Master's Thesis

The effect of shore characteristics on *Fucus* macroalgae on the West coast of Scotland

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Rocky shores are fascinating habitats to study due to their varying conditions. Exposure is an important factor determining the geographic distribution and size of many marine algal species. A brown marine macroalgae *Fucus spiralis var. platycarpus* was given species status as *F. guiryi* in 2011. Though it was previously thought to have been a subspecies of *F. spiralis,* it is also similar to *F. vesiculosus* in morphology. The size and abundance of these three species have not yet been correlated to their environment and especially *F. guiryi* is not well known. This study aimed to shed light on how we can separate *F. spiralis*, *F. guiryi*, and *F. vesiculosus* along the west coast of Scotland. The second aim was to compare their zonation in the north to the zonation in their more southern range, including Portugal. The third aim was to understand the role that shore shelteredness played in the size and abundance of these species. Aspect (compass direction), slope, and substrate were recorded for eighteen shores. Transects were laid out to span the intertidal zone inhabited by the species, allowing calculation of percentage cover and zonation. Individuals of each species were measured for their length, maximum circumference, and thallus width. The species were so different in size as well as morphology that it was possible to distinguish them. The zonation patterns found in the species' southern range are reflected in their northern distribution apart from not having a zone with all three species. *F. vesiculosus* preferred sheltered shores whilst *F. guiryi* and *F. spiralis* showed no distinct preference.

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Hakusanat: *Fucus guiryi*, *Fucus spiralis*, *Fucus vesiculosus*, kivikkorannat, merilevät, runsaus, suojaisuus, vuorovesivyöhyke

Merien kivikkorantoihin vaikuttavat voimat luovat monipuolisen ja vaihtelevan ympäristön, missä voidaan tutkia suojaisuuden vaikutusta lajien kasvuun ja levinneisyyteen. Vuonna 2011, ennen *Fucus spiralis* -lajin alalajina pidetty *Fucus spiralis var. platycarpus* sai lajinimen *Fucus guiryi*. Laji on myös läheistä sukua lajille *F. vesiculosus*. Näiden kolmen lajin kokoa ja runsautta ei ole vielä verrattu niiden elinympäristön altistuneisuuteen. Tämän tutkimuksen tavoitteena oli tarkastella kuinka selkeästi nämä kolme lajia eroavat toisistaan Skotlannin länsirannikolla. Toisena tavoitteena oli verrata lajien vyöhykkeitä Skotlannissa eteläisen levinneisyysalueen vyöhykkeisyyteen Portugalissa. Tämän lisäksi tavoitteena oli selvittää kuinka rannan suojaisuus vaikuttaa lajien kokoon ja runsauteen. Suojaisuuden määrittämiseen käytettiin rannan kompassisuuntaa, kaltevuutta ja kasvualustaa. Aineiston keruuta varten käytettiin vuorovesivyöhykkeen yli kulkevia laskentalinjoja. Yksilöiltä mitattiin pituus, ympärysmitta ja varren paksuin kohta. Pituuden ja ympärysmitan avulla laskettiin yksilön tuuheus. Tulokseksi saatiin, että koon ja morfologian perusteella lajit on mahdollista erottaa toisistaan kyseisellä levinneisyysalueella. Eteläisen levinneisyysalueen vyöhykkeisyys on verrattavissa pohjoisemman alueen vyöhykkeisyyteen, vaikka vastaavaa kolmen lajin vyöhykettä ei löytynyt. Koon ja runsauden perusteella *F. vesiculosus* suosi suojaisempia rantoja, *F. guiryi* kasvoi samalla lailla suojaisuudesta riippumatta ja *F. spiralis* menestyi vaihtelevasti kummankinlaisilla rannoilla.

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1 INTRODUCTION

1.1 The rocky shore environment

Rocky shores are intertidal areas of coast mostly composed of medium to large rock formations. Rocky shores are an ecotone where a terrestrial and a marine habitat meet. This type of ecosystem includes characteristics of both habitats, as well as their overlapping area. This creates a unique shifting environment of tides and the challenging conditions caused by them. These challenges include desiccation, wave exposure, temperature changes, and changing light conditions. Tides are one of the most important features of a rocky shore environment (Harley 2008). This means that organisms living on rocky shores not only have to survive the daily changes in desiccation and submersion, but also monthly changes in the time exposed. This variable environment creates many available niches to fill. The species are often highly specialized and adapted to their specific environments and can also be very responsive to environmental change (Mieszkowska et al. 2006, Hawkins et al. 2008). Indeed, rocky shores are home to a highly diverse collection of species (Thompson et al. 1996) including macroalgae, barnacles, and limpets. These species are sessile which facilitates easy sampling of whole ecosystems on rocky shores.

