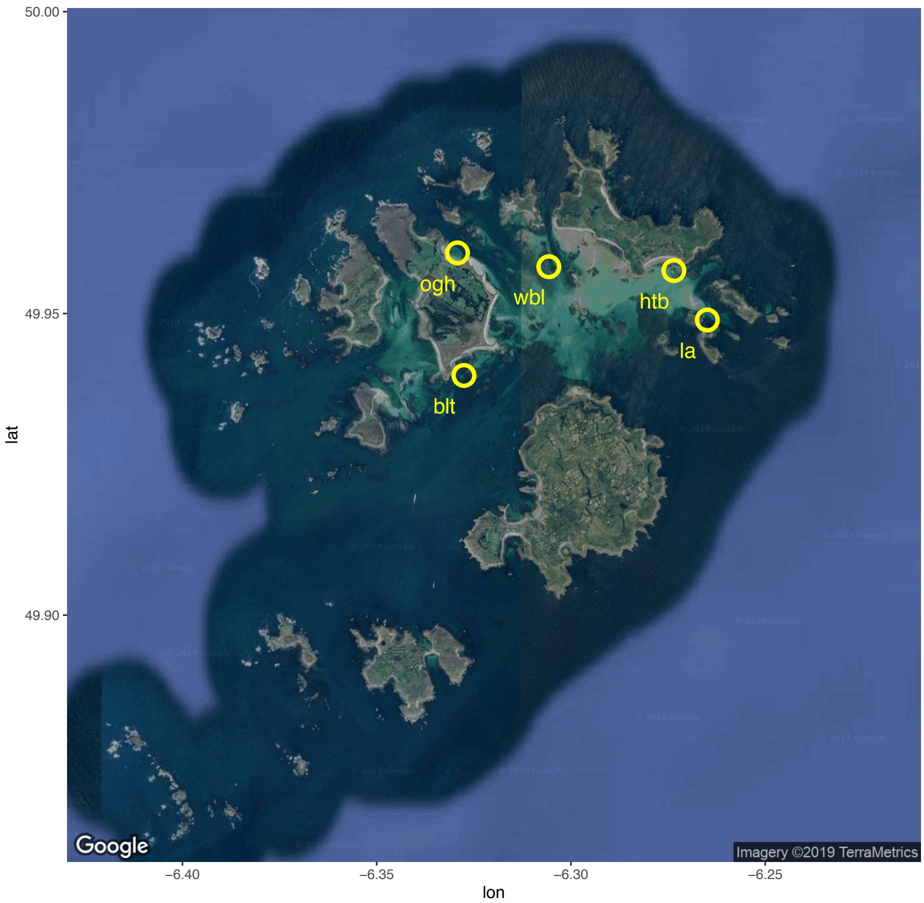

Figure 1b Locations of the five survey sites around the Isles of Scilly. Yellow circles indicate sites. Clockwise from bottom-left: Broad Ledges Tresco (blt), Old Grimsby Harbour (ogh), West Broad Ledges (wbl), Higher Town Bay (htb), and Little Arthur (la).

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 this year's Isles of Scilly eelgrass survey comprised Catherine and Olle Åkesson (OSPAR), Chiara Bertelli (Swansea University), James Bull (Swansea University), Fiona Crouch (Marine Biological Association, UK), Emma Kenyon (Sussex University), and Max Robinson (Swansea University). 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

Site	Latitude	Longitude	Date surveyed
Broad Ledges Tresco (blt)	49°56.371′N	06°19.764′W	01 / 08 / 2019
Higher Town Bay (htb)	49°57.445′N	06°16.445′W	31 / 07 / 2019
Little Arthur (la)	49°56.919′N	06°15.927′W	28 / 07 / 2019
Old Grimsby Harbour (ogh)	49°57.612′N	06°19.799′W	28 / 07 / 2019
West Broad Ledges (wbl)	49°57.388′N	06°18.266′W	27 / 07 / 2019

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 (Trudy Russell, 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 the current year, as well as on temporal trends through the whole period of the current Isles of Scilly eelgrass survey (1996-present). 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 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 over-dispersed 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, $logit[p] = ln[p / (1-p)]$) the proportions with Gaussian (Normal) GLMs.

All statistical analyses were undertaken using R version 3.6.1 (R Core Team, 2019).

4.1 Survey results from the current year

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 both quadrat occupancy ($\chi^2_{df=4} = 23.9$, $p < 0.001$) and shoot count ($\chi^2_{df=4} = 13.7$, $p = 0.008$) between sites.

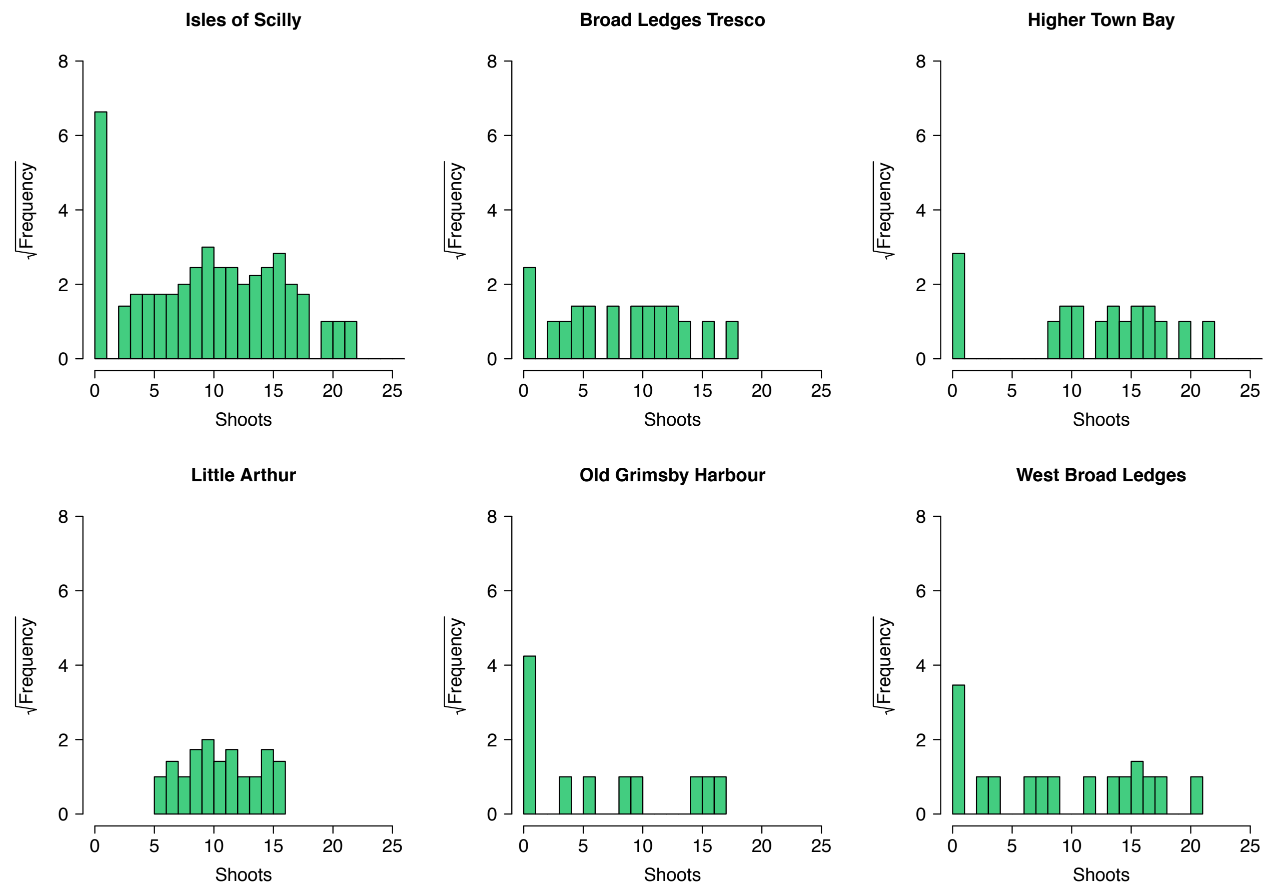

Figure 2 Frequency histogram of the number of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations (Note square root frequency scale)

Quadrat occupancy can be ranked (highest to lowest) as Little Arthur, Broad Ledges Tresco, Higher Town Bay, West Broad Ledges, and Old Grimsby Harbour. Percentage occupancy estimates are given in Table 2a. Shoot density can be ranked (highest to lowest) as Higher Town Bay, West Broad Ledges, Little Arthur, Old Grimsby Harbour, and Broad Ledges Tresco. Shoot density estimates are given in Table 2b.

Table 2a Percentage (lower, upper 95% c.i.) of quadrats occupied

Site	blt	htb	la	ogh	wbl
Estimate	80 (60, 91)	68 (48, 83)	100 (NA)	28 (14, 48)	36 (37, 74)

Table 2b Mean (lower, upper 95% c.i.) shoot density in occupied quadrats

Site	blt	htb	la	ogh	wbl
Estimate	9.3 (7.7, 11)	15 (13, 18)	11 (9.4, 13)	11 (8.1, 15)	11 (9.3, 14)

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 ($\chi^2_{df=4} = 65.2$, $p < 0.001$).

