

Isles of Scilly Eelgrass Bed Voluntary Monitoring Programme – 2021 Annual Survey

April 2024

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Report details

Author(s)

Dr James Bull

Dr Emma Kenyon

Natural England Project Manager

Kate Sugar

Contractor

In partnership with [Project Seagrass](#)

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Foreword

Project Seagrass have an ongoing voluntary seagrass survey in the Isles of Scilly which Natural England part fund. The purpose of this project is to continue to collect data to contribute to the ongoing condition assessment of the seagrass beds which are a feature of the Isles of Scilly Complex Special Area of Conservation (SAC).

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

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1 Executive summary

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 26 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 substantial variation in shoot density between survey sites this year, as is often the case. Canopy height was also found to differ between sites but this may simply be a feature of environmental differences between sites, such as depth or turbidity. 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. Substantial differences in LAI were observed between the five survey sites. However, longer-term trends reveal that considerable annual fluctuations in shoot metrics show no consistent changes through time across the Isles of Scilly. At the spatial scale of shoot density within eelgrass patches, there is no evidence to indicate concern.

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 (67.9 %) over the duration of the annual monitoring, while other sites are relatively stable over time.

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 substantially between survey sites. However, trends in disease and epiphyte community are not the same and 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 indicates concerning declines in eelgrass at Old Grimsby Harbour since the start of monitoring in 1996 and with no obvious change in downward trajectory 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. Elsewhere across our sampling locations within the Isles of Scilly SAC, eelgrass remains in good condition.

2 Introduction

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.

Zostera marina (eelgrass) is the predominant seagrass species of the north Atlantic and the focus of this survey.

2.2 Wasting disease

In the 1930s, a 'wasting disease' (*Labyrinthula zosterae*) substantially reduced populations of eelgrass. Along the Atlantic coasts of Europe and North America, up to 90% loss was estimated (Muehlstein 1989), with dramatic knock-on effects to fishing industries and waterfowl populations (Orth et al. 2006). Wasting disease continues to affect eelgrass beds, but with no outbreaks as dramatic as the epidemic of the 1930s (Short et al. 1988). Various theories have been put forward to explain the occurrence of wasting disease (review in den Hartog 1987). In particular, environmental stresses, especially high summer temperatures, have been suggested as a likely trigger for epidemics (Rasmussen 1977).

Wasting disease was reported to have reappeared around the Isles of Scilly in the early 1990s, and this was a key motivation for the 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 *Z. 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 eelgrass habitats around the UK is located in the shallow, relatively sheltered waters between the numerous islands and rocks that make up the Isles of Scilly, UK. Lying approximately 25 miles 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 eelgrass 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 eelgrass populations (Zipperle et al. 2010, van der Teide et al. 2012), or the marine turtles and sirenians of tropical seagrass habitats (Thayer et al. 1984, Fourqurean et al. 2012). In addition, our survey location is an archipelago with little industrial or agricultural impact or urbanisation (Figure 1). Here, eelgrass grows substantially as a natural monoculture and we are able to make rare baseline observations of an eelgrass 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.

2.5.1 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 macroalgae, found attached to the small material. The site does have yachts anchoring but this is infrequent due to the more exposed nature of the location. The bed is close to the works that took place in 2008 to repair and extend the pier at Carn Near. This site is accessible for sampling at most states of the tide although currents present a challenge at certain times.

2.5.2 Higher Town Bay

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 macroalgae, found attached to the small material.

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2.5.3 Little Arthur

This bed lies in the Eastern Isles and to the east of Little Arthur, where it is sheltered from the prevailing southwesterly winds and strong currents that flow round the islands. A much larger expanse of eelgrass lies to the west of Little Arthur but this is not accessible for 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 macroalgae. The eelgrass bed, however, lies in a small patch of medium sand and, despite the surrounding macroalgae, the eelgrass bed is relatively free from any covering vegetation. This is one of the deepest beds surveyed in the islands and although small in area, exists as a complete single bed with few significant patches of sand. This site is best sampled at either lower or high water slack.

2.5.4 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 macroalgae. 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.

2.5.5 West Broad Ledges

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

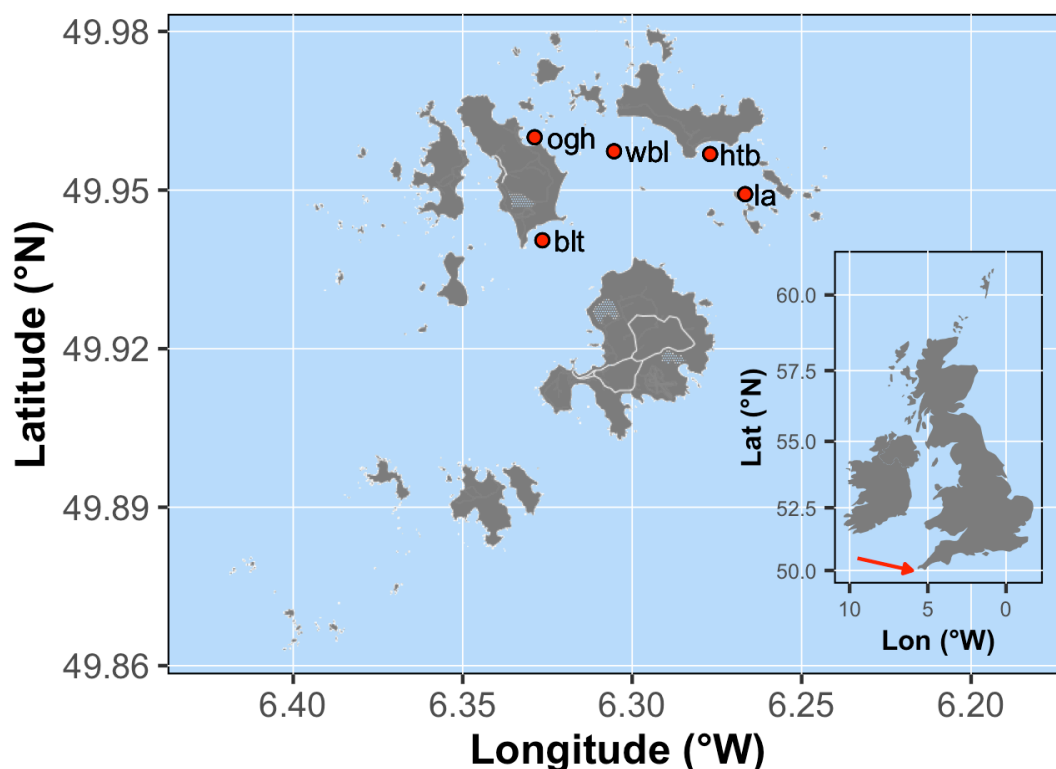


Figure 1. Locations of the five survey sites around the Isles of Scilly. Red points indicate sites. Clockwise from bottom-left: Broad Ledges Tresco (blt), Old Grimsby Harbour (ogh), West Broad Ledges (wbl), Higher Town Bay (htb), and Little Arthur (la). Inset map of the United Kingdom & Ireland. Red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

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 over-arching aim of this survey is to build a long-term evidence base of eelgrass condition.

The objectives 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 Methods

3.1 Survey methods

3.1.1 Survey team

The team for this year's Isles of Scilly eelgrass survey comprised Lisa Benson, James Bull, Blaise Bullimore, Ross Bullimore, Fiona Crouch, Emma Kenyon, and Angus Jackson. All participants were volunteers and did not receive payment for their contributions to the survey (indeed in all cases, volunteers contributed to survey costs). Volunteers have appropriate training through approved agencies such as BSAC and RYA.

3.1.2 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. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Sites	Latitude (°N)	Longitude (°W)
blt	49.94051	6.32649
htb	49.95682	6.27700
la	49.94923	6.26666
ogh	49.95999	6.32877
wbl	49.95734	6.30535

3.1.3 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 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 eelgrass survey methodology (Trudy Russell, *pers. comm.*).

3.1.4 Shoot count

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.

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

3.1.6 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 this is based on the longest leaf and, additionally, no leaf widths were 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.

3.1.7 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.

3.1.8 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. Where nonlinear trends through time were assessed, we used Generalised Additive Models (GAMs), which are based on GLMs but with the facility to fit nonlinear trends.

3.2.1 Shoot count

We combined information on presence or absence of eelgrass shoots within quadrats with information on shoot density within occupied quadrats. This was analysed using 'zero-inflated' mixture models. These are GLMs that simultaneously quantify the proportion of occupied quadrats assuming a binomial distribution of presence and absence, with quantification of non-zero shoot density assuming a zero-truncated negative binomial distribution.