The intertidal zone lies between the highest and lowest tide marks and can include several zones. Different categories of shore exposure can be formed based on biological criteria. One is based on Ballantine's categorization which relates species composition to varying degrees of shelteredness (Ballantine 1961). Macroalgae species in the genus *Fucus* are typically found on the three most sheltered shores (Ballantine 1961) but can extend into more exposed habitats as well (Lewis 1964). *Fucus vesiculosus* is capable of growing over a meter long but tends to do so only in sheltered environments.

1.2 Effects of climate change on rocky shores

As global climate changes and most likely creates warming sea waters (Meehl et al. 2005), the distributional ranges of marine species will change as well. Therefore, it is important to know the distribution of species so that changes in their distribution and abundance can be followed (Thomas et al. 2004). For example, species of plankton (Beaugrand et al. 2001), fish (Genner et al. 2004), and benthos (Hiscock et al. 2004) have shown distributional shifts towards the poles. Distributional shifts of intertidal species have been noticed as well (Southward et al. 2005). Since the intertidal zone is affordable to sample and manage experimentally, it is an excellent habitat to observe these broader scale changes in marine biota (Hawkins et al. 2009).

Many species are predicted to track temperature changes with distributional shifts often towards cooler habitats, and in the case of marine species, poleward (Stenseth et al. 2002, Chen et al. 2011). However, the response of a single species to warmer temperatures can be highly variable (Martínez et al. 2012). For example, in a study done by Lima et al. (2007), it was discovered that a similar number of species shifted north as did to the south. All warm-water species expanded their range northwards (Lima et al. 2007). All the different forces resulting from climate change on individuals are complex (Gaylord 1999, Helmuth and Denny 2003), so, it is not always easy to predict how each species will respond to these changes.

Rising sea levels due to climatic change will also affect the zonation of species on shores. The main limitation for their high shore limits being physical stress, such as desiccation (Lubchenco 1980). Whilst lower shore limits are most likely guided by biotic interactions, such as herbivory (Connell 1972, Underwood 1979). The effect of rising sea levels can also be seen in changes in desiccation and submersion times. The shape of the shore, including its slope, will have an effect on how various species will change their distribution.

Wave action creates another gradient in conjunction with rising sea levels. It can be thought of as an environmental gradient, though it does not affect the shoreline in such clearly defined limits as does desiccation (Raffaelli and Hawkins 2012). Especially high shore dwelling species can have an easier time inhabiting exposed shores due to wave spray abating desiccation problems. On the other hand, exposure to large wave forces creates a risk of dislodgement (Carrington 1990, Blanchette 1997). A case study was made with *Fucus gardneri* in which individuals from exposed shores (shores experiencing strong wave action) were transplanted to sheltered shores (shores protected from strong wave action) and vice versa. The individuals transplanted to exposed sites decreased in size significantly and the ones transplanted to sheltered sites increased in size (Blanchette 1997). This could suggest that as the climate warms and strong storms and waves become more frequent, algal species might adapt to the changing conditions by becoming smaller. Zonation of rocky shore habitats would be expected to also shift from communities dominated by fucoid algae to communities dominated by more hardy species, including barnacles and limpets (Ballantine 1961, Southward et al. 1995).

1.3 *Fucus* algae and zonation of rocky shores

The family *Fucaceae* includes seven species of brown algae, as well as their subspecies (Hardy et al. 2006). Many of these species are important bioengineers on northern rocky shores. This means that they modify habitats, increase spatial complexity, and facilitate the presence of other species (Seed and O'Connor 1981). Associated with high biodiversity on rocky shores, they provide shelter and act as important primary producers in the oceans (Thompson et al. 1996). *Fucus* canopies are also important in protecting high-shore sub-canopy algae and the settling of barnacles (Hawkins 1983, Leonard 2000, Ingolfsson and Hawkins 2008). Macroalgal species also provide ecosystem services like nourishment, medicine, and storm protection (Rönnbäck et al. 2007).