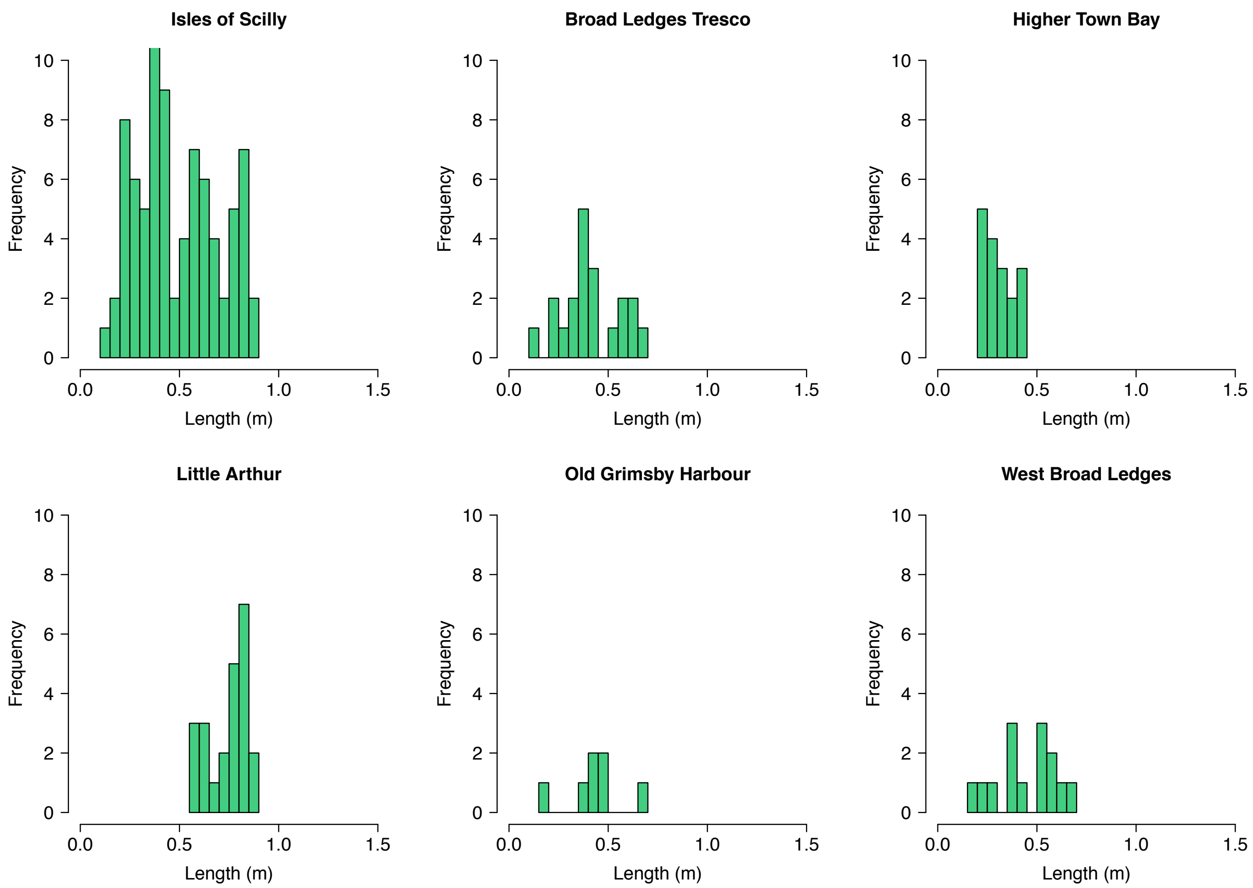

Figure 3 Frequency histogram of the 'canopy height' of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations

Canopy height can be ranked (highest to lowest) as Little Arthur, West Broad Ledges, Old Grimsby Harbour, Broad Ledges Tresco, and Higher Town Bay. Estimates are given in Table 3.

Table 3 Mean (lower, upper 95 % c.i.) canopy height in centimetres

Site	blt	htb	la	ogh	wbl
Estimate	42 (37, 47)	31 (27, 35)	75 (67, 84)	43 (35, 53)	45 (39, 53)

Leaf area index Distributions of leaf area index (LAI) across quadrats, at each of the sampling locations, are presented in Figure 4 and Table 4. There <u>is</u> a significant difference in LAI between sites ($\chi^2_{df=4}$ = 17.4, p = 0.002).

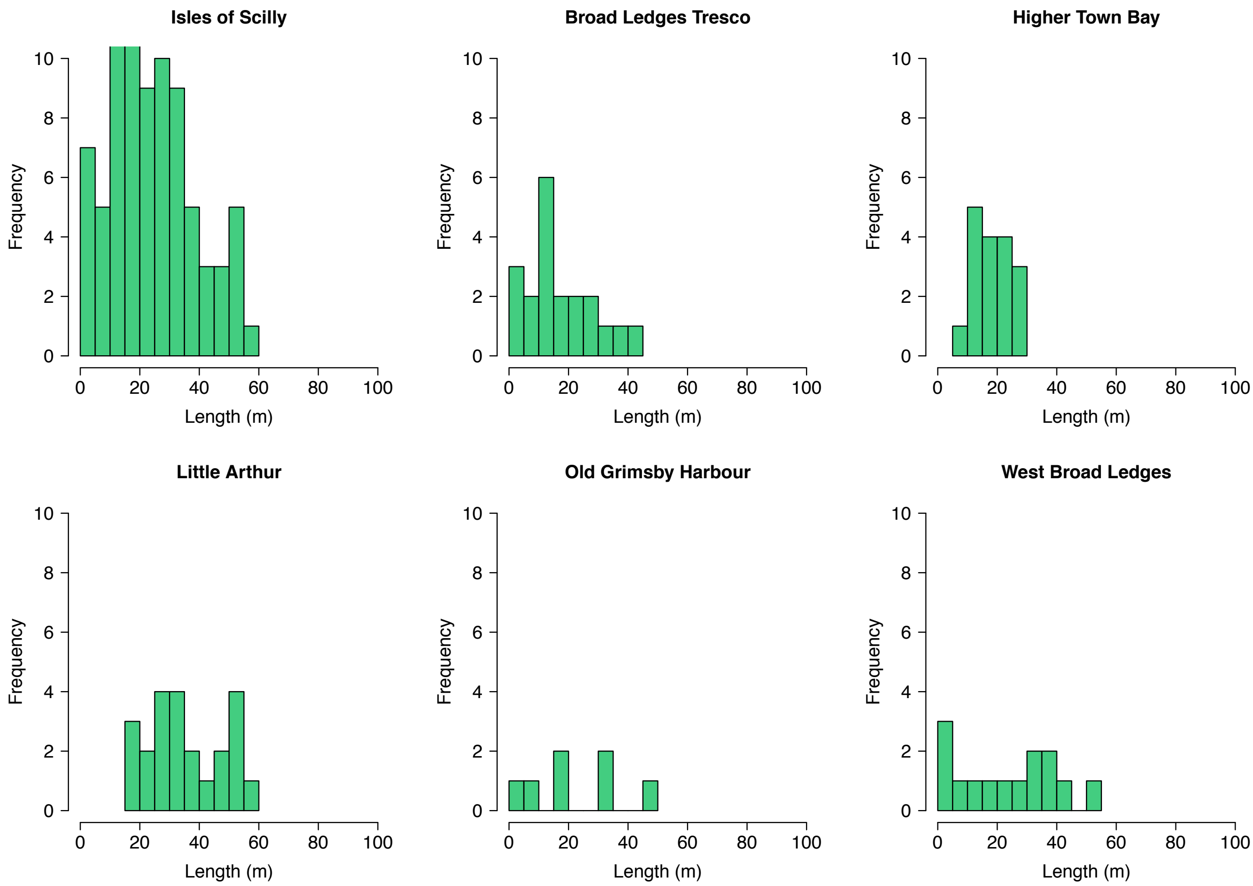

Figure 4 Frequency histogram of the 'leaf area index' (LAI) of eelgrass recorded per 25 x 25cm quadrat at each of the five survey locations

Leaf area index can be ranked (highest to lowest) as Little Arthur, West Broad Ledges, Old Grimsby Harbour, Higher Town Bay, and Broad Ledges Tresco. Estimates are given in Table 4.

Table 4 Mean (lower, upper 95% c.i.) leaf area index

Site	blt	htb	la	ogh	wbl
Estimate	17 (13, 22)	18 (14, 24)	36 (29, 45)	22 (15, 33)	24 (18, 32)

Wasting disease Distributions of disease prevalence across quadrats, at each of the sampling locations, are presented in Figure 5 and Table 5. There <u>are</u> significant differences in the proportion of infected leaves per shoot between survey sites ($F_{df=4} = 6.91$, $p < 0.001$).

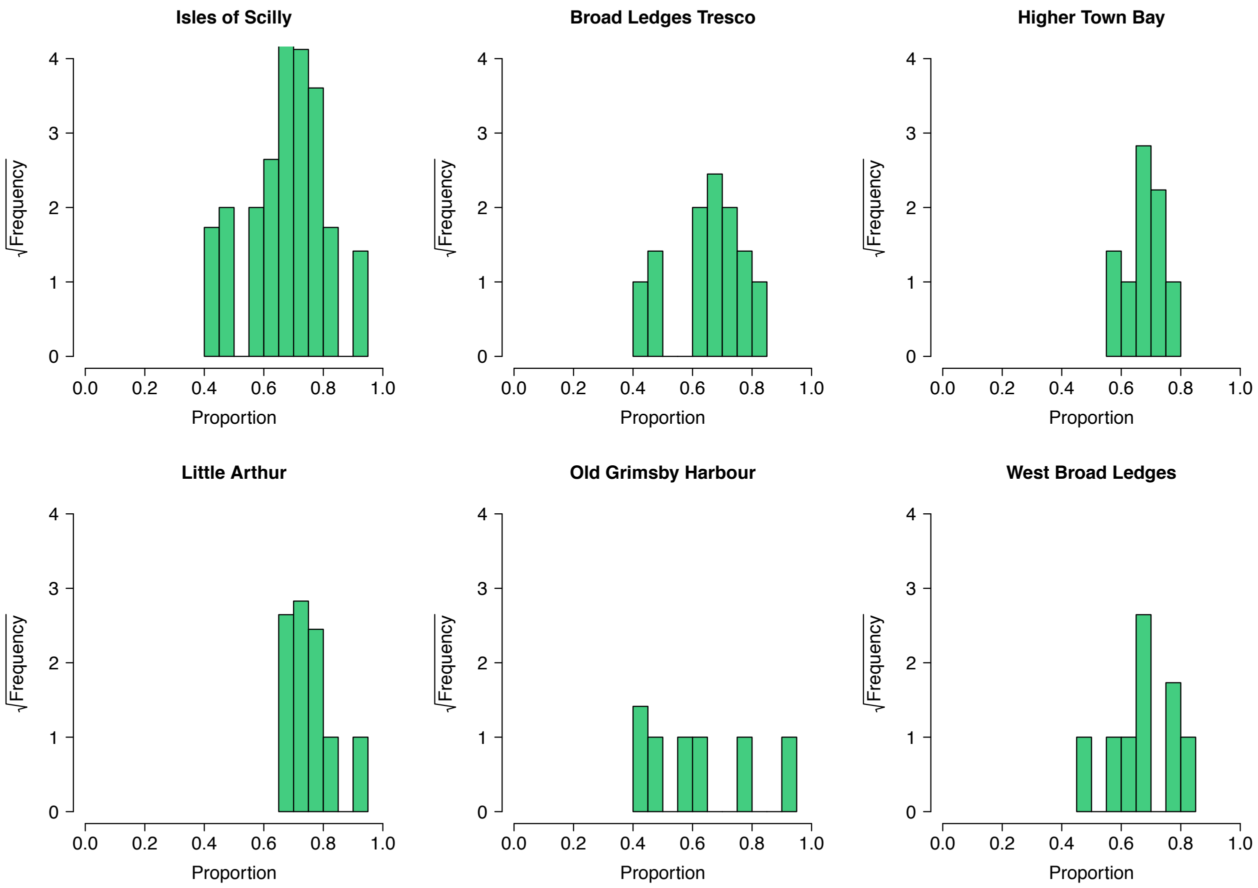

Figure 5 Frequency histogram of the proportion of infected eelgrass leafs recorded per 25 x 25cm quadrat at each of the five survey locations (Note square root frequency scale)

Disease prevalence can be ranked (highest to lowest) as Little Arthur, West Broad Ledges, Higher Town Bay, Broad Ledges Tresco, and Old Grimsby Harbour. Estimates are given in Table 5.