3.2.2 Presence / absence

Wasting disease was recorded as 'infected' or 'uninfected' on a leaf-by-leaf basis. In the current study, this presence / absence data was modelled using over-dispersed binomial GLMs. Results are presented as proportions of leaves infected.

3.2.3 Continuous data

Canopy height and leaf area index data are continuous but with a lower boundary of zero. This results in 'skewed' data distributions with increasing variance-mean ratios (i.e. variability in leaf lengths is greater among sets of longer leaves). We model this type of bounded data using gamma GLMs.

3.2.4 Ordinal data

Epiphyte scores are recorded as percentage cover brackets. Here we converted these scores (0-5) to proportion data (0-1), first by averaging scores across quadrats, then dividing by five. Here, we modelled proportion data using beta GLMs.

3.2.5 Software and reproducibility

All statistical analyses were undertaken using R version 4.0.2 (R Core Team, 2020). This report was prepared using R Markdown to produce a final Word document while preserving analysis code as an integral part of the work flow. Full code is available from the authors on request.

4 Results

4.1 Survey results from the current year

4.1.1 Shoot count

Distributions of shoot counts across quadrats at each of the sampling sites are presented in Figure 2, with analysis presented in Table 2.

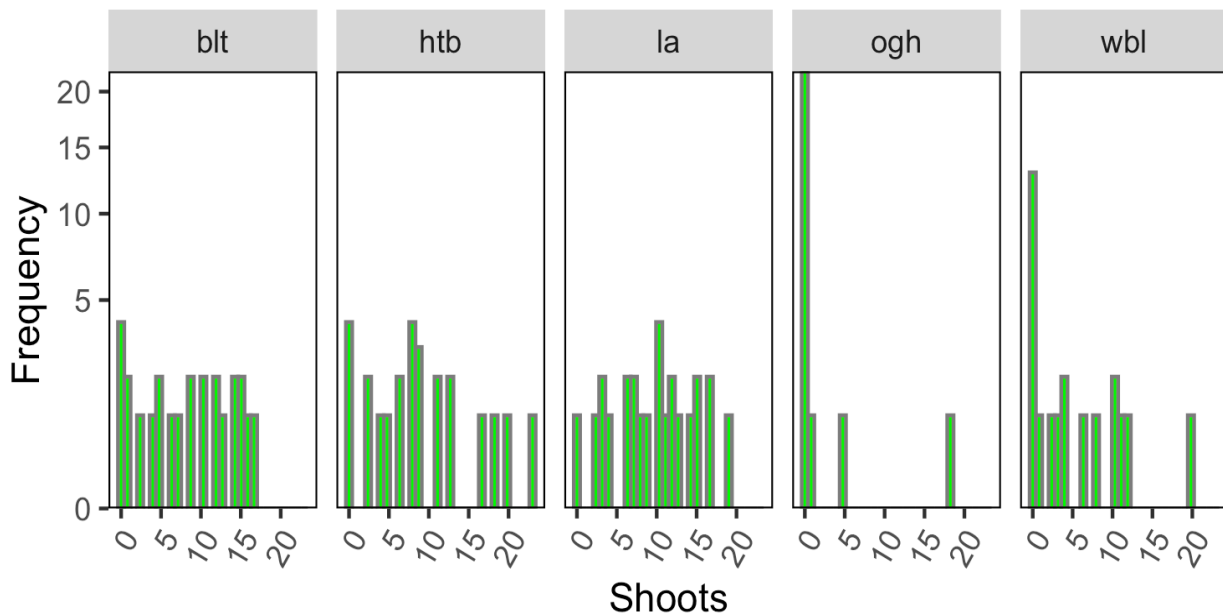


Figure 2. Frequency histogram of the number of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). (Note square root frequency scale due to the high number of zero counts.)

A negative binomial-binomial mixture model was fitted to quantify differences between survey sites in both shoot counts and quadrat occupancy.

Mean shoot density per quadrat, in ascending order, was: wbl (mean = 7.47, 95% c.i. = [5.18, 10.76]), ogh (mean = 7.89, 95% c.i. = [3.83, 16.26]), blt (mean = 9.3, 95% c.i. = [7.13, 12.13]), htb (mean = 9.93, 95% c.i. = [7.64, 12.91]), la (mean = 9.93, 95% c.i. = [7.77, 12.69]).

The proportion of occupied quadrats, in ascending order, was: ogh (mean = 0.12, 95% c.i. = [0.04, 0.32]), wbl (mean = 0.49, 95% c.i. = [0.3, 0.68]), blt (mean = 0.85, 95% c.i. = [0.64, 0.95]), htb (mean = 0.85, 95% c.i. = [0.64, 0.94]), la (mean = 0.97, 95% c.i. = [0.71, 1]).

To assess whether substantial differences exist between sites, a negative binomial model was fitted to describe differences between sites in shoot counts but not quadrat occupancy, and a binomial model was fitted to describe differences between sites in quadrat occupancy but not shoot counts. Model comparison, based on AICc, was used to identify the best descriptor of eelgrass shoot distribution.

Table 1. Model comparison for shoot counts. The lowest AICc value denotes the best fitting model, with a difference ($\Delta AICc$) of 2 indicating a substantial difference between models.

Modnames	K	AICc	$\Delta AICc$	ModelLik	AICcWt	LL	Cum.Wt
Binomial	7.00	613.48	0.00	1.00	0.97	-299	0.97
Neg. Binom.-Binom.	11.00	620.74	7.26	0.03	0.03	-298	1.00
Negative Binomial	7.00	667.00	53.52	0.00	0.00	-326	1.00

This year, the binomial model was the best fitting model. This indicates that there were significant differences between sites in the proportion of occupied quadrats but not in shoot density.

4.1.2 Canopy height

Distributions of canopy heights across quadrats at each of the sampling sites are presented in Figure 3.

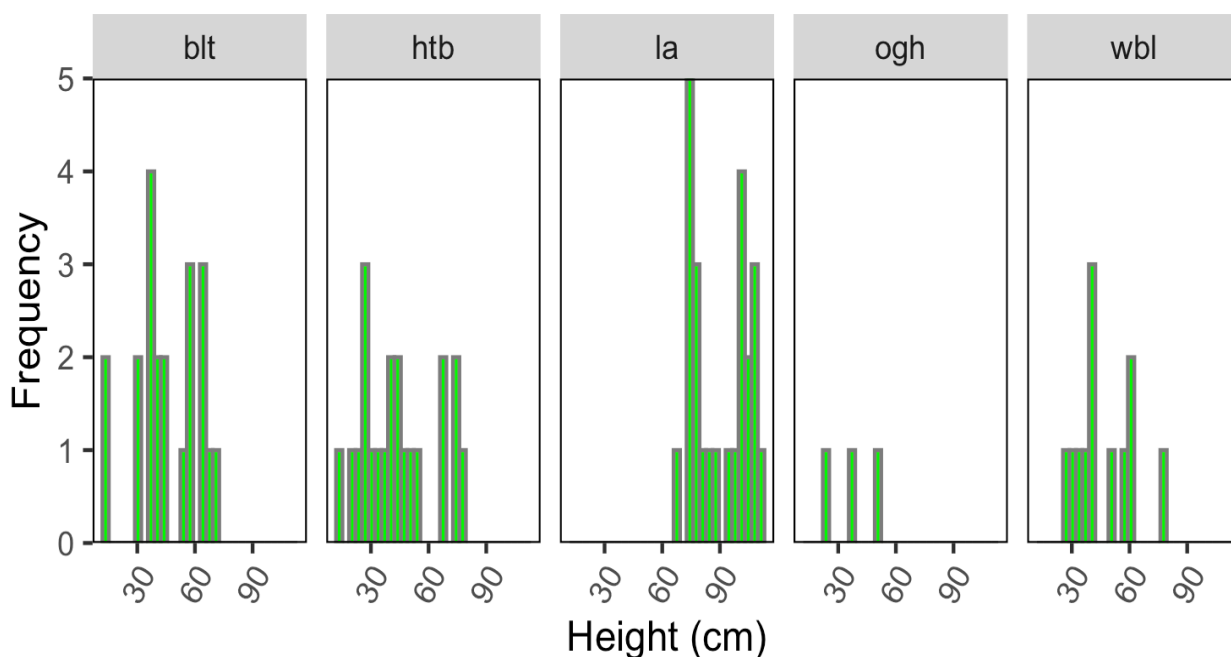


Figure 3. Frequency histogram of canopy heights recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl) (empty quadrats excluded).

Mean canopy height per quadrat, in ascending order, was: ogh (mean = 37.17 cm, 95% c.i. = [25.27, 54.66]), htb (mean = 44.19 cm, 95% c.i. = [38.19, 51.13]), blt (mean = 45.64 cm, 95% c.i. = [39.45, 52.81]), wbl (mean = 46.25 cm, 95% c.i. = [38.14, 56.09]), la (mean = 90.19 cm, 95% c.i. = [78.69, 103.37]).