Fucus species are predominantly found on more sheltered shores in their northern distribution. However, they can also be found on more exposed shores (Lewis 1964). Wave exposure is one of the most important constraining factors to plant growth on intertidal shores (Blanchette 1997). Individuals on more exposed shores are often smaller than on sheltered shores (Lewis 1968, Menge 1976). *Fucus* need a stable enough substrate to adhere to e.g. large rocks or bedrock, though they can also attach themselves to smaller rocks (personal observation). More exposed shores will have mostly large rocks and bedrock as opposed to sheltered ones which can exhibit more sand, silt, mud or small rocks. The way the shore is oriented affects the way it experiences wave and solar radiation exposure. Shores facing directly to the west on the west coast are likely to be more exposed than shores oriented to the south for example. On the other hand, in the northern hemisphere, north-facing surfaces will remain cooler than south-facing or flatter surfaces because south-facing shores experience more direct sunlight and thus will be more susceptible to harsh desiccation (Helmuth and Hofmann 2001, Harley and Helmuth 2003). The slope of the shore is important because the steeper the slope the smaller the available living space is for all species. The tide also goes down and comes back up more rapidly on flatter shores compared to the gradual change on a steep slope. Because of this, a steeply sloped shore will most likely exhibit more clearly separated zones than a gently sloped one. It is also more likely to be exposed to harsher wave action (Helmuth and Denny 2003).

Phenotypic plasticity means that even though the individuals all have the same genotype, they can have varying morphology, e.g. size and color, in different environments. Essentially, it is a direct response to environmental variables like temperature or physical disturbance and has been recorded in *Fucus* species (Norton 1991, Chapman 1995). There is a large amount of within-species morphological variation in the *Fucus* genus (Sideman and Mathieson 1985, Bäck et al. 1993, Bäck 1993) which is due to both genetic and environmental factors (Mathieson et al. 1981). However, there also exist stable morphotypes in different geographical locations, which indicates that these groups within the species have adapted to their specific conditions (Kalvas and Kautsky 1998).

In the Eastern Atlantic Ocean, three species of fucoid algae exist in distinct morphotypes whilst still having some hybridization: *Fucus spiralis, Fucus guiryi* (previously *Fucus spiralis var. platycarpus*) and *Fucus vesiculosus*. In their study, Zardi et al. (2011) suggested that *F. spiralis var. platycarpus* should be elevated to species status as *F. guiryi*. This was based on genetic, morphological, and physiological traits. Though it was previously thought to have been a subspecies of *F. spiralis*, *F. guiryi* is also similar to *F. vesiculosus* in morphology. It can be distinguished from the other species by its unique receptacle sterile rim and monopodial branching (Zardi et al. 2011, see results section for images). *F. spiralis* has characteristically spiraled fronds (Fish and Fish 2011), hence its name. Because the species are in their fertile stage during the summer months, it is easier to distinguish *F. guiryi* from *F. spiralis* in summer when the receptacle sterile rim can be identified (Mathieson et al. 1976, Berger et al. 2001). *F. vesiculosus* has characteristic bladders along the fronds (Fish and Fish 2011) making it distinctive from the other two species.

F. guiryi can be found on the shores of Portugal and Northwestern Africa in areas of cold water, upwelling (Lourenço et al. 2016) and, after a gap on the shores of France, it reappears in Brittany and the British islands (G. I. Zardi personal observation). *F. spiralis var platycarpus* has been recorded as far north as the Scottish Orkney Islands and described as not uncommon (Batters 1902. Figure 1). However, the distribution of *F. guiryi* has not been recorded since its taxonomic split from *F. spiralis,* and thus cannot be assumed to be conclusively accurate. In addition, *F. guiryi* is not always recognized as distinct from *F. spiralis.* For example, in The Marine Life Information Network database, *F. spiralis* is described as having a sterile rim on the reproductive bodies (White 2008), a distinguishing characteristic of *F. guiryi*. This can cause confusion and suggests that at least some recorded instances of *F. spiralis* might actually represent *F. guiryi.*