Table 5 Mean (lower, upper 95% c.i.) wasting disease prevalence proportion

Site	blt	htb	la	ogh	wbl
Estimate	0.68 (0.64, 0.71)	0.68 (0.65, 0.72)	0.73 (0.71, 0.76)	0.57 (0.51, 0.63)	0.69 (0.66, 0.73)

Epiphytes Distributions of average epiphyte scores across quadrats, at each of the sampling locations, are presented in Figure 6 and Table 6. There are significant differences in the average epiphyte scores per quadrat between survey sites ($F_{df=4}$ = 4.16, p = 0.004).

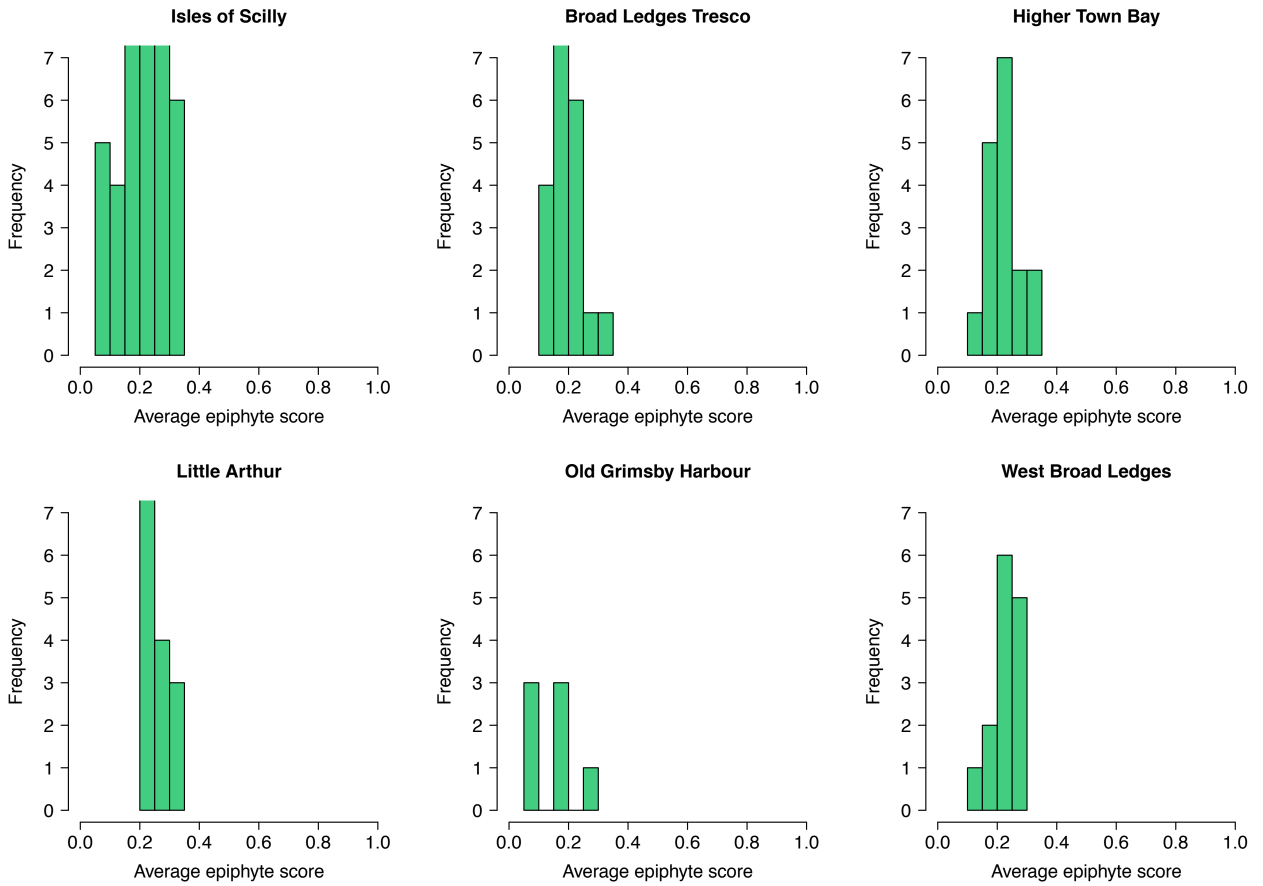

Figure 6 Frequency histogram of the average epiphyte score recorded per 25 x 25cm quadrat at each of the five survey locations

Epiphyte score can be ranked (highest to lowest) as Little Arthur, Higher Town Bay, West Broad Ledges, Broad Ledges Tresco, and Old Grimsby Harbour. Estimates are given in Table 6.

Table 6 Mean (lower, upper 95% c.i.) epiphyte score

Site	blt	htb	la	ogh	wbl
Estimate	0.20 (0.18, 0.23)	0.24 (0.22, 0.27)	0.24 (0.22, 0.27)	0.16 (0.13, 0.21)	0.24 (0.21, 0.26)

4.2 Time series results from 1996 - present

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 ($F = 3.09$, $p < 0.001$). There are also significant differences in the trends between sites ($F = 28.2$, $p < 0.001$). In particular, at Higher Town Bay shoot density has declined over the length of the study (Figure 7).

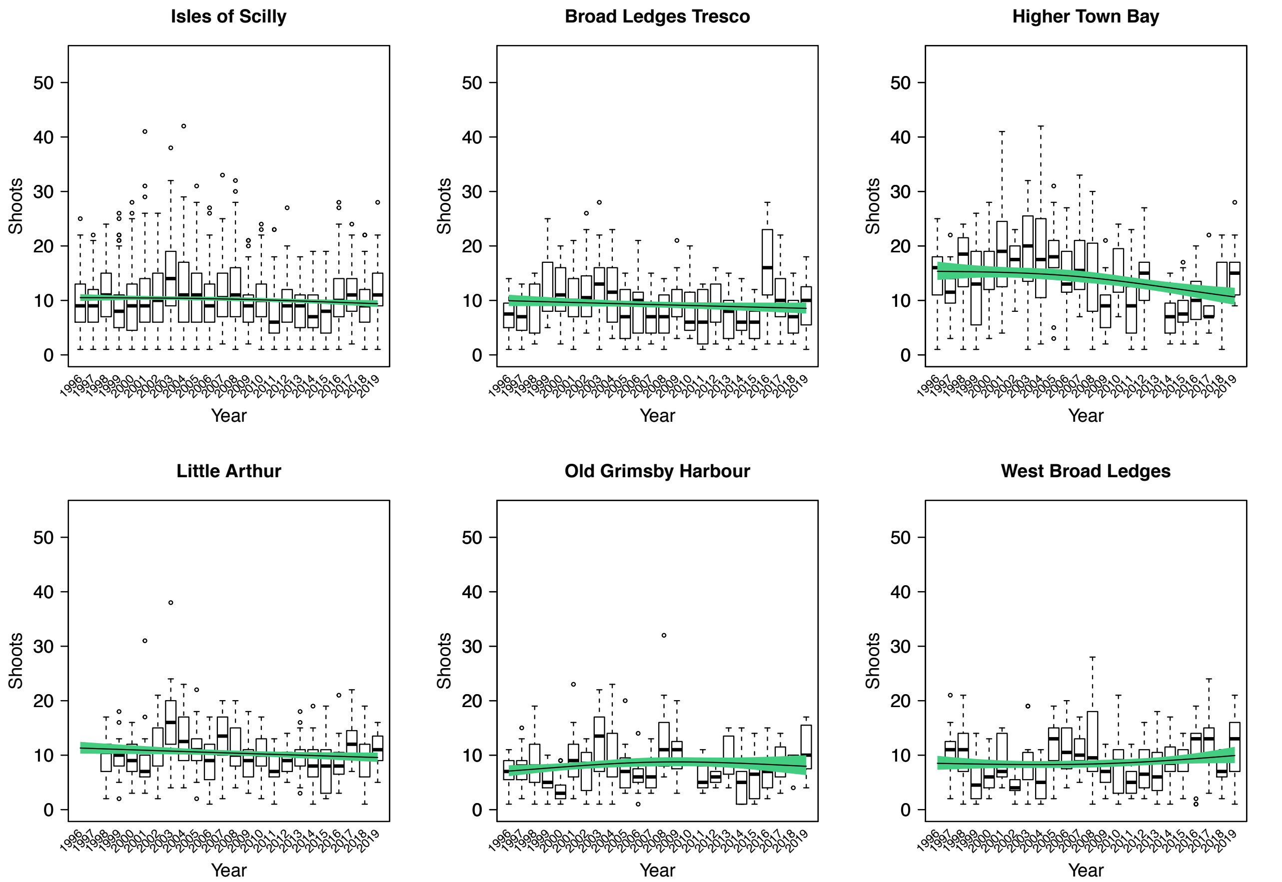

Figure 7 Time series of eelgrass shoot densities for all quadrats at each of the five survey sites. Box-whisker plots show median (centre line), interquartile range (box), Tukey whiskers covering data points within an additional 1.5 x interquartile range, with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model). 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 summary (p < 0.05 in bold)

Site	$F_{degrees\ of\ freedom}$	p-value
blt	$F_{df=1.00,\ 1.00} = 2.809$	0.094
htb	$\mathbf{F_{df=1.77,\ 1.95} = 9.739}$	**< 0.001**
la	$F_{df=1.00,\ 1.00} = 3.564$	0.059
ogh	$F_{df=1.71,\ 1.92} = 2.682$	0.120
wbl	$F_{df=1.60,\ 1.84} = 1.322$	0.180

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 ($F = 2.28$, $p = 0.007$). There are also significant differences in the trends between sites ($F = 164$, $p < 0.001$). In particular, at Little Arthur, canopy height has declined on average; whereas at Broad Ledges Tresco a slight increase is observed through time. At Higher Town Bay, there is variation through time but with no overall trend (Figure 8).