4.1.3 Leaf area index

Distributions of leaf area index across quadrats at each of the sampling sites are presented in Figure 4. Leaf area index was calculated as the length of the longest leaf per shoot multiplied by the number of leaves per shoot, summed over all shoots in a given quadrat. As such, this is an over-estimate (as only the longest leaf was measured) but provides a comparable measure across sites and years.

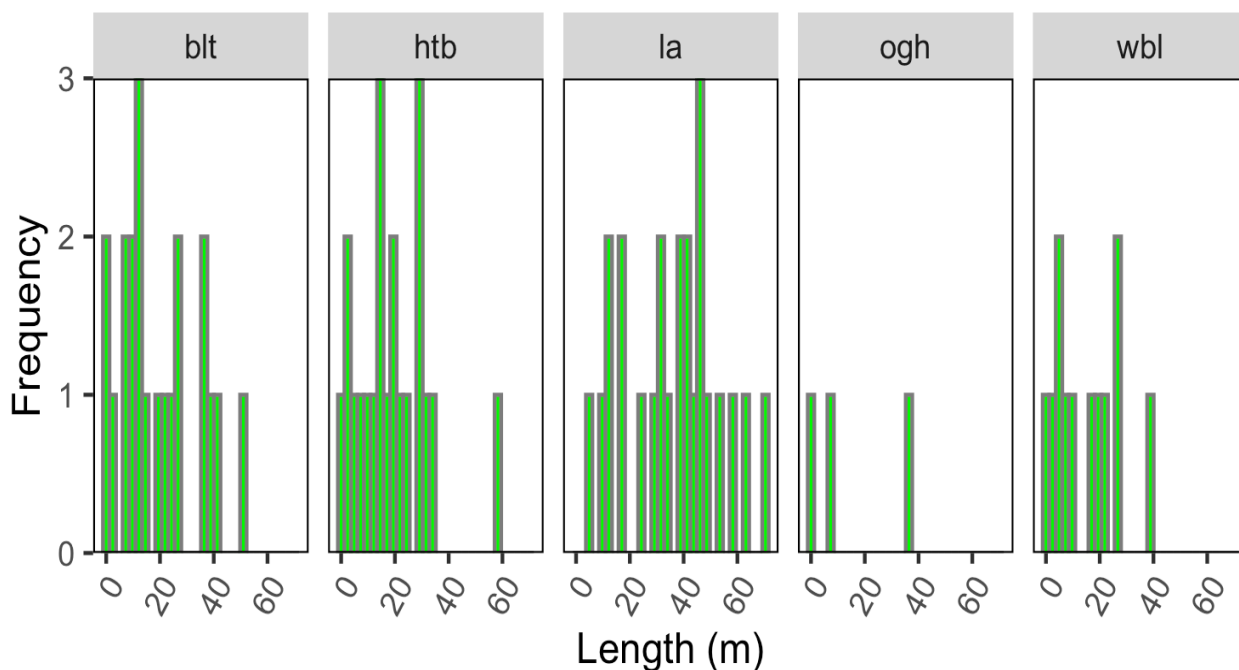


Figure 4. Frequency histogram of leaf area index recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl) (empty quadrats excluded).

Mean leaf area index per quadrat, in ascending order, was: ogh (mean = 14.71 m, 95% c.i. = [6.56, 32.97]), wbl (mean = 14.86 m, 95% c.i. = [9.93, 22.25]), htb (mean = 18.75 m, 95% c.i. = [13.82, 25.44]), blt (mean = 19.6 m, 95% c.i. = [14.45, 26.59]), la (mean = 35.94 m, 95% c.i. = [27.02, 47.8]).

4.1.4 Wasting disease

Distributions of wasting disease prevalence across quadrats at each of the sampling sites are presented in Figure 5. Prevalence is measured as the proportion of infected leaves per shoot, averaged across a given quadrat.

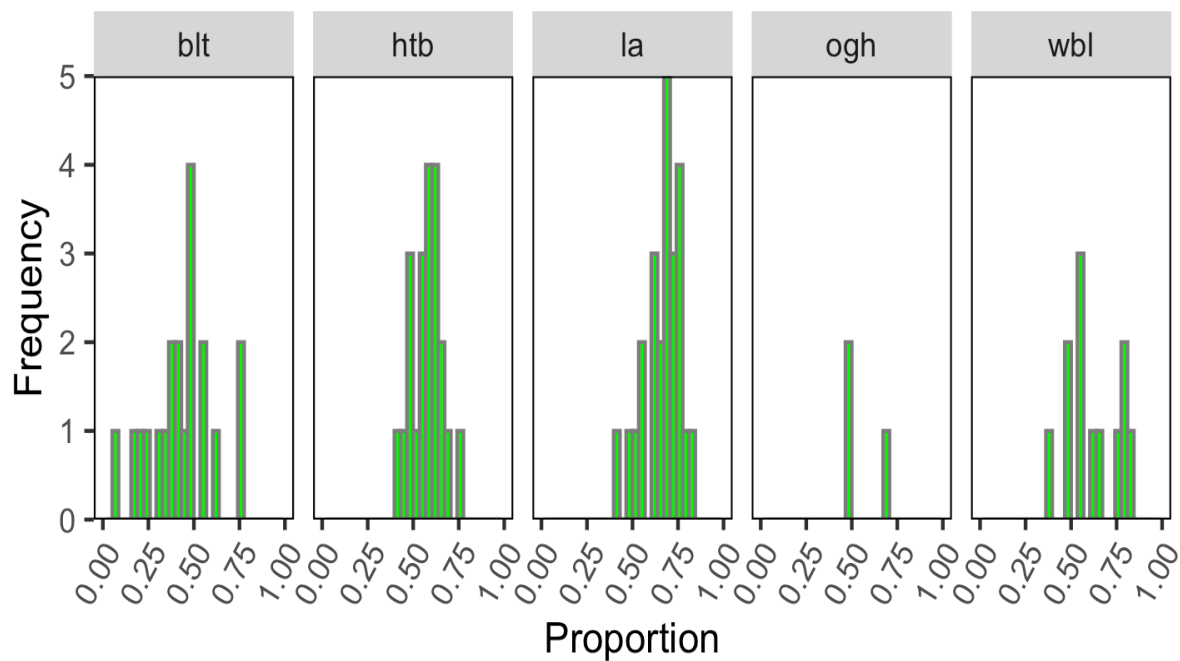


Figure 5. Frequency histogram of wasting disease prevalence recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl) (empty quadrats excluded).

Mean proportion of infected leaves per quadrat, in ascending order, was: blt (mean = 0.4, 95% c.i. = [0.35, 0.45]), ogh (mean = 0.54, 95% c.i. = [0.4, 0.68]), htb (mean = 0.55, 95% c.i. = [0.5, 0.6]), wbl (mean = 0.62, 95% c.i. = [0.54, 0.69]), la (mean = 0.68, 95% c.i. = [0.64, 0.73]).

4.1.5 Epiphytes

Distributions of average epiphyte scores across quadrats at each of the sampling sites are presented in Figure 6.

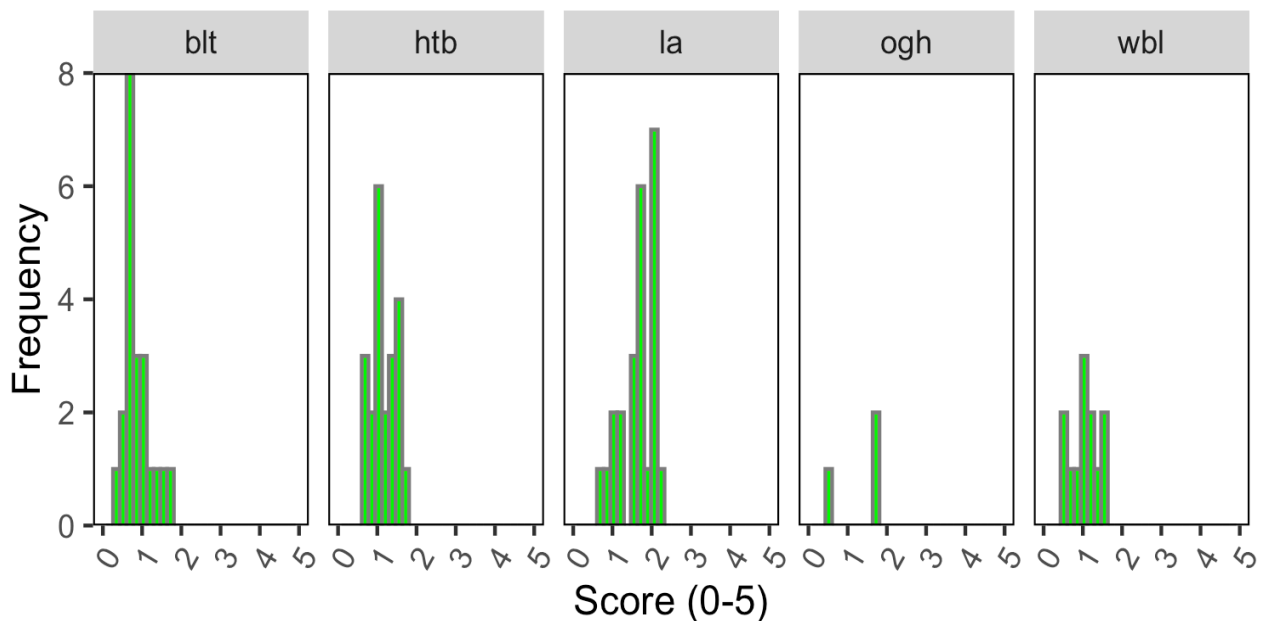


Figure 6. Frequency histogram of average epiphyte scores recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl) (empty quadrats excluded).