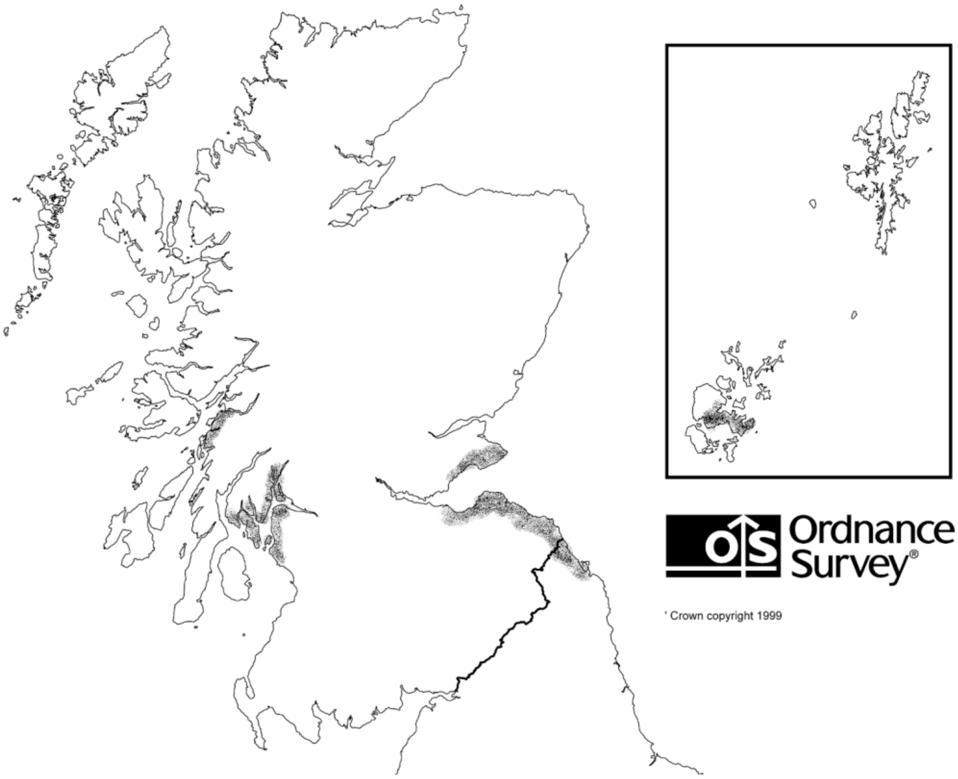

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Figure 1. Shaded areas show the distribution of *Fucus spiralis* var. *platycarpus* in Scotland based on Batters 1902. Outline map of Scotland and Orkney and Shetland Islands (inset) obtained from the Ordnance Survey, UK.

Based on these observations, *F. guiryi* might be more common than previously thought, since it is often mistaken as *F. spiralis* (Coyer et al. 2011). It is known that north from Portugal, *F. vesiculosus* and *F. spiralis* can be found in sympatry, both species being present on the open coast as well as in sheltered habitats. *F. spiralis* can be found from northern Norway to the Azores and Canary Islands, as well as on western Atlantic shores (Lüning 1990, Haroun et al. 2002). *F. spiralis* is widespread on all coasts of Britain and Ireland (Hardy et al. 2006), and thus, it can be hypothesized that *F. guiryi*, should be found in the same range.

On the shores of Portugal and France, sympatry and zonation of the three species have been described in more detail. Zardi et al. (2011) described distinct zones, some with species overlapping. *F. spiralis* inhabiting the zone closest to the shore and *F. vesiculosus* the zone furthest from the shore, with *F. guiryi* in between (Zardi 2011). It is not yet known if they exhibit the same clear zonation in other parts of their range. However, their zonation does overlap to some degree, and *F. vesiculosus* are known to move closer to the shore when *F. spiralis* is removed (Hawkins and Hartnoll 1985, Chapman and Johnson 1990). This suggests that their zonation is a result of competitive exclusion, not just physiological limitations of the algae. For example, *F. spiralis* is outcompeted by *F. vesiculosus* in the mid-shore region (Chapman 1990). Desiccation experiments show that the species are adapted to their respective vertical zones by withstanding different times of emersion (Zardi et al. 2011), with *F. spiralis* being the most able to withstand this type of stress (Davidson and Pearson 1996). Its zone was found to be the same, uppermost intertidal, in the Great Bay estuary system of New Hampshire, USA (Niemeck and Mathieson 1976). This could suggest that the zonation of this species is similar in Scotland if it can be found to be the same across the Atlantic.