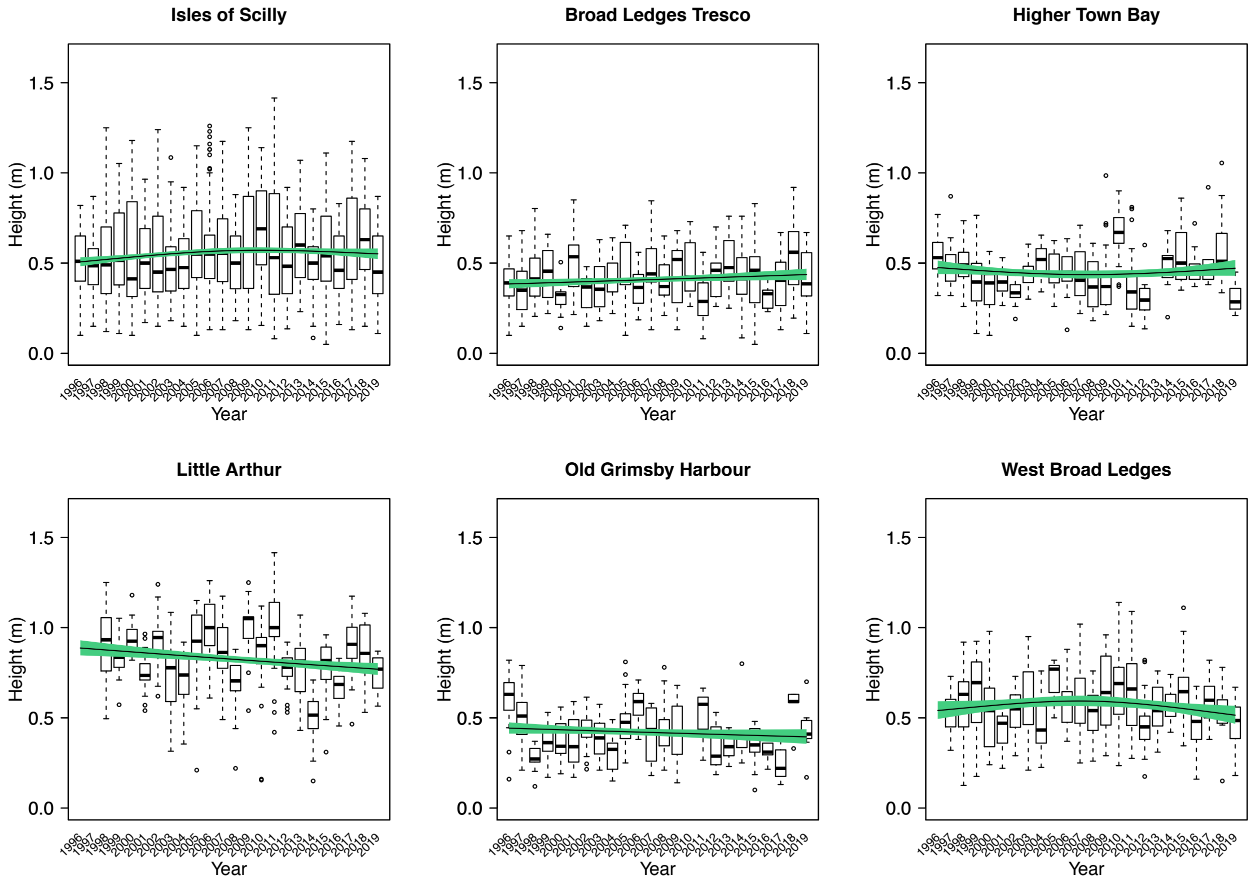

Figure 8 Time series of eelgrass 'canopy heights' for all quadrats at each of the five survey sites. Box-whisker plots show median (centre line), interquartile range (box), Tukey whiskers covering data points within an additional 1.5 x interquartile range, with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model). 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 summary ($p < 0.05$ in bold)

Site	$F_{degrees\ of\ freedom}$	p-value
blt	$\mathbf{F_{df=1.00,\ 1.00} = 5.954}$	**0.015**
htb	$F_{df=1.77,\ 1.95} = 2.008$	0.153
la	$\mathbf{F_{df=1.00,\ 1.00} = 6.932}$	**0.009**
ogh	$F_{df=1.00,\ 1.00} = 2.872$	0.090
wbl	$F_{df=1.83,\ 1.97} = 2.677$	0.061

Leaf area index 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 ($F = 2.72$, $p = 0.003$). There are also significant differences in the trends between sites ($F = 76.6$, $p < 0.001$).In particular, at Higher Town Bay and Little Arthur, LAI has declined through time (Figure 9).

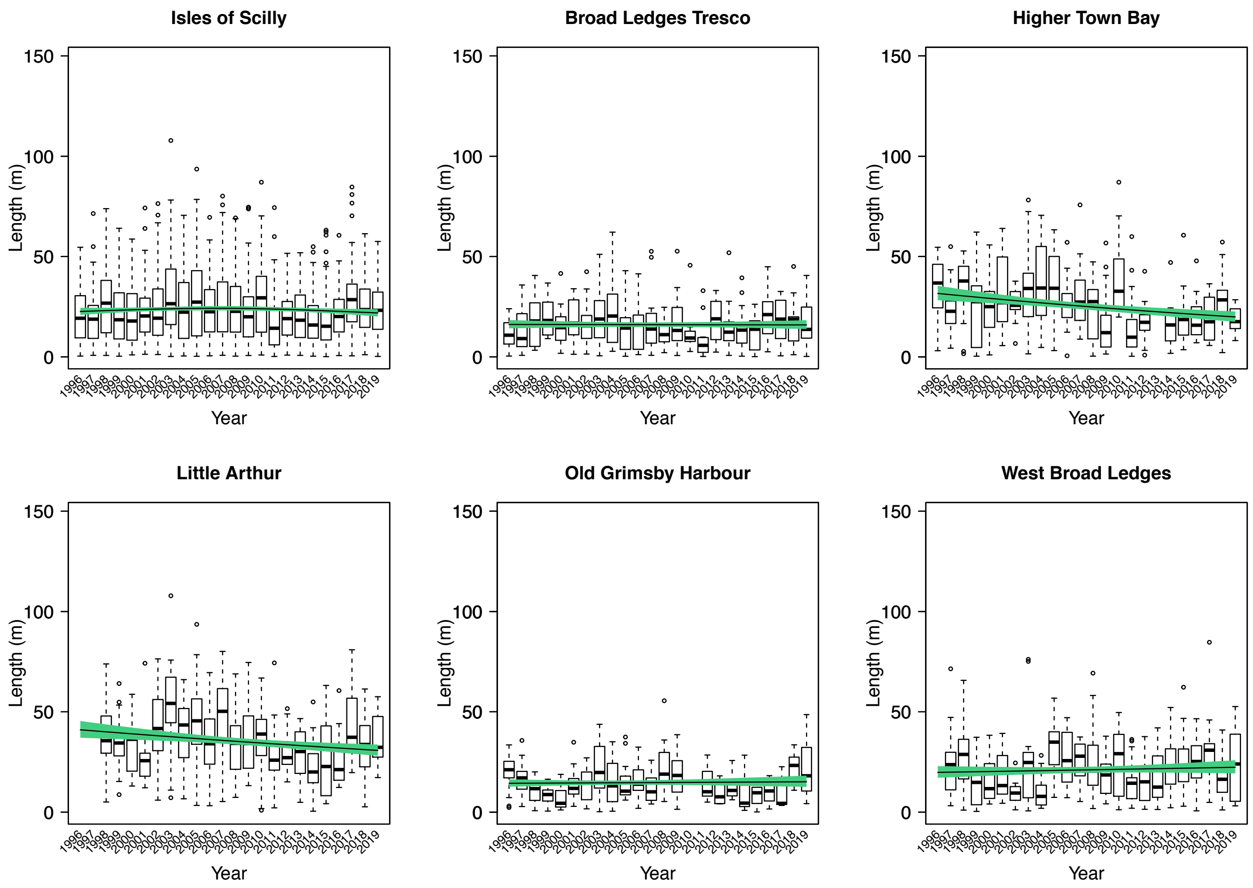

Figure 9 Time series of the ‘leaf area index’ (LAI) of eelgrass for all quadrats at each of the five survey sites. Box-whisker plots show median (centre line), interquartile range (box), Tukey whiskers covering data points within an additional 1.5 x interquartile range, with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model). 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 summary (p < 0.05 in bold)

Site	$F_{degrees\ of\ freedom}$	p-value
blt	$F_{df=1.00,\ 1.00} = 0.017$	0.896
htb	**$F_{df=1.00,\ 1.00} = 19.00$**	**< 0.001**
la	**$F_{df=1.00,\ 1.00} = 7.555$**	**0.006**
ogh	$F_{df=1.00,\ 1.00} = 0.146$	0.702
wbl	$F_{df=1.00,\ 1.00} = 1.072$	0.301

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 ($F = 3.95$, $p < 0.001$). There are also significant differences in the trends between sites ($F = 11.0$, $p < 0.001$). This trend is particularly striking at Old Grimsby Harbour, where quadrat occupancy has declined through time (Figure 10).