Mean quadrat-averaged epiphyte score per quadrat, in ascending order, was: blt (mean = 0.9, 95% c.i. = [0.75, 1.05]), wbl (mean = 1.05, 95% c.i. = [0.9, 1.3]), htb (mean = 1.2, 95% c.i. = [1.05, 1.35]), ogh (mean = 1.2, 95% c.i. = [0.85, 1.7]), la (mean = 1.65, 95% c.i. = [1.5, 1.8]).

4.2 Time series results from 1996 - present

4.2.1 Quadrat occupancy

Time series are presented in Figure 7 and Table 3. No statistically significant trends were observed with the exception of a monotonic decrease in quadrat occupancy at Old Grimsby Harbour.

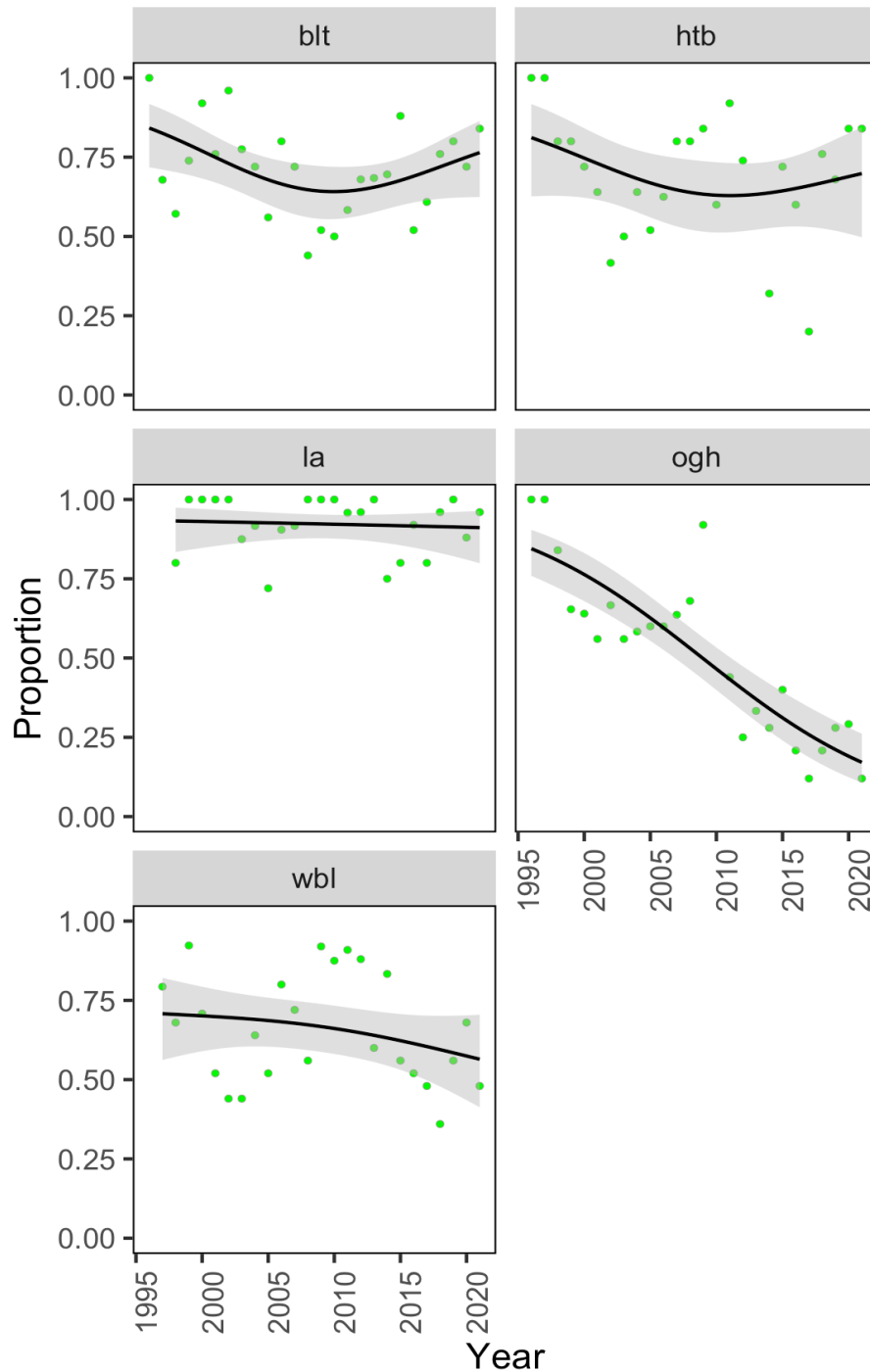


Figure 7. Time series plot of the proportion of occupied quadrats recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 2. Statistical summary of a GAM for the proportion of occupied quadrats recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	F	p.value
blt	1.761	1.943	1.706	0.152
htb	1.728	1.926	1.729	0.134
la	1.000	1.000	0.121	0.728
ogh	1.000	1.000	36.238	0.000
wbl	1.346	1.572	1.626	0.314

4.2.2 Shoot count

Time series of shoot counts throughout the monitoring period, at each of the sampling locations, are presented in Figure 8 and Table 4. Shoot density showed a statistically significant decline at Broad Ledges Tresco and Higher Town Bay.