Changes in emersion times create competition for the settlement of juveniles. These species do not have planktonic larvae which leads to settlement near the parent algae (Zardi et al. 2011) further helping to maintain the zonation of species. The rate of growth of *F. spiralis* has been studied on the Argyll coast (Knight and Parke 2009) as well as genetic studies focusing on the presence of distinct morphotypes (Coyer et al. 2011). The size and abundance of the species have not yet been correlated to their environment and especially *F. guiryi* is not well known because of its new species status. The west coast of Scotland is exposed to the forces of the Atlantic Ocean, but it is sheltered by close-by islands and archipelagos as well as the shape of the individual shores. This creates shores of different exposure, which enables the comparison of sheltered and exposed shores.

1.6 The aims and hypotheses

The first aim of this study was to clarify the distribution of *F. guiryi* on the west coast of Scotland using morphological features to identify *F. spiralis*, *F. guiryi*, and *F. vesiculosus* in the field. The second aim was to compare the zonation found in Scotland to the zonation found in previous studies in Portugal. The third aim was to see if shore exposure affected the size and abundance of these species in this part of their range. This was done by collecting data of the three species on shores of varying exposure. Exposure was determined by using environmental variables substrate, aspect/compass direction, and slope to get a general degree of exposure. My research questions and their accompanying hypotheses were:

1) Are there enough morphological differences between *F. spiralis* and *F. guiryi* to tell them apart along the west coast of Scotland?

   H0: The species are not easily distinguishable from one another, especially in the field.

   H1: The species are significantly different in size and/or morphology.

2) Does the zonation of the species on the shore in the northern part of their range (Scotland) resemble zonation patterns on shores in the southern part of their range (Portugal)?

   H0: The zonation patterns are identical

   H1: A difference can be found in the zonation patterns

3) Does the shelteredness of the shore affect the size and abundance of the species?

   H0: Shore shelteredness has no effect on algae abundance and/or size.

   H1: Larger individuals and higher abundance can be found on more sheltered shores.

2 METHODS

2.1 Locations and shore characteristics

This study was done in collaboration with SAMS, the Scottish Association for Marine Science, which is based in Oban. Surveys were conducted along the west coast of Scotland and its adjacent islands, Isle of Skye and Isle of Mull during June and July of 2018. In total 18 shores were sampled (see results for precise locations). These included five local shores near Oban and 13 more distant shores, including two from Dumfries and Galloway, six from Ayrshire, and five from the Isle of Skye and Arisaig. The average distance between shores sampled in Ayr was about 10 km. On the Isle of Skye, shores sampled were on average 50 km apart. The distance between the most northern shore and the most southern sampled shore was 340 km.

For each shore, latitude and longitude was determined using the app Map Coordinate version 1.19 by makeSmile. Shelteredness was determined based on openness to sea and the presence of nearby islands. Based on this, all shores were originally divided into four groups but were then later merged into two (sheltered or exposed) due to the small number of shores sampled. The aspect of the shore, which is the compass direction perpendicular to the shoreline, was also determined using the app Map Coordinate version 1.19 by makeSmile.

2.2 Transects

To determine zonation and abundance of algae, a line transect starting from the beginning of the *Fucus* zone to the end of it was laid out perpendicular to the shore (Figure 2). This was done during low tide for easy sampling. The location of the transect was chosen to be a representative sample of the *Fucus* zone.

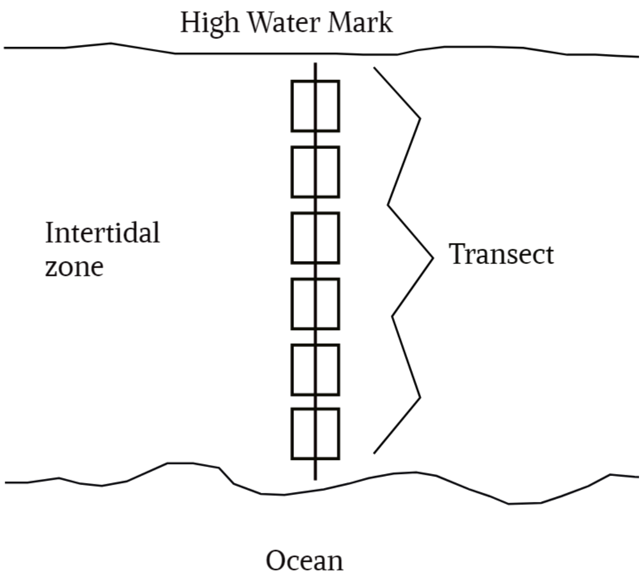

Figure 2. A diagram of a line transect spanning the intertidal zone, including six quadrats. High water mark donating the highest point where water rises and the end of the algae zone.