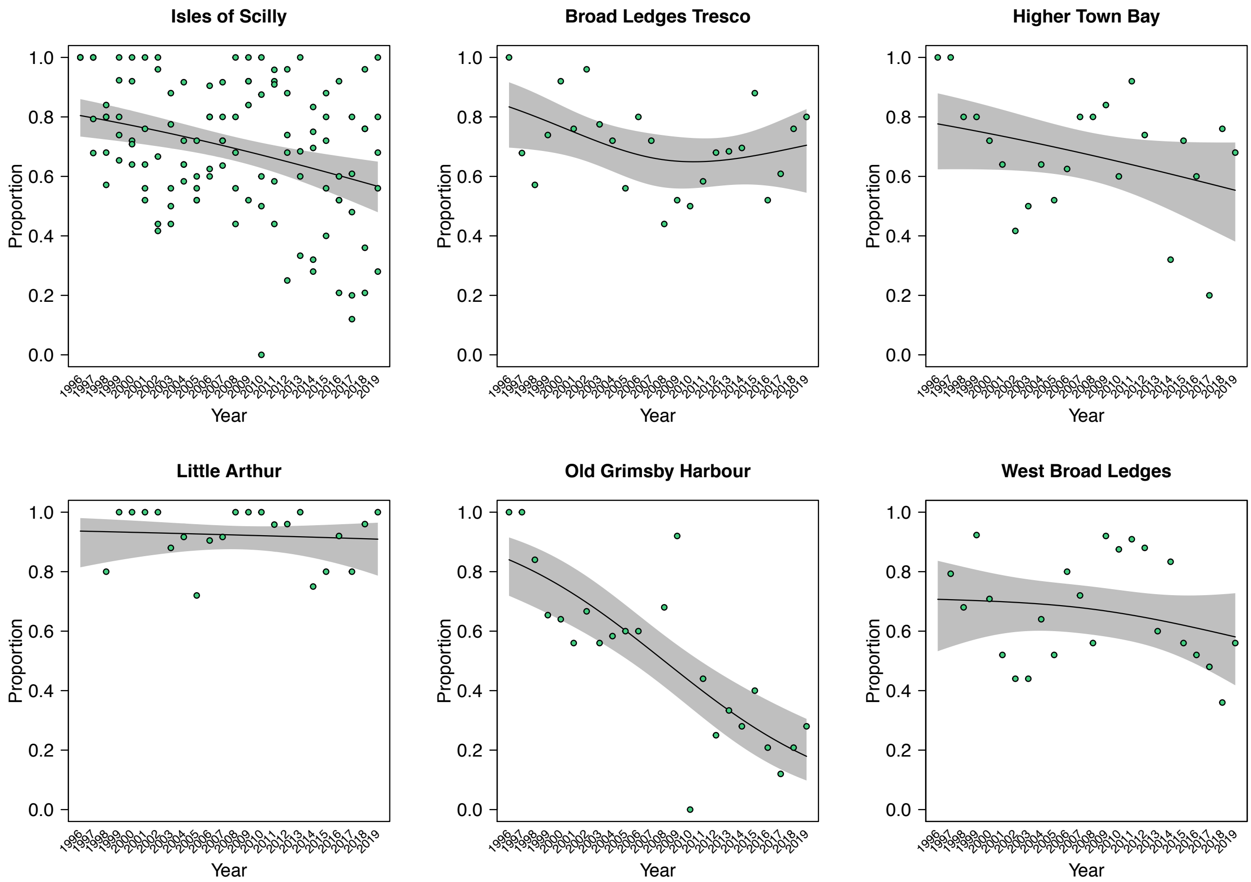

Figure 10 Time series of the proportion of occupied quadrats at each of the five survey sites. Green points indicate proportions of quadrats occupied at each site. Solid lines show overall temporal trends (Generalised Additive Model). Trend lines are surrounded by 95% confidence envelopes in grey.

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

Site	$F_{\text{degrees of freedom}}$	p-value
blt	$F_{df=1.60,\ 1.84} = 1.941$	0.238
htb	$F_{df=1.00,\ 1.00} = 3.708$	0.057
la	$F_{df=1.00,\ 1.00} = 0.133$	0.716
ogh	$\mathbf{F_{df=1.00,\ 1.00} = 29.04}$	**< 0.001**
wbl	$F_{df=1.14,\ 1.25} = 0.617$	0.372

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 ($F = 9.45$, $p < 0.001$). There are also significant differences in the trends between sites ($F = 11.3$, $p < 0.001$). At Little Arthur and Old Grimsby Harbour disease prevalence has increased through time. However, at Broad Ledges Tresco, Higher Town Bay, and West Broad Ledges disease prevalence increased through approximately the first half of the study but then decreased (Figure 11).

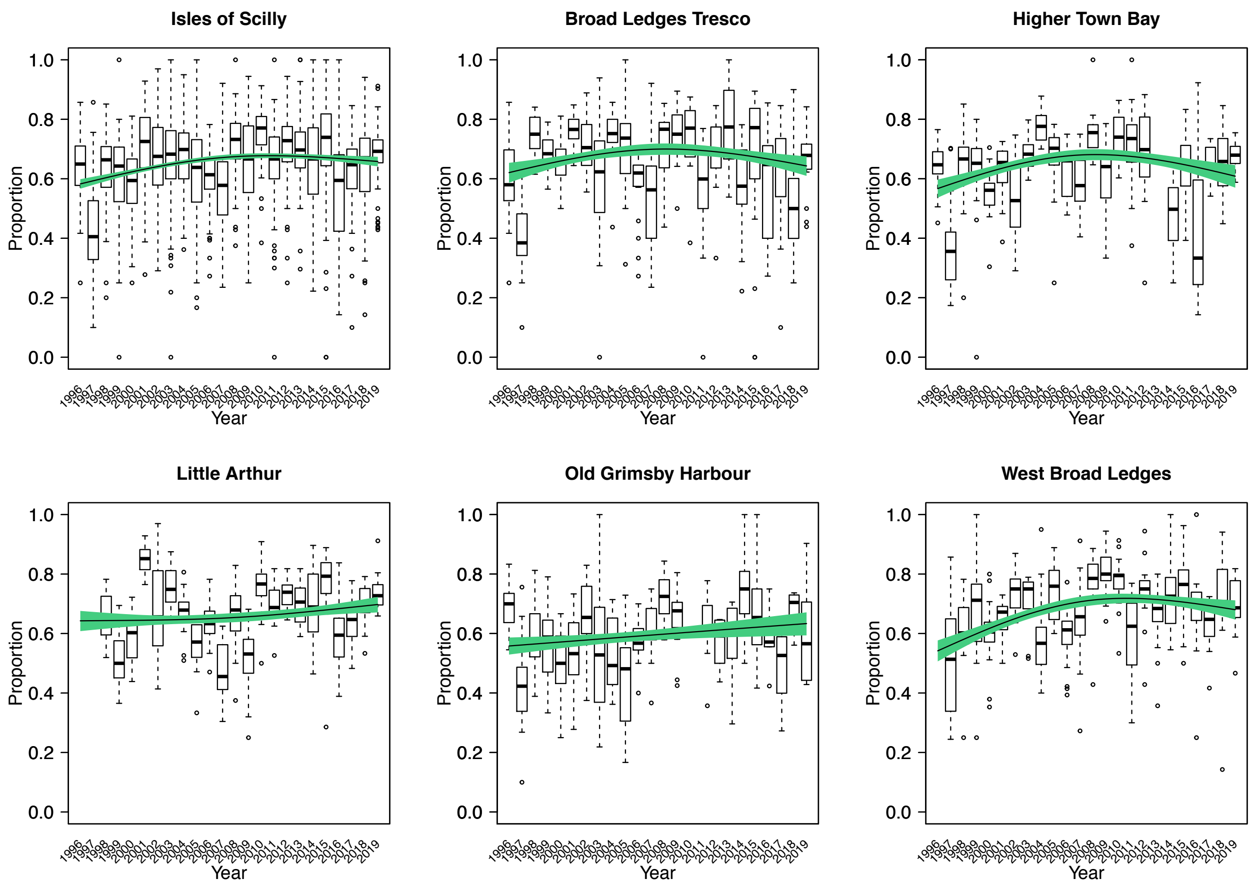

Figure 11 Time series of the disease prevalence per quadrat at each of the five survey sites. Box-whisker plots show median (centre line), interquartile range (box), Tukey whiskers covering data points within an additional 1.5 x interquartile range, with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model). 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 summary (p < 0.05 in bold)

Site	$F_{\text{degrees of freedom}}$	p-value
blt	$\mathbf{F_{df=1.92,\ 1.99} = 6.458}$	**0.002**
htb	$\mathbf{F_{df=1.97,\ 2.00} = 22.18}$	**< 0.001**
la	$\mathbf{F_{df=1.53,\ 1.78} = 4.349}$	**0.010**
ogh	$\mathbf{F_{df=1.00,\ 1.00} = 6.317}$	**0.012**
wbl	$\mathbf{F_{df=2.00,\ 2.00} = 28.25}$	**< 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 = 12.5, p < 0.001). There are also significant differences in the trends between sites (F = 46.2, p < 0.001). All sites show an increase through approximately the first half of the survey period, followed by a deceleration (Figure 12). At Higher Town Bay, Old Grimsby Harbour, and West Broad Ledges, the trend has reversed.

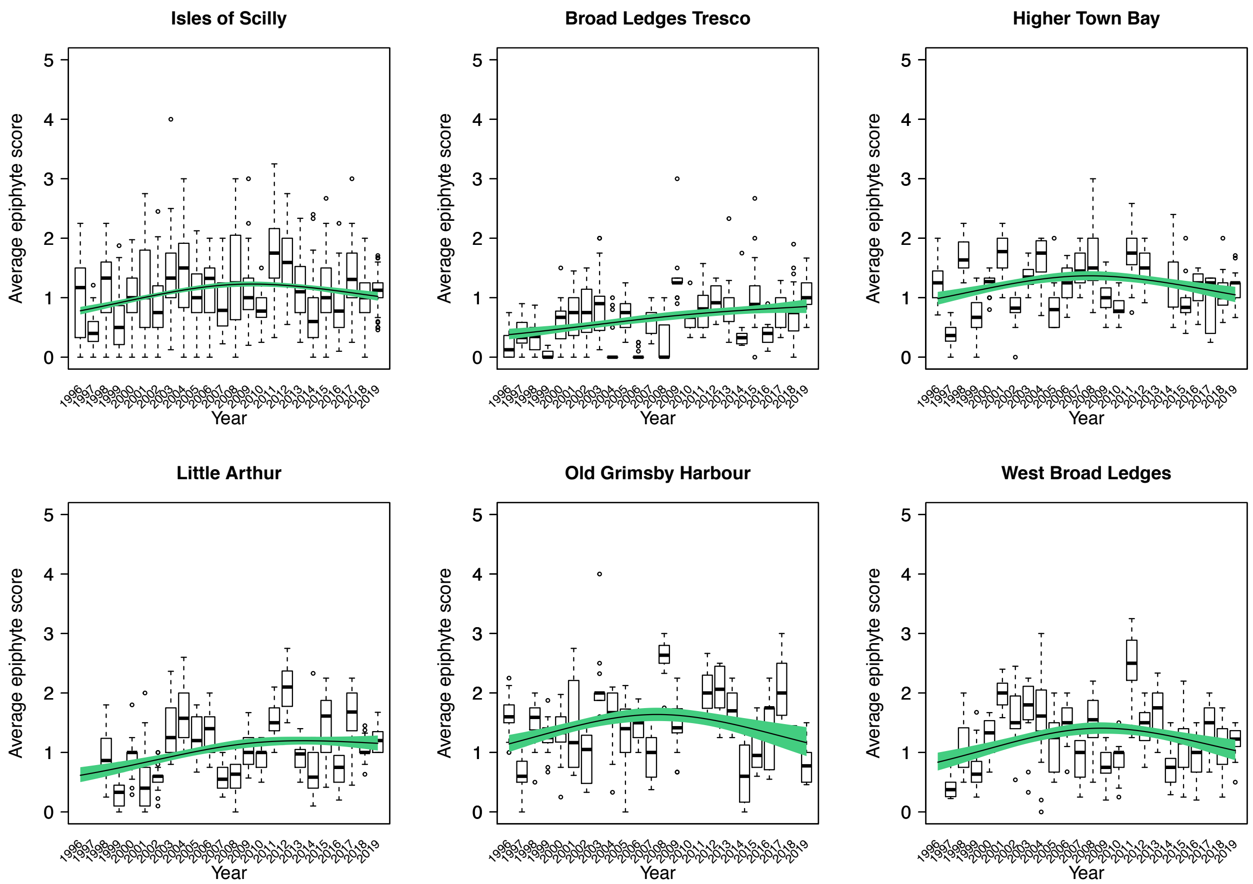

Figure 12 Time series of the average epiphyte scores per quadrat at each of the five survey sites. Box-whisker plots show median (centre line), interquartile range (box), Tukey whiskers covering data points within an additional 1.5 x interquartile range, with outliers shown as open circles. Solid lines show overall temporal trends (Generalised Additive Model). 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 summary (p < 0.05 in bold)