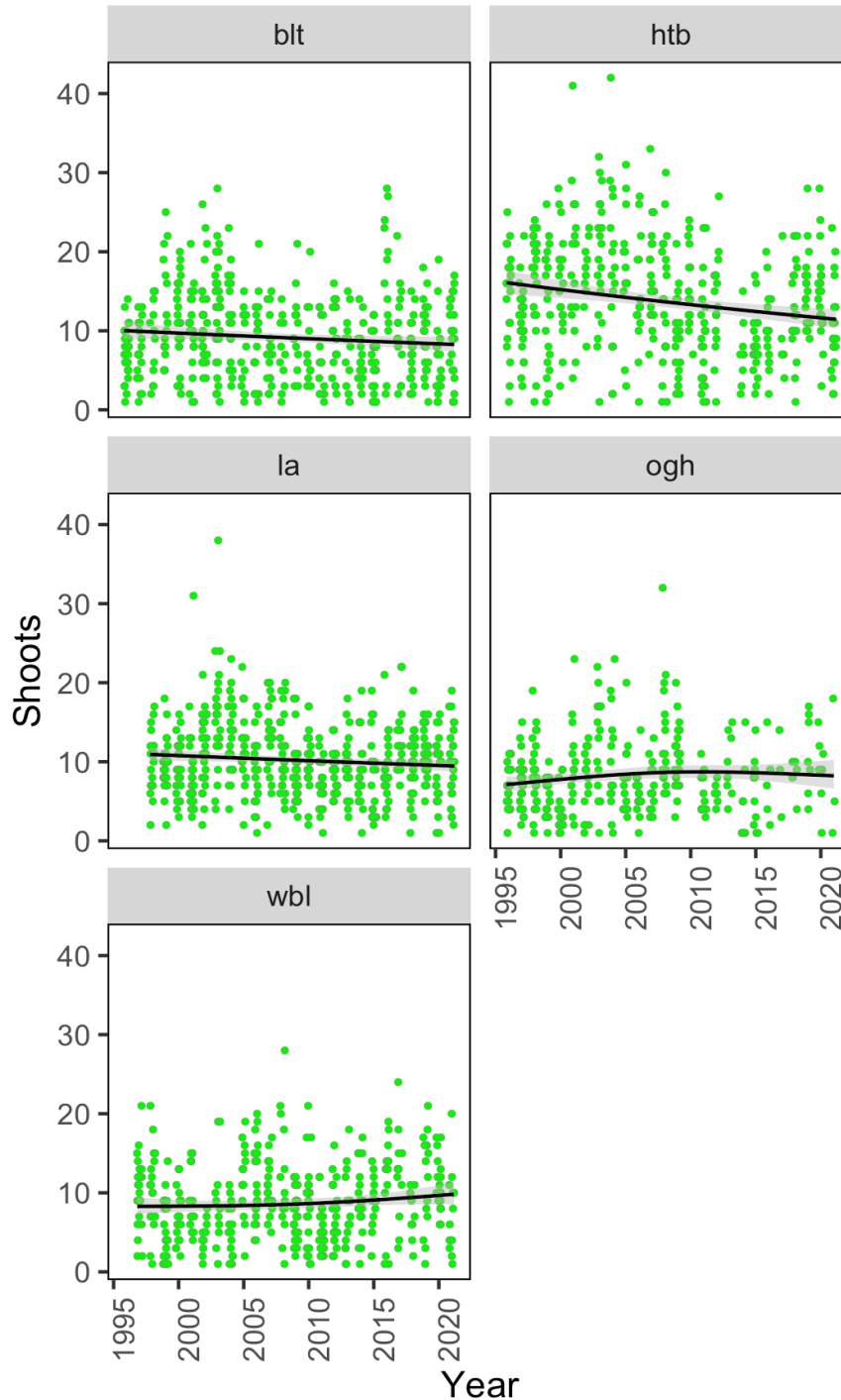


Figure 8. Time series plot of the number of eelgrass shoots recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 3. Statistical summary of a GAM for the number of shoots per quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	Chi.sq	p.value
blt	1.002	1.004	5.088	0.024
htb	1.002	1.005	16.900	0.000
la	1.002	1.004	3.187	0.075
ogh	1.660	1.884	5.321	0.119
wbl	1.490	1.740	2.448	0.159

4.2.3 Canopy height

Time series of canopy heights throughout the monitoring period, at each of the sampling locations, are presented in Figure 9 and Table 5. No statistically significant trends in canopy height were observed with the exception of a monotonic increase at Broad Ledges Tresco.

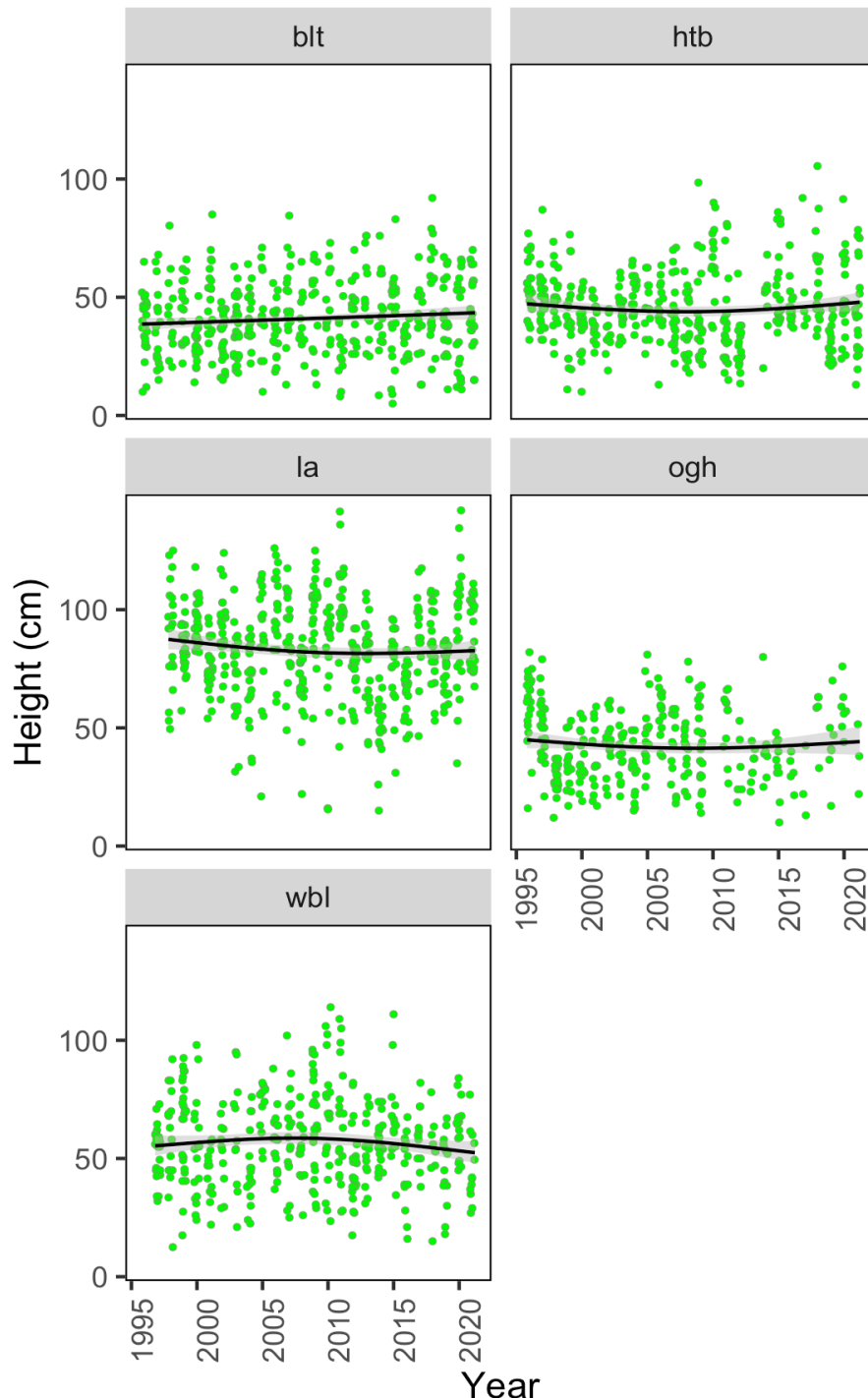


Figure 9. Time series plot of canopy heights recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 4. Statistical summary of a GAM for the canopy heights per quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	F	p.value
blt	1.000	1.001	5.249	0.022
htb	1.775	1.949	1.885	0.143
la	1.354	1.583	0.689	0.345
ogh	1.647	1.875	1.533	0.275
wbl	1.758	1.942	1.784	0.139

4.2.4 Leaf area index

Time series of leaf area index (LAI) throughout the monitoring period, at each of the sampling locations, are presented in Figure 10 and Table 6. Statistically significant declines in LAI were observed at Higher Town Bay and Little Arthur.