Leveling measurements to estimate the slope of the shore were done using two, meter long poles (Figure 3). The first pole was positioned at the beginning of the transect. The second pole was taken down the transect at intervals to determine the slope of the shore and where the quadrats would be laid. Because every shore is unique in its topography, a finer scale was used to measure the slope of flatter shores. This was done in order to sample as many individuals per transect as possible. Depending on the length of the *Fucus* zone, this was 5-9 quadrats per transect, and on average 6 quadrats per transect. For some shores, this meant a 0.5 m vertical drop for each interval quadrat point, whereas for others a 0.1 m vertical drop was used. After this, a 50x50 cm quadrat divided into 100 5x5 cm squares was laid in the transects at the measured intervals. The middle of the quadrat was placed at the point in the transect that was measured. For each quadrat, the substrate was determined visually. The substrate could be bedrock, boulders, cobbles or sand.

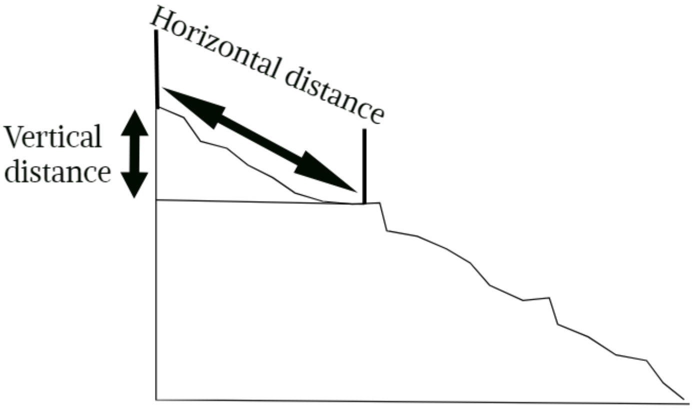

Figure 3. Diagram of the leveling protocol used for determining the slope of the shore. The diagram shows a hypothetical cross-section of a shore with two poles (dark vertical lines) one positioned at the shoreline, beginning the transect, and the other at a horizontal distance along the shore toward the sea. The vertical distance, measuring the difference in height of the seafloor from the shoreline was measured using a scale on the two poles. The horizontal and vertical measurements were used to calculate slope.

Slope (S) is the change in vertical distance in relation to horizontal distance (Equation 1).

$$S = \frac{y2 - y1}{x2 - x1}, \qquad (1)$$

In the equation above, y2 - y1 = Δy, or vertical change, while x2 - x1 = Δx, or horizontal change.

Slope steepness categories were determined by dividing the shores into three groups based on the measured slope. The larger the value is the steeper the slope. Slope steepness category 1 represented flat shores with measured slopes ranging from 0.00 to 0.01, slope steepness category 2 represented moderately sloped shores with measured slopes ranging from 0.01 to 0.05, and slope steepness category 3 represented steep shores with measured slopes ranging from 0.05 to 0.15.

2.3 Determining species and measuring size

To distinguish the species from one another, their morphology was compared visually in the field. To help with this, the morphology of the species was studied using pictures compiled by Holly Brown and Martin Wilkinson, School of Life Sciences, Heriot-Watt University, Edinburgh, Scotland. *F. vesiculosus* is distinguished from the others by the presence of vesicles in the fronds. *F. spiralis* and *F. guiryi* resemble each other, but *F. guiryi* can be distinguished by receptacle sterile rims, monopodial branching, and a generally straighter appearance of the fronds.

The percentage coverage was determined visually for each studied *Fucus* species using the 5x5 cm squares of the quadrats in each transect (Dethier et al. 1993, Benedetti-Cecchi et al. 1996). The percentage cover for each species on a shore is an average of all quadrats on that shore. A minimum of two haphazardly chosen individuals of each species present were measured from each quadrat. Individuals that had reproductive vesicles were chosen, indicating that they were at a comparable fertile age. Individuals were measured using a flexible tape measure and a slide ruler for thallus width (Figure 4). The width of the thallus was measured from the widest part of the thallus approximately 1 cm from the holdfast to the accuracy of 0.5 mm. The overall length of the individual was measured from the beginning of the holdfast to the tip of the longest frond to the closest half centimetre. The circumference of the algae was measured by holding the individual in a bunch and measuring the thickest part loosely to the closest half centimetre. Bushiness of an individual was calculated according to Zardi et al. (2015) as the maximum circumference/maximum length.