Site	$F_{\text{degrees of freedom}}$	p-value
blt	$\mathbf{F_{df=1.64,\ 1.84} = 17.62}$	**< 0.001**
htb	$\mathbf{F_{df=1.95,\ 2.00} = 10.98}$	**< 0.001**
la	$\mathbf{F_{df=1.92,\ 1.99} = 20.12}$	**< 0.001**
ogh	$\mathbf{F_{df=1.96,\ 2.00} = 15.46}$	**< 0.001**
wbl	$\mathbf{F_{df=1.97,\ 2.00} = 17.93}$	**< 0.001**

5.1 Key findings

This year, the overall picture was one of slightly higher than average eelgrass shoot density but slightly lower than average canopy height. It would be interesting to assess this against sunshine records for the year (and compare with other years), as this pattern might be expected to result from higher than average levels of available light (Abal et al. 1994). These metrics combine with the number of leaves per shoot to result in a measure of productivity described as leaf area index (LAI). The opposite findings for shoot density and canopy height effectively cancelled each other out to result in an average level of within-quadrat productivity this year, compared to long-term trends. However, a single year snapshot in a highly variable ecosystem is comparatively uninformative. Here, we focus on long-term trends:

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 until 2015 (Figure 7). However, the last four years (2016-2019) have shown shoot density at a consistently higher level when averaged across all five sampling sites. As recently as last year, this reversal of fate had not reached statistically significant levels and we were predicting a sustained long-term decline in the near future (Bull & Kenyon in press). The more recent picture is encouraging; however, we caution too much optimism on two counts: 1) no single metric is, on its own, a reliable indicator of seagrass status (Jones & Unsworth 2016), and 2) we are not confident about the causes of decline up to 2015 and do not know the reasons for apparent recovery more recently.

The other key estimator of eelgrass abundance is '**patch occupancy**', measured as the proportion of sampled quadrats with eelgrass, as opposed to bare sand. Averaged across all five sampling sites, patch occupancy has consistently decreased throughout the whole of the study period. Overall, there has been a **23.6% <u>decline</u> since monitoring began in 1996**. Separated by survey location, percentage changes at each of the monitoring sites are: Broad Ledges Tresco: 13.9% <u>decline</u>, **Higher Town Bay: 22.3% <u>decline</u>,** Little Arthur: 2.7% <u>decline</u>, **Old Grimsby Harbour: 66.1% <u>decline</u>,** West Broad Ledges: 12.8% <u>decline</u>. (Declines greater than 20% in bold.)

A key strength of our multi-year, annual study is the ability to identify long-term trends with a high degree of (statistical) confidence. This is not possible with one-off or occasional monitoring. The emerging picture is that where a quadrat is located within an eelgrass patch, within-quadrat measures do not show any striking long-term trends. Some years are better than others but this largely averages away over time. However, the probability of a randomly allocated quadrat being located on bare sand is consistently increasing over time - eelgrass 'patchiness' within meadows is increasingly substantially. Our long-term monitoring and analysis is revealing that processes and mechanisms underpinning the transition between eelgrass cover and bare sand at the patch scale are likely to be responsible for the long-term resilience and stability of eelgrass around the Isles of Scilly.

This fits well with other theoretical and empirical studies demonstrating 'bistability' in seagrass meadows. A bistable system is one where two distinct average levels (say of shoot density) are found. In either stable state, small pushes away from average levels are quickly compensated for and the system returns to equilibrium. However, a larger push by some external pressure, beyond a critical tipping point, causes the ecosystem to 'flip' to its alternative stable state. Once changed, the system is now resistant to small pushes away from that new state, so a return to the previous level is hard to achieve - an overall scenario known as 'hysteresis'. In seagrass meadows the two stable states appear to be 'some' (seagrass) and 'none' (bare sand). Across the Isles of Scilly, this would account for clear transitions between areas of eelgrass and bare sand, as opposed to a gradual fade-out across a gradient (either through time or across space).

Establishing an empirical pattern that is consistent with the hypothesis of bistability provides a promising lead to establish the causes of eelgrass decline across the Isles of Scilly. However, it is well understood that more than one cause can result in the same pattern and testing causality from its end result is notoriously hard (an 'inverse problem' in maths). Having analysed our long-term observational data to identify the role of spatial scale on dynamics, we suggest that it is possible and desirable to develop existing statistical 'diagnostic tests' for the existence of alternative stable states in this ecosystem (Sheffer & Carpenter 2003). Additionally, identifying the causes of pressures that lead to regime shifts between these stable states - essentially what drives eelgrass patch creation and destruction - could be achieved through a mixture of mechanistic modelling (e.g., van der Heide et al. 2011, McGlathery et al. 2013) and short-term manipulative experiments in mesocosms or in the field (e.g., van Katwijk et al. 1998).

5.2 Individual site summaries

Broad Ledges Tresco Shoot density and overall leaf area index (LAI) for this site remain relatively constant. There has been a gradual increase in canopy height and epiphyte cover here. The most noticeable feature is a continuing reversal of the previous decline in 'patchiness' (proportion of occupied quadrats). While coverage (patchiness) is currently increasing, it is important to continue to closely monitor this site to see if this improvement is transient.

Higher Town Bay Shoot density is higher this year than in recent years but canopy height is lower. 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. However, shoot density and canopy height combine with leaf counts per shoot to result in a continuing decline in above ground productivity, as measured by LAI. The decline in patch occupancy is even more worrying, with **over 20% loss** since the start of the survey. This site remains one of two that is particularly in trouble (the other being Old Grimsby Harbour).

Little Arthur This remains the site with the most continuous expanse of eelgrass on our survey. In addition, shoot density was above average this year. Continuing, gradual declines in canopy height and resulting LAI are statistically significant, which is a concern as this site has always represented a benchmark for seagrass in the Isles of Scilly and no local adverse pressures are evident.

Old Grimsby Harbour Trends at Old Grimsby Harbour are strikingly different to all other monitored locations around the Isles of Scilly. Within-quadrat metrics (shoot density, canopy height, and LAI) remain relatively constant over the long term and this year was unremarkable in that respect. The observation that sets Old Grimsby Harbour apart is the over **60% decline in patch occupancy** since our monitoring began in 1996. While this year's proportion of occupied quadrats was higher than last year's, this year's record is still within the 95% confidence interval for our predicted long-term decline - in other words, one slightly less bad year is nothing to celebrate and complete loss of seagrass at this site seems highly probable within a few years.

West Broad Ledges This site is relatively exposed to prevailing weather and currents, leading to striking emergent patterns in the seagrass vegetation when viewed using remote sensing (Irvine et al. 2018). However, the exposure level here may well flush through any local pollution and discourages local threats from boat traffic and anchorage. While cause and effect is unestablished through Scilly, this may well be the reason that all eelgrass metrics (shoot density, canopy height, LAI, and quadrat occupancy) remain relatively constant in the long term here.

5.3 Wasting disease

The first appearance of wasting disease in the Isles of Scilly, reported in a survey in 1991 (Fowler 1992) was, in part, the motivation for the continued monitoring to this day. Since then, it is interesting to see that wasting disease has remained evident at relatively consistent 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. Since our report on the 2017 survey, we have started to analyse the long-term trends in wasting disease prevalence. Statistically significant nonlinear trends in disease prevalence are seen across the Isles of Scilly. Interestingly, trends differ between sites, suggesting local influences have a substantial role to play in disease dynamics. Related work, using seagrass in the Isles of Scilly as a case study, has indicated that there is a complex interplay between the spatial pattern of seagrass and the transmission and prevalence of pathogens. This seems to involve an eco-evolutionary feedback loop, whereby disease transmission is affected by host plant distribution but also certain host plant spatial configurations are promoted by disease (Irvine et al. 2016c). Given the clear differences in patch occupancy between sites, as well as changes in patch occupancy over time, the future likelihood of disease outbreak here is unknown but the fundamental research is in place to be able to get a handle on this if given sufficient priority.

5.4 Epiphyte cover

This is also the third annual report where we have analysed long term trends in epiphyte cover. Epiphyte cover has shown a very similar nonlinear trend at all sites in our survey, increasing through approximately half of our monitoring period, and decelerating thereafter. This pattern is 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-four 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.

However, we now believe that our focus on spatial scale has put us in a place where future research could be done that has a realistic prospect of identifying causes of this decline. This would be a necessary first step towards developing effective mitigation strategies. The priority should be on validating the hypothesis of alternative stable states amongst eelgrass populations, coupled with an experimental approach to identifying the key drives of eelgrass patch creation and loss.