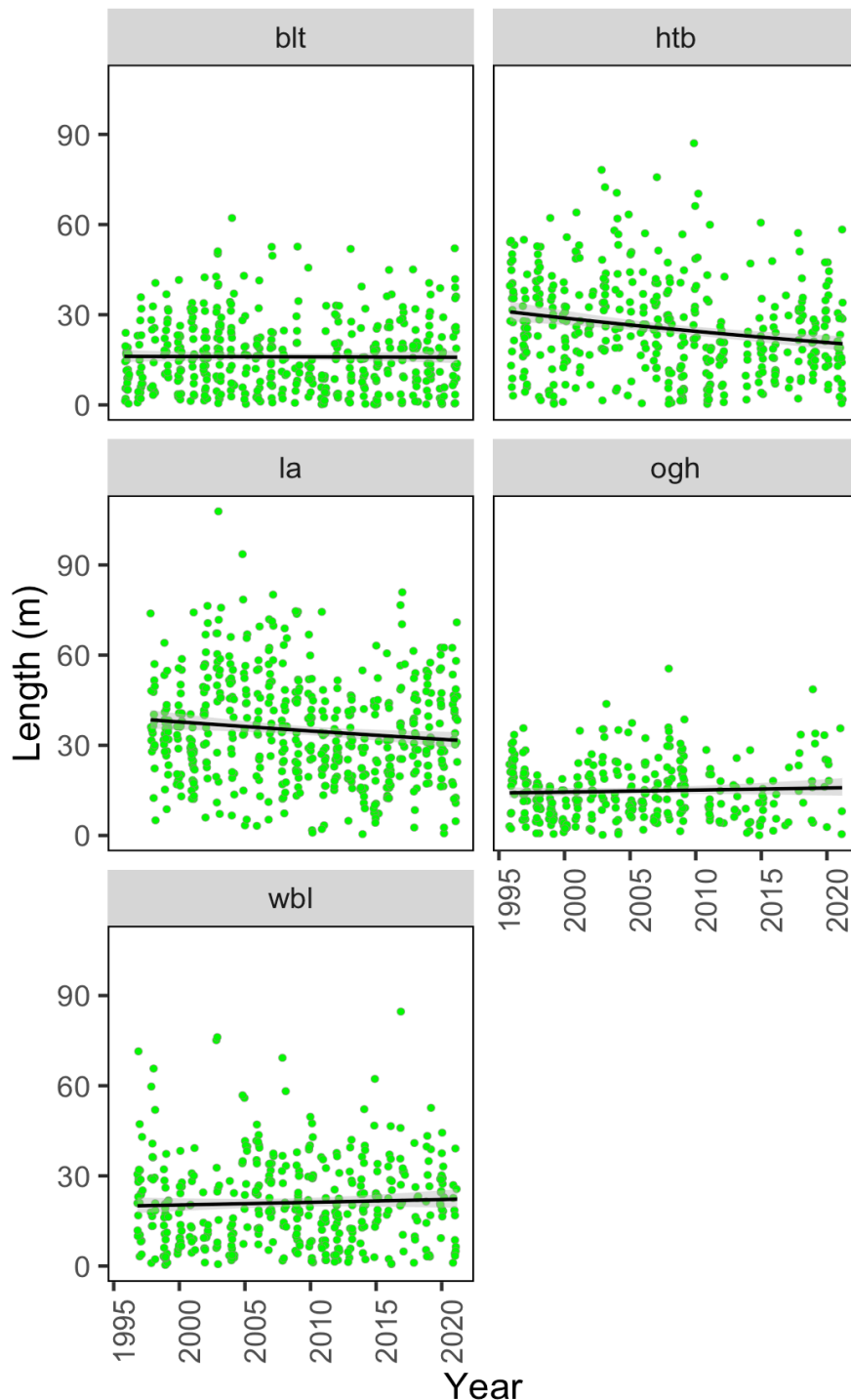


Figure 10. Time series plot of leaf area index recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 5. Statistical summary of a GAM for the leaf area index per quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	F	p.value
blt	1.000	1.000	0.035	0.852
htb	1.000	1.000	17.984	0.000
la	1.000	1.000	4.558	0.033
ogh	1.000	1.001	0.748	0.387
wbl	1.000	1.000	0.846	0.358

4.2.5 Wasting disease

Time series of the proportion of infected leaves per quadrat throughout the monitoring period, at each of the sampling locations, are presented in Figure 11 and Table 7. Statistically significant increases in wasting disease were observed at all sites except Old Grimsby Harbour. At Broad Ledges Tresco, Higher Town Bay, and West Broad Ledges this initial increase peaked around 2010 with subsequent decline.

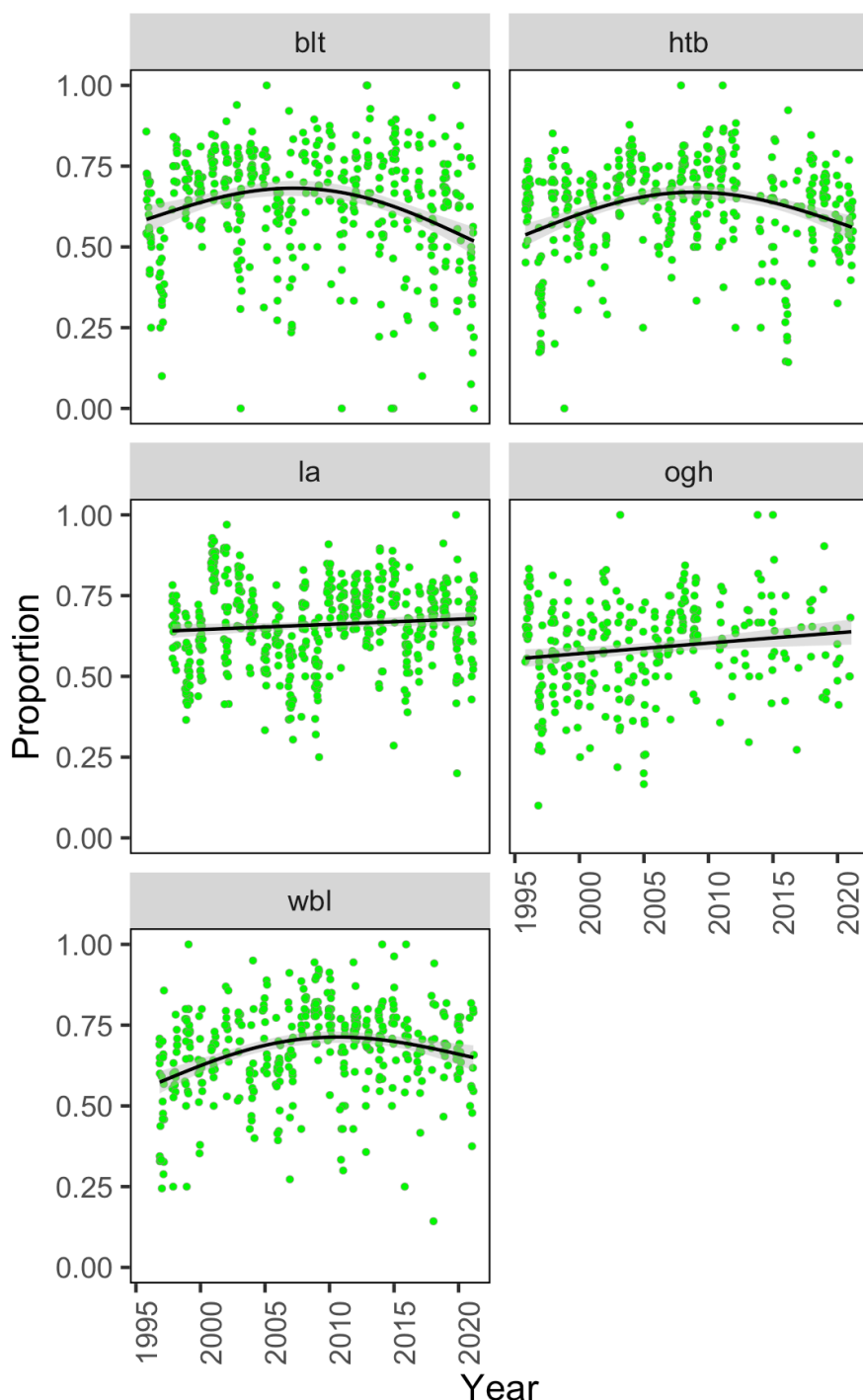


Figure 11. Time series plot of wasting disease prevalence recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 6. Statistical summary of a GAM for the wasting disease prevalence per quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	F	p.value
blt	1.979	2.000	29.382	0.000
htb	1.983	2.000	30.748	0.000
la	1.000	1.000	5.722	0.017
ogh	1.434	1.680	3.132	0.115
wbl	1.969	1.999	28.102	0.000

4.2.6 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 8. Statistically significant increases in epiphyte cover were observed at all sites except Old Grimsby Harbour. At Higher Town Bay and West Broad Ledges this initial increase peaked around 2010 with subsequent decline, while at Little Arthur the peak was around 2012.