Figure 4. Location of where thallus measurement was taken marked in white. *F. vesiculosus* as an example individual.

2.4 Statistical analyses

The data were analyzed using IBM SPSS (version 24). To determine the differences among species in overall length, thallus width, and bushiness, mean values were compared with one-way analysis of variance tests. Test of homogeneity of variances was performed with Levene's statistic and normality was tested with the Shapiro-Wilk test. Pairwise comparisons were conducted using Tukey's test when there was homogeneity of variances in the studied data. If this was not the case, Tamhane's test was used. One-way ANOVA was used in order to test whether there were differences in the algae size or cover from sheltered and exposed shores. Possible correlation of species cover, between *F. guiryi* and *F. spiralis* was tested with Pearson correlation. The limit of statistical significance for all tests was 0.05. Principal components analysis was done with PRIMER v6 software (Clarke and Gorley 2006). The analysis included aspect, substrate, slope, shelteredness, and the percentage coverage of each species to determine which shores shared characteristics.

3 RESULTS

3.1 Locations, distribution, and shore characteristics

The shores were sampled using, for the majority, two independent transects, but some shores were sampled with just one transect due to time constraints. On the shores where only one transect was sampled a larger number of quadrats was used along the single transect to ensure a sufficient sample size. Some shores did not have any *F. guiryi* individuals in the samples (Figure 5, triangles). Many shores had abundant *F. guiryi* but no clear *F. spiralis* individuals (Figure 5, diamonds). All shores except Troon beach had *F. vesiculosus*. Five out of eighteen of the shores were categorized as exposed (Table 1). Slope steepness categories were more uniform among the samples with five category 1, six category 2, and seven category 3 shores out of the total eighteen shores sampled.

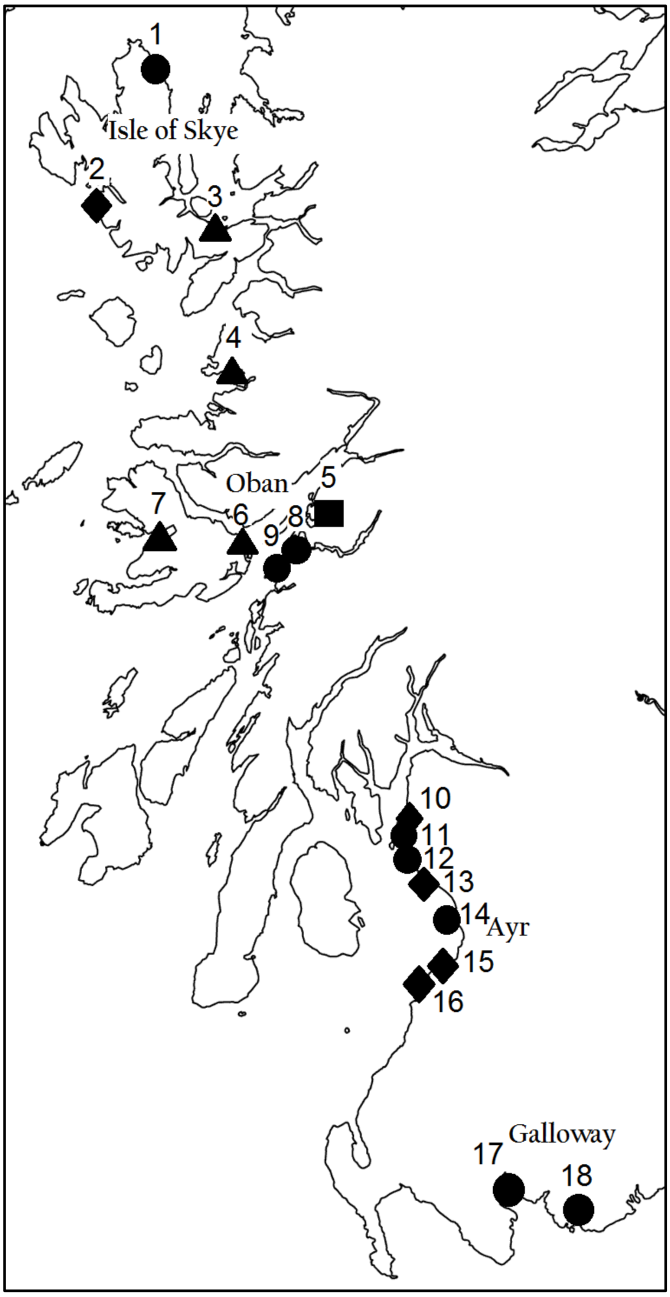

Figure 5. Locations of the shores studied. Circles represent shores where all three species were present, triangles represent shores with *F. spiralis*, and diamonds represent shores with *F. guiryi*, and the square represents the shore where only *F. vesiculosus* was sampled.