6 ACKNOWLEDGMENTS

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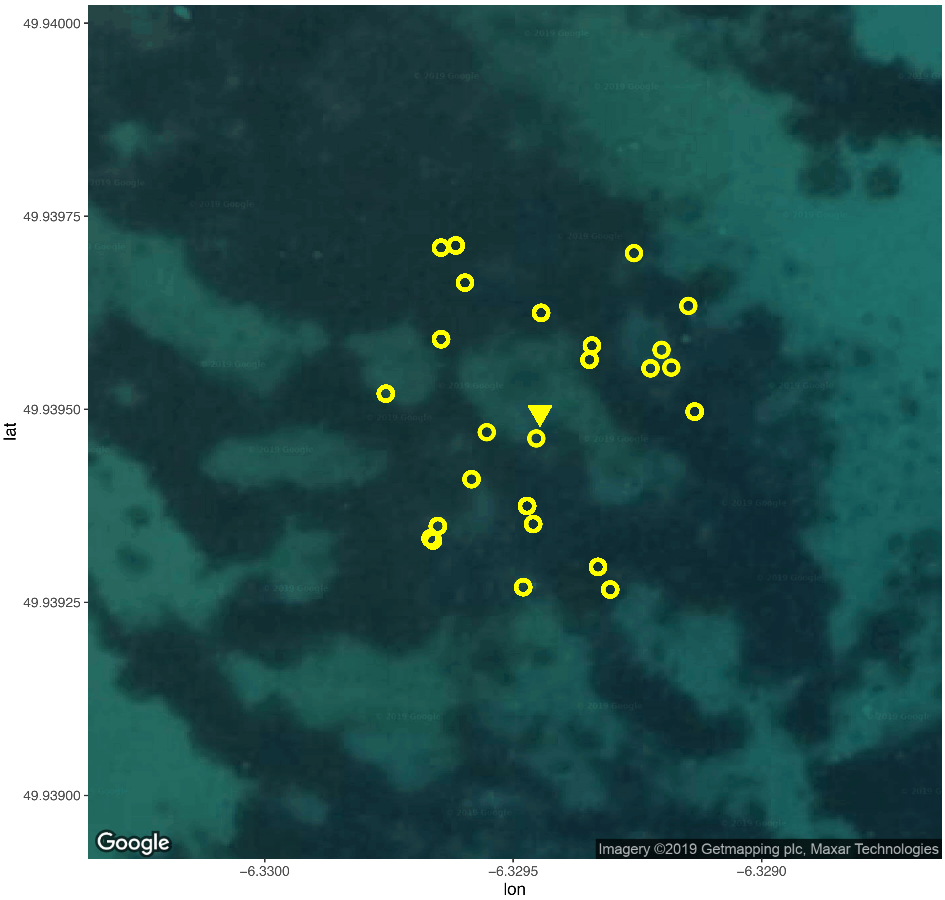
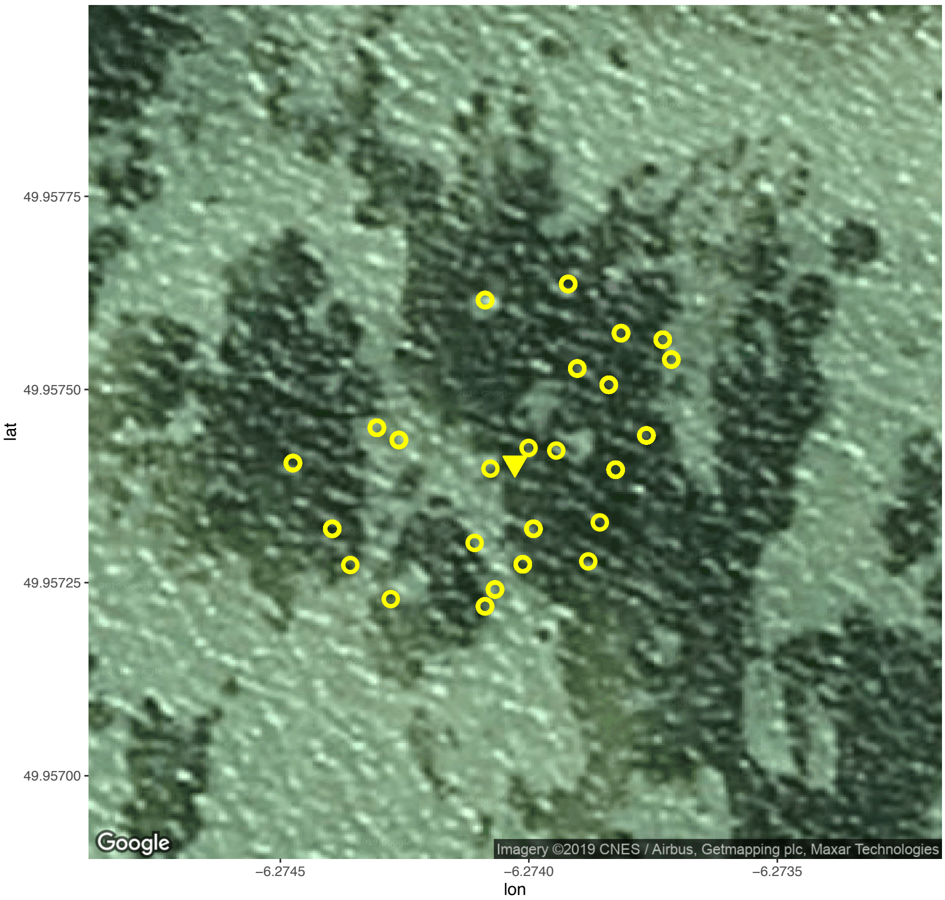
Appendix 1 - Locations of quadrats used in the current survey. Yellow triangles show the central datum (anchor) for each survey. Yellow circles show individual quadrats (not to scale, quadrats do not overlap). Google Earth images are the most recent available but these are primarily illustrative to give 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.