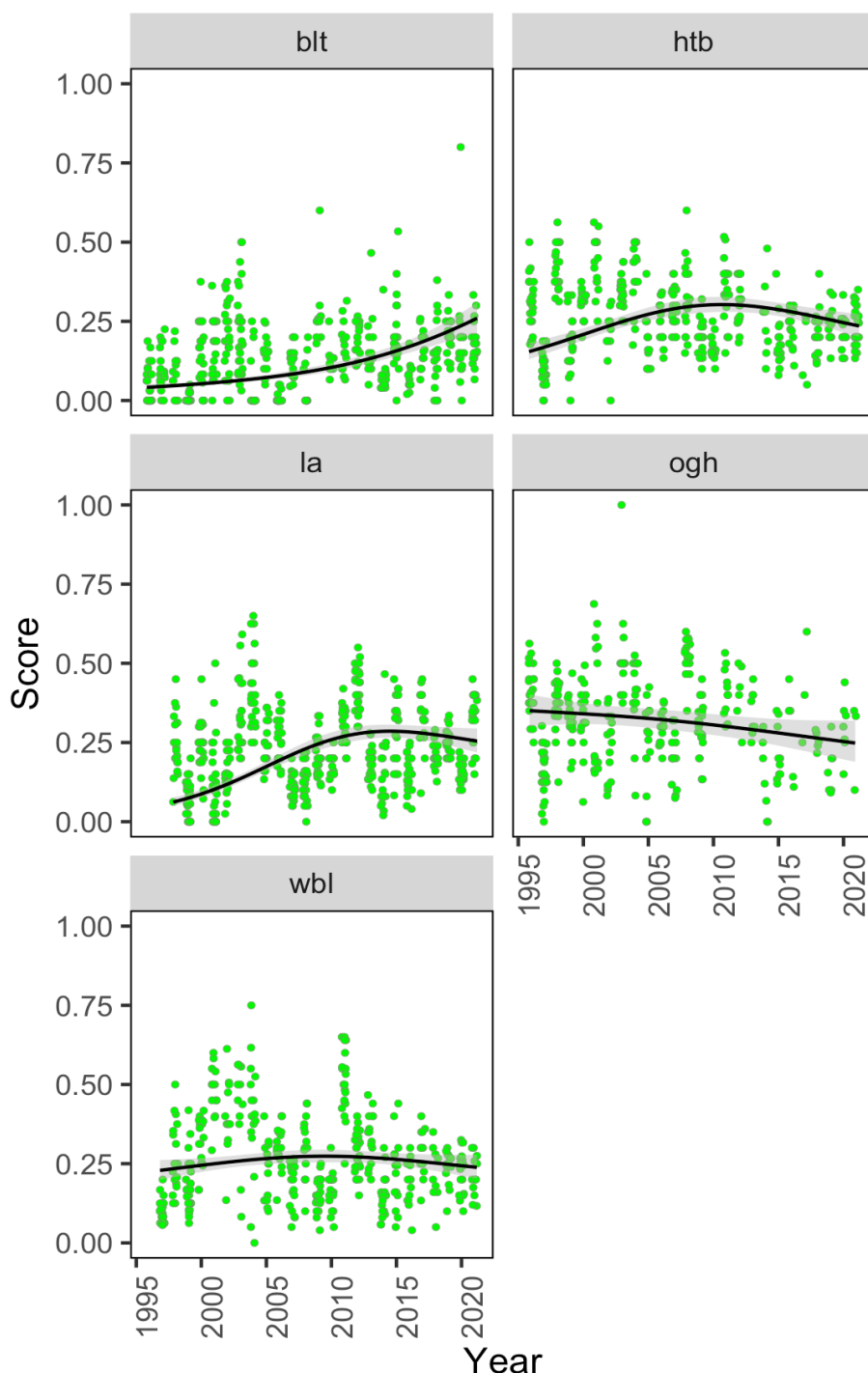


Figure 12. Time series plot of average epiphyte scores recorded per 25 x 25cm quadrat at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl).

Table 7. Statistical summary of a GAM for the average epiphyte pers quadrat recorded at each of the five survey locations. Broad Ledges Tresco (blt), Higher Town Bay (htb), Little Arthur (la), Old Grimsby Harbour (ogh), and West Broad Ledges (wbl). A p-value of greater than 0.05 indicates no statistically significant trend over time. An edf ('effective degrees of freedom') value of one indicates a linear trend, with larger values indicating greater complexity in the trend.

Sites	edf	Ref.df	Chi.sq	p.value
blt	1.784	1.953	311.587	0.000
htb	1.964	1.999	52.946	0.000
la	1.981	2.000	213.834	0.000
ogh	1.347	1.574	0.554	0.538
wbl	1.845	1.976	11.849	0.006

5 Discussion

5.1 Key findings for eelgrass

This year, the overall picture was one of slightly lower than average eelgrass shoot density and slightly higher than average canopy height. These metrics combine with the number of leaves per shoot to result in a measure of productivity described as leaf area index (LAI), with 2021 showing lower than average LAI. 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 lower than average levels of available light (Abal et al. 1994). However, a single year snapshot in a highly variable ecosystem is comparatively uninformative. Next, 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. Broad Ledges Tresco and Higher Town Bay showed small but statistically significant declines. However, while we see some idiosyncrasies between survey sites, there is little evidence of any long-term trend overall across our sampling locations. This picture is encouraging; however, we caution too much optimism on two counts: 1) no single metric is, on its own, a reliable indicator of eelgrass status (Jones & Unsworth 2016), and 2) our long-term survey of temporal and spatial patterns does not focus on identifying underlying processes and mechanisms.

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 decreased throughout the whole of the study period. Overall, there has been a 18.6 % decline since monitoring began. Separated by survey location, percentage changes at each of the monitoring sites are: Broad Ledges Tresco: 18.7 % decline, Higher Town Bay: 20.3 % decline, Little Arthur: 2.2 % decline, Old Grimsby Harbour: 67.9 % decline, and West Broad Ledges: 13.7 % decline. However, we have seen improvements at Broad Ledges Tresco and Higher Town Bay, and only Old Grimsby Harbour is consistently showing a concerning decline over the whole monitoring period.

5.2 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. Notable 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: initial increases in wasting disease reverse around 2010 at Broad Ledges Tresco, Higher Town Bay, and West Broad Ledges, but with a consistent increase at Little Arthur and no change at Old Grimsby Harbour. Related work, using eelgrass in the Isles of Scilly as a case study, has indicated that there is a complex interplay between the spatial pattern of eelgrass 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.

5.3 Epiphyte cover and *Sargassum muticum*

Since 2017, we have also used our complete records from 1996 onwards to analyse long-term trends in epiphyte cover. Epiphyte cover has shown nonlinear trends at several sites in our survey, but with no consistency in the timing of increases and decreases between sites: initial increases were observed at all sites except Old Grimsby Harbour, this accelerated at Broad Ledges Tresco but reversed at Higher Town Bay, Little Arthur, and West Broad Ledges. *S. muticum* has spread invasively 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.

5.4 Synthesis

More than two decades 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. The picture for eelgrass around the Isles of Scilly is one of relative stability across the archipelago. This is highly encouraging against a backdrop of serious global decline for the species. However, we do see both short-term fluctuations and longer-term trends that indicate susceptibility to change even in this relatively pristine environment. In particular, the eelgrass at Old Grimsby Harbour continues to fragment and this is a matter of serious local concern. With its range of environmental and anthropogenic influences, the Isles of Scilly SAC would make an excellent candidate for investigation of the mechanisms and processes underpinning resilience in eelgrass, and this is our key recommendation to move from observation to understanding of ecosystem change. This would be a necessary first step

towards developing effective mitigation strategies in the face of environmental and climate change. Annual monitoring remains the bedrock of understanding resilience, with inter-annual fluctuations and rates of change being needed to quantify the two most widely recognised elements of ecosystem resilience; namely 'resistance' to, and 'recovery' from perturbation. In this way, baseline monitoring can be elevated to empower ecologists and conservation managers to understand the causes and consequences of change. We also urge developing an integrated approach through linking experimental studies, studies of population genetics, socio-economics, and detailed quantification of hydrodynamic forcing, in order to seize the opportunity to develop the Isles of Scilly SAC into an ecosystem resilience study site of global importance. Building on the unrivalled baseline data on eelgrass now available here, this ambitious aim is both desirable and achievable.

6 Acknowledgments

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 Bed & Breakfast for putting us up and putting up with us. We are very grateful to the many residents of the Isles of Scilly who helped us overcome numerous logistical issues and make the survey a success.

7 References

Abal EG, Loneragan N, Bowen P, Perry CJ, Udy JW, Dennison WC (1994) Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers, to light intensity. *J. Expt. Mar. Biol. Ecol.* 178: 113-129.

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 Algal* 6: 239-251.

den Hartog C (1987) Wasting disease and other dynamics phenomena in *Zostera* beds. *Aquat. Bot.* 27: 3-14.

den Hartog C (1989) Early records of wasting disease-like damage patterns in eelgrass *Zostera marina*. *Dis. Aquat. Organ.* 7: 223-226.

Duarte CM (2002) The future of seagrass meadows. *Envir. Cons.* 29: 192-206.

Duarte CM, Chiscano CL (1999) Seagrass biomass and production: A reassessment. *Aquat. Bot.* 65: 159-174.

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.

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.

Irvine MA, Bull JC, Keeling MJ (2016c). Disease transmission promotes evolution of host spatial patterns. *Journal of The Royal Society Interface* 13(122): p.20160463.

Irvine MA, Bull JC, Keeling MJ (2018). Conservation of pattern as a tool for inference on spatial snapshots in ecological data. *Scientific reports* 8(1): p.132.

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.

McGlathery KJ, Reidenbach MA, D'Odorico PA, Fagherazzi S, Pace ML, Porter JH (2013) Nonlinear dynamics and alternative stable states in shallow coastal systems. *Oceanography* 26: 220-231.

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.

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

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

Potouroglou M, Bull JC, Krauss KW, Kennedy HA, Fusi M, Daffonchio D, Mangora MM, Githaiga MN, Diele K, Huxham M, (2017) Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports* 7: 11917.