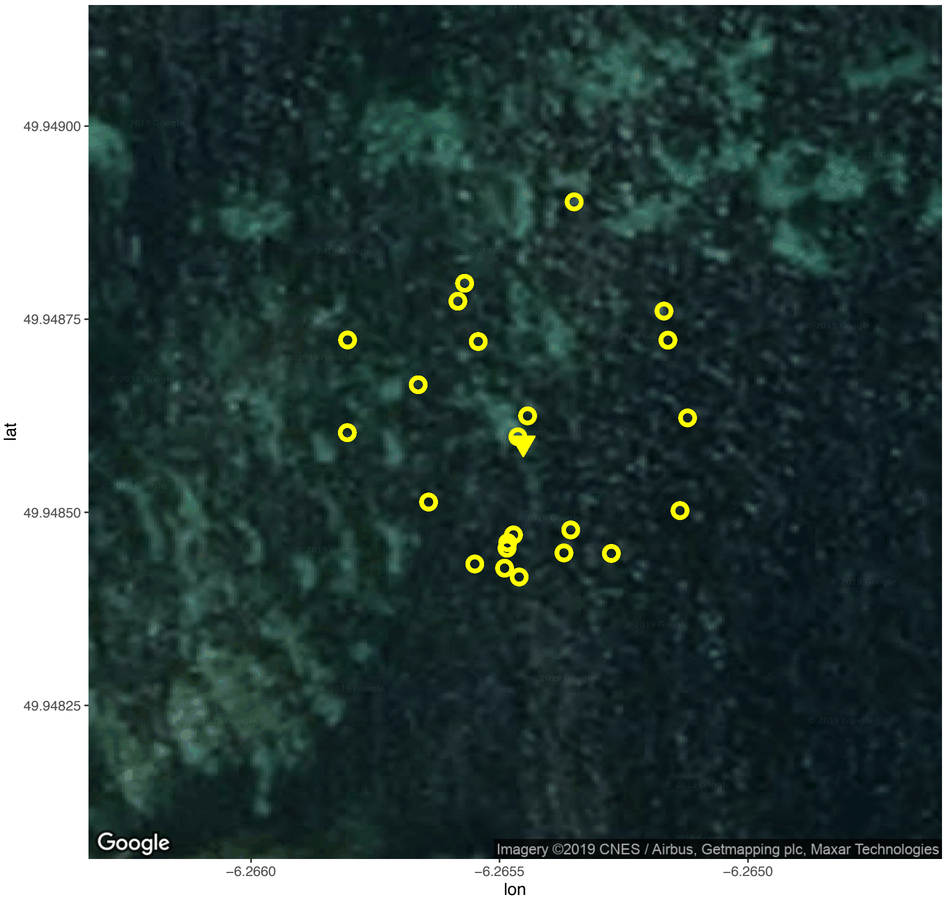
Broad Ledges Tresco



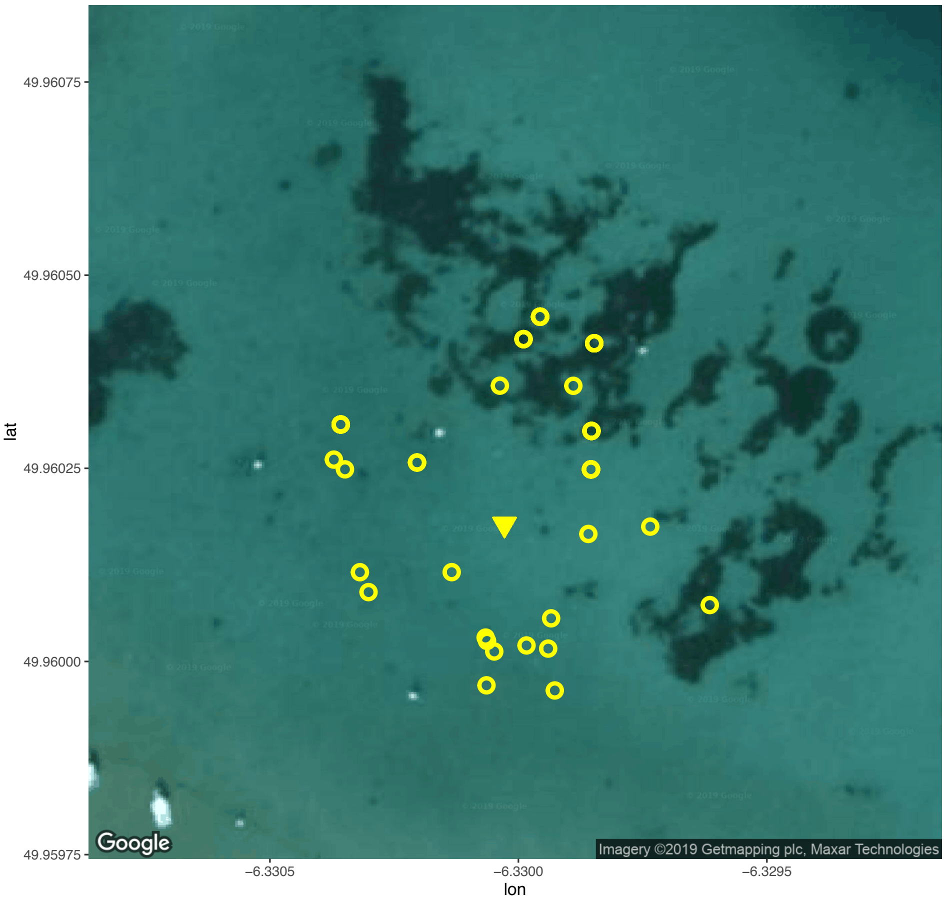
Higher Town Bay



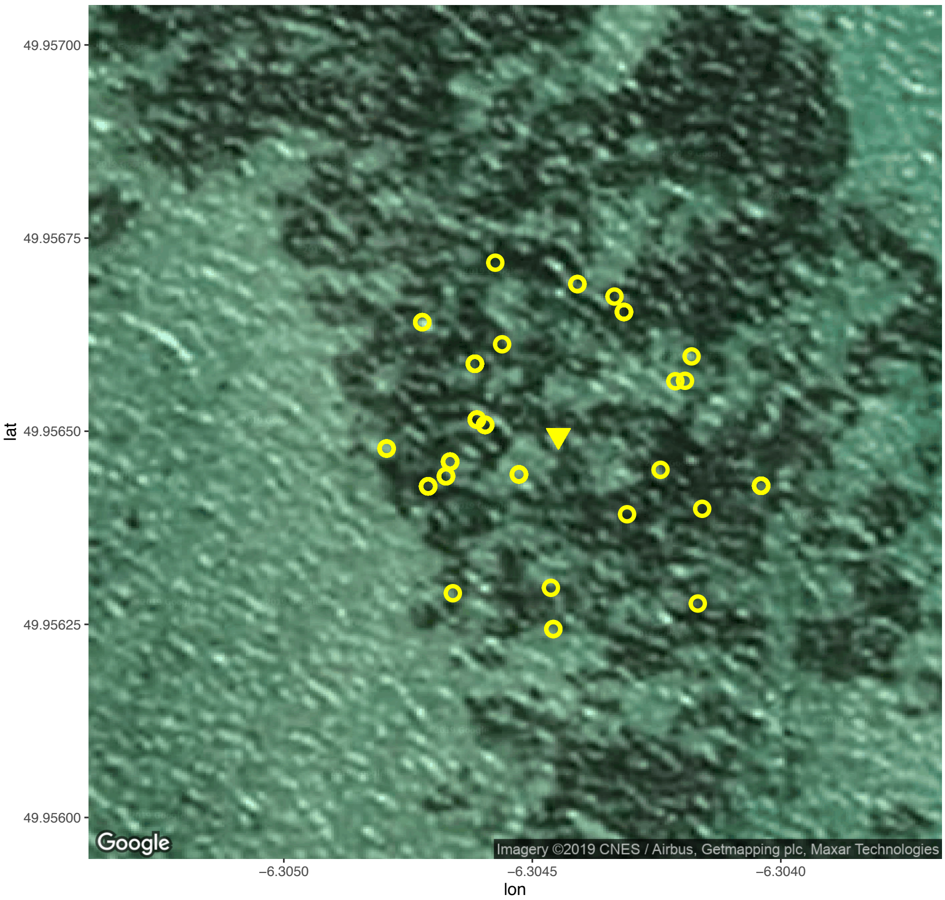
Little Arthur



Old Grimsby Harbour



West Broad Ledges



Appendix 2 - Summary data for the current year

Broad Ledges Tresco

quadrat	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	23	54	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	16.4	64	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	16.8	74	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	6.5	211	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	11.5	246	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	25.3	224	10	32	12	46	4	2	6	2	0	3	0.58	0	1.39
7	7.2	37	6	37	17	45	4	3	5	2	2	3	1	0.52	1.2
8	9.1	31	11	26	16	34	3	2	4	3	2	4	1.25	0.75	2.75
9	19.2	297	14	64	38	77	4	3	5	3	2	4	1	0.43	1.61
10	25.1	272	12	38	19	44	4	3	5	3	1	4	1.1	0.38	1.31
11	27.3	223	16	41	22	54	4	2	5	3	1	4	1.25	0.7	2.24
12	23.7	27	1	11	11	11	2	2	2	1	1	1	1	1	1
13	27.8	322	10	59	50	76	5	4	23	4	3	16	1.25	1.04	1.61
14	19.6	95	12	38	19	55	4	2	4	3	2	3	1.25	0.82	1.86
15	27.5	191	11	25	13	37	4	2	5	2	1	3	1	0.56	1.44
16	28.3	165	6	39	31	55	4	3	14	3	2	14	1.67	0.89	3.97
17	26.8	326	11	59	20	94	4	2	24	4	0	19	1.5	0.25	1.71
18	17.1	228	4	31	17	39	4	4	4	3	2	3	0.88	0.75	1.46
19	27.3	222	6	43	22	51	4	3	5	3	2	3	0.9	0.62	1.22
20	18.3	192	8	39	25	55	3	2	4	2	1	3	1.1	0.67	2.35
21	24.7	167	13	65	44	80	5	3	6	3	2	4	1	0.48	1.47
22	12.8	348	13	54	41	76	4	2	5	2	2	4	0.75	0.5	1.92
23	21.7	321	5	67	37	73	5	3	5	3	2	3	0.6	0.51	1.28
24	13.9	71	3	25	20	32	4	3	4	2	1	2	0.5	0.26	0.66
25	16	197	19	44	21	65	4	2	32	2	2	19	1	0.49	1.91

Higher Town Bay

quadrat	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	19.3	123	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	25.9	230	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	13.6	188	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	25.7	213	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	21.7	138	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	9.9	91	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	2.8	172	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	5.9	88	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	17.4	48	14	41	19	49	4	3	5	3	2	4	1.12	1	2.09
10	29.5	64	9	45	22	57	4	3	6	2	2	4	1	0.7	1.35
11	23	85	13	38	22	48	4	3	5	3	2	4	1.25	0.86	1.47
12	26.5	26	11	36	30	55	4	3	4	3	2	3	1.25	1	1.63
13	17.3	163	20	33	24	47	4	2	5	2	1	4	1.25	1	2
14	25.5	49	17	35	21	51	4	3	5	3	2	4	1.25	1	1.84
15	19.8	62	16	42	24	54	4	2	6	3	1	4	1	0.84	1.51
16	22.6	181	10	27	14	37	3	2	4	2	1	3	1	0.5	1.93
17	13.2	150	16	27	17	38	4	3	5	3	2	3	1.25	0.84	2
18	29.8	58	15	22	15	34	3	3	5	2	1	3	0.67	0.56	1.83
19	18.7	99	14	24	11	36	4	2	5	3	0	4	1.2	0.24	1.89
20	20.2	177	11	31	20	39	4	3	5	3	0	3	1	0.17	2.15
21	25.2	243	10	22	12	36	3	3	4	2	1	2	1.42	1.06	1.93
22	21.5	359	28	21	12	33	4	2	5	3	1	4	1.71	0.61	2.06
23	12.9	276	22	28	14	47	4	2	4	2	0	3	1.33	0.26	2
24	28.2	266	17	28	17	37	3	2	4	2	1	4	1.67	0.8	2.33
25	16.3	281	18	23	15	34	3	2	4	2	1	3	1	0.51	1.55

Little Arthur

quadrat	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	20.1	161	9	71	30	80	4	2	5	3	2	4	1.6	1.04	1.96
2	21	187	8	56	34	68	4	2	5	3	1	4	1.43	1	1.94
3	25.8	182	10	60	50	68	4	4	5	4	3	4	1.68	1.27	2.19
4	23.6	97	5	81	67	89	4	4	5	3	3	3	1	1	1.36
5	27.6	126	13	81	52	93	5	3	5	3	2	4	1	0.62	1.23
6	23	166	10	77	45	85	4	3	5	3	2	4	1.37	0.81	1.63
7	25.6	151	12	64	36	71	4	3	5	3	2	4	1.12	0.76	1.65
8	27	288	11	67	44	76	4	3	26	3	2	25	1.2	0.76	2.51
9	26.2	259	17	64	52	74	5	3	34	3	3	26	1.25	1	2.05
10	17	325	15	78	51	88	4	3	5	3	2	4	1.4	1	1.75
11	5.7	191	7	76	69	88	4	3	5	3	3	4	1.33	1.21	1.48
12	2.6	173	11	86	53	117	5	2	15	3	1	7	1	0.44	1.35
13	23.6	58	9	80	40	90	5	2	5	3	2	4	1	0.64	1.69
14	22.2	68	15	87	68	97	4	2	6	3	2	5	1	0.75	1.33
15	19.8	185	11	77	65	101	4	2	5	2	1	4	1	0.5	2.52
16	24.7	187	7	59	49	68	5	3	5	4	2	4	1.2	1	1.73
17	21.8	187	11	72	54	91	4	3	5	3	2	4	1.25	1	1.58
18	18.7	332	13	87	76	103	5	4	15	3	2	13	1.2	0.65	1.54
19	15.6	277	13	85	40	94	5	3	14	3	2	8	1	0.67	1.2
20	29.1	14	14	85	45	97	5	3	5	3	2	4	1	0.65	1.23
21	20.5	223	16	82	64	93	4	3	5	3	2	4	1.55	1	1.75
22	25	197	9	68	55	85	4	4	5	3	2	4	1.25	1.04	1.74
23	10.6	320	15	85	33	97	4	4	5	3	2	4	1.25	0.84	1.78

Old Grimsby Harbour

quadrat	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	13.9	231	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	20	171	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	26.1	171	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	19.3	180	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	9.5	110	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	18	97	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	29.7	117	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	25.7	193	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	15.8	167	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	20.7	193	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	19.1	198	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	25.6	250	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
13	19.5	197	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
14	19.3	20.5	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
15	26.9	283	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
16	18.5	348	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
17	28.8	285	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
18	25.6	243	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	11.1	57	17	47	23	64	4	3	5	2	0	4	0.5	0	1
20	26.1	22	10	41	24	50	5	4	5	2	0	3	0.5	0	1.24
21	28.1	4	16	40	19	49	5	3	6	3	0	4	0.78	0.12	1.1
22	14.9	39	9	50	28	66	3	2	4	3	2	4	1.5	1	1.93
23	24.8	359	6	17	10	29	3	3	4	1	0	3	0.46	0	1
24	29.6	295	15	70	45	84	5	3	6	3	2	4	1	0.45	1.57
25	17.3	294	4	36	29	48	3	3	3	2	2	3	1	0.67	2.18

West Broad Ledges

quadrat	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	12.4	131	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	14.3	97	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3	19.7	56	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	21.5	110	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	20.9	58	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	25.1	219	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
7	24.4	18	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	28.7	137	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
9	18.8	185	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10	23.7	52	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	29.7	341	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	22.8	23	9	45	24	57	5	3	5	4	2	4	1.4	0.84	1.93
13	18.5	317	22	67	27	89	4	2	13	3	2	6	1.5	0.81	2
14	16.2	268	18	40	16	52	4	2	5	3	0	4	1.37	0.21	1.6
15	19.8	258	14	53	17	69	4	2	5	2	1	3	1.25	0.33	2
16	6.7	249	17	54	25	70	4	3	5	3	1	4	1.2	0.63	1.37
17	25.4	273	7	18	12	33	3	2	4	3	0	3	1.33	0.11	2.28
18	29	98	17	58	39	77	4	2	14	3	1	8	1.2	0.56	1.84
19	18.5	332	1	52	52	52	6	6	6	4	4	4	0.83	0.83	0.83
20	12.1	293	15	56	24	69	4	4	5	3	2	4	1.2	0.44	1.5
21	17	261	12	38	20	59	4	3	5	2	1	4	1.1	0.69	1.54
22	28.1	314	8	38	26	53	4	4	5	3	3	4	1.45	1.04	1.8
23	24.7	183	3	30	23	43	4	3	4	3	3	3	1.25	1.01	1.65
24	13.5	294	17	64	38	85	4	3	21	3	2	19	1	0.5	1.57
25	25.1	5	4	21	15	25	4	3	4	2	1	2	0.5	0.35	0.5