R Core Team (2020) 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.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18: 648-656.

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, van Nes EH, van Katwijk MM, Olf H, Smolders AJ (2011) Positive feedbacks in seagrass ecosystems - evidence from large-scale empirical data. *PLoS ONE* 6: e16504.

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.

van Katwijk MM, Schmitz GH, Hanssen LS, den Hartog C (1998) Suitability of *Zostera marina* populations for transplantation to the Wadden Sea as determined by a mesocosm shading experiment. *Aquatic Botany* 60: 283-305.

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.

8 Appendix 1 - Summary data for the current year

Note that some cells in the following tables have been left blank.

8.1 Broad Ledges Tresco

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
0.00						135.00	6.90
0.00						211.00	9.10
0.00						89.00	4.70
0.00						358.00	25.00
13.00	66.00	4.00	36.10	0.54	0.75	288.00	21.00
10.00	45.00	4.00	18.79	0.78	0.71	57.00	14.50
5.00	57.00	5.00	13.15	0.62	0.33	170.00	15.10
9.00	36.00	4.00	13.08	0.34	0.67	33.00	18.90
6.00	36.00	4.00	8.85	0.43	0.58	331.00	27.90
12.00	57.00	4.00	25.61	0.48	0.90	63.00	23.50
17.00	70.00	5.00	52.10	0.22	0.75	168.00	18.70
15.00	64.00	4.00	35.46	0.42	0.75	63.00	21.90
7.00	31.00	3.00	7.46	0.39	0.50	343.00	19.60
14.00	37.50	4.00	22.64	0.17	0.78	220.00	29.50
10.00	56.00	4.00	24.57	0.39	0.90	182.00	12.00
2.00	43.00	4.00	3.44	0.25	0.75	274.00	20.10
1.00	15.00	3.00	0.45	0.00	1.67	249.00	16.80
12.00	29.50	3.00	12.36	0.07	0.67	123.00	22.60
1.00	15.00	4.00	0.60	0.75	1.00	72.00	27.50
5.00	55.00	4.00	9.70	0.50	1.50	330.00	30.00

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
15.00	38.00	4.00	25.97	0.32	1.00	289.00	23.20
14.00	64.00	4.00	39.09	0.48	1.25	282.00	26.80
16.00	64.00	4.00	41.86	0.40	1.00	159.00	21.30
9.00	39.00	3.00	13.74	0.56	1.33	174.00	9.50
4.00	40.50	3.50	6.53	0.47	0.90	4.00	8.60

8.2 Higher Town Bay

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
						102.00	18.50
0.00						205.00	20.60
0.00						168.00	23.70
0.00						217.00	28.80
2.00	25.50	3.00	1.84	0.67	1.00	31.00	28.60
17.00	47.00	4.00	30.56	0.62	1.00	19.00	12.00
9.00	43.00	3.00	14.16	0.55	0.67	337.00	17.00
13.00	29.00	3.00	17.08	0.55	1.00	174.00	13.10
9.00	25.00	4.00	8.73	0.57	0.75	207.00	29.90
8.00	75.00	4.00	23.37	0.62	1.23	94.00	18.80
13.00	69.00	4.00	34.04	0.44	1.00	65.00	23.90
20.00	41.50	3.50	28.63	0.40	1.00	154.00	16.00
8.00	54.00	4.00	19.05	0.49	0.78	299.00	15.50
5.00	28.00	3.00	5.27	0.69	1.33	43.00	15.90
9.00	42.00	4.00	15.41	0.63	1.50	276.00	22.10
6.00	67.50	4.00	15.71	0.64	0.88	77.00	28.50
8.00	76.00	5.00	29.19	0.50	1.27	74.00	25.10
6.00	36.00	3.50	7.19	0.62	0.88	140.00	18.70
2.00	13.00	2.00	0.52	0.50	1.75	301.00	16.50
18.00	78.50	5.00	58.34	0.54	1.63	63.00	26.00
23.00	34.00	3.00	28.79	0.59	1.60	134.00	18.60
11.00	28.00	4.00	12.95	0.52	1.00	357.00	21.20
8.00	51.50	4.50	19.01	0.57	1.33	46.00	26.30
11.00	45.00	4.00	21.18	0.60	1.40	338.00	23.70
4.00	19.50	3.00	2.72	0.77	1.54	18.00	7.20

8.3 Little Arthur

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
0.00						283.00	3.10
17.00	108.00	4.00	70.90	0.54	0.75	189.00	18.30
8.00	86.50	4.00	24.46	0.67	1.00	220.00	15.80
13.00	104.00	4.00	46.60	0.61	1.67	257.00	12.10
6.00	73.50	4.00	17.78	0.67	2.00	296.00	19.50
15.00	75.00	4.00	43.62	0.71	1.00	249.00	21.00
2.00	67.50	3.50	4.73	0.43	0.92	188.00	17.70
6.00	74.50	4.00	16.92	0.52	1.75	295.00	30.00
12.00	83.00	4.00	40.91	0.75	1.63	234.00	29.40
7.00	104.00	4.00	31.02	0.55	1.60	77.00	29.30
7.00	103.00	5.00	31.97	0.69	1.60	99.00	13.80
3.00	107.00	4.00	12.60	0.50	1.75	123.00	20.80
11.00	100.00	4.00	39.16	0.61	1.75	338.00	25.00
15.00	74.00	4.00	38.35	0.72	1.25	215.00	28.00
17.00	80.00	4.00	58.09	0.68	1.25	249.00	21.90
10.00	106.50	5.00	46.37	0.68	1.80	108.00	27.90
10.00	111.00	5.00	48.67	0.80	1.73	292.00	13.50
19.00	78.00	4.00	62.44	0.77	2.00	238.00	22.10
10.00	75.50	4.50	30.25	0.71	1.92	219.00	20.20
9.00	95.00	4.00	34.06	0.63	2.00	67.00	25.00
14.00	77.00	4.00	45.30	0.71	2.00	309.00	20.20
3.00	99.00	4.00	10.78	0.73	2.25	80.00	27.20
12.00	102.50	4.50	53.54	0.76	2.00	70.00	15.30
10.00	101.50	4.00	41.82	0.76	2.00	37.00	19.70
4.00	78.50	4.00	12.12	0.81	2.00	301.00	27.10

8.4 Old Grimsby Harbour

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
0.00						30.00	23.60
0.00						169.00	28.50
0.00						122.00	11.40
0.00						84.00	12.70
0.00						94.00	14.70
0.00						176.00	3.10
0.00						169.00	25.20
0.00						148.00	26.80
0.00						354.00	25.40
0.00						318.00	20.60
0.00						296.00	27.90
0.00						197.00	26.90
0.00						111.00	13.10
0.00						153.00	19.20
0.00						202.00	29.50
0.00						154.00	27.80
0.00						165.00	26.60
0.00						204.00	29.70
0.00						138.00	28.70
0.00						353.00	17.70
0.00						154.00	15.10
0.00						143.00	21.60
1.00	22.00	2.00	0.44	0.50	0.50	9.00	15.90
18.00	51.50	4.00	35.64	0.50	1.75	65.00	27.40
5.00	38.00	5.00	8.05	0.68	1.67	177.00	27.30

8.5 West Broad Ledges

shoots	canopy	leaf	LAI	wasting	epiphytes	bearing	distance
0.00						137.00	19.60
0.00						305.00	22.80
0.00						90.00	25.80
0.00						120.00	21.10
0.00						256.00	27.10
0.00						168.00	27.10
0.00						86.00	25.90
0.00						179.00	29.90
0.00						72.00	29.90
0.00						306.00	29.30
0.00						246.00	24.10
0.00						312.00	16.10
0.00						308.00	17.50
6.00	35.00	4.00	8.66	0.77	1.50	235.00	21.00
10.00	60.00	4.00	22.65	0.79	1.50	52.00	27.10
1.00	27.00	4.00	1.08	0.50	1.00	242.00	17.90
8.00	77.00	4.00	26.93	0.62	0.75	350.00	24.10
12.00	61.50	4.00	25.62	0.55	1.38	90.00	18.10
20.00	56.50	4.00	39.11	0.56	0.88	289.00	14.00
4.00	41.50	4.00	6.42	0.80	0.58	152.00	12.70
11.00	42.00	4.00	18.56	0.48	1.00	66.00	20.00
10.00	49.50	4.00	16.84	0.66	1.29	86.00	20.50
3.00	39.00	4.00	4.13	0.82	1.25	51.00	18.60
4.00	29.00	4.50	4.98	0.56	1.00	22.00	25.60
2.00	37.00	4.00	3.38	0.38	0.60	37.00	14.50