Table 1. Shore characteristics

Number	Shore	Latitude	Longitude	Shelteredness	Slope steepness
1	Staffin Bay	57.63476	-6.217656	**Exposed**	2
2	Talisker	57.281796	-6.459726	**Exposed**	1
3	Broadford	57.242132	-5.905373	Sheltered	2
4	Arisaig	56.895485	-5.740803	Sheltered	3
5	Loch na Keil	56.463990	-6.039822	Sheltered	1
6	Craignure	56.470556	-5.695556	Sheltered	2
7	Dunstaffnage	56.454167	-5.435833	Sheltered	1
8	Wee Ganavan	56.431389	-5.483889	Sheltered	3
9	Pencil point	55.77879	-4.859626	Sheltered	2
10	Fairlie marina	55.767639	-4.858993	Sheltered	3
11	Seamill	55.683265	-4.863815	**Exposed**	3
12	Ardrossan	55.637981	-4.810607	Sheltered	3
13	Troon beach	55.539983	-4.67173	**Exposed**	3
14	Greenan castle	55.440558	-4.669537	Sheltered	1
15	Culzean castle	55.355401	-4.787963	**Exposed**	1
16	Creetown	54.871883	-4.36851	Sheltered	2
17	Kirkcudbright	54.830587	-4.060591	Sheltered	3
18	Dallachulish	56.546667	-5.287500	Sheltered	2

3.2 Differentiating the species

In general, the species exhibited different morphology, as predicted by previous reports on identification. The majority of *F. guiryi* individuals sampled exhibited a sterile rim around their receptacles (Figure 6). They are also generally larger in size (Figure 7) and have straighter fronds rather than the spiraled ones found on *F. spiralis* (Figure 8). *F. vesiculosus*, on the other hand, is usually much longer than either species and has vesicles (Figure 9). So, all individuals that had vesicles were typed as *F. vesiculosus.* There were some *F. guiryi* individuals which did not have a sterile rim. Distinguishing individuals that exhibited both *F. spiralis* and *F. guiryi* characteristics was done based on the general size and spiral shape of the fronds if no receptacle sterile rim was present. Fortunately, most (about 70%) *F. guiryi* individuals had a sterile rim. On the other hand, about 75% of *F. spiralis* identification were certain.

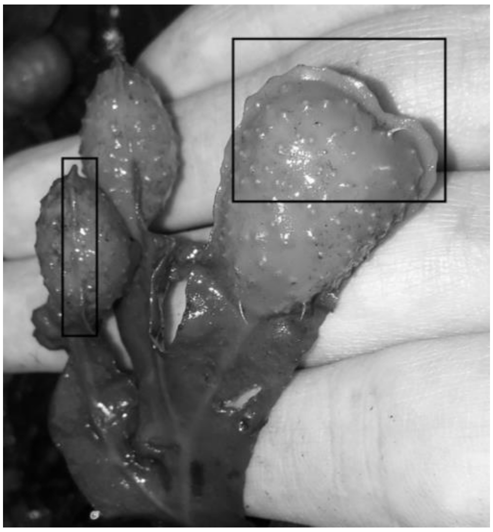

Figure 6. An example of the sterile receptacle rims of *F. guiryi* inside black boxes

Figure 7. An *F. guiryi* individual (grey box) beside *F. spiralis* (other individuals) demonstrating the differences in length

Figure 8. *Fucus spiralis* on the left exhibiting spiraled fronds and *Fucus guiryi* on the right with flatter fronds

Figure 9. *Fucus vesiculosus* individual with clearly recognizable vesicles

There was a statistically significant difference between the length of the three species determined by one-way ANOVA ($F_{2,389}$ = 115.391, p = 0.000, Figure 10). The mean length of *F. spiralis* was 24 cm, compared to *F. guiryi,* 32 cm, and *F. vesiculosus,* 60 cm.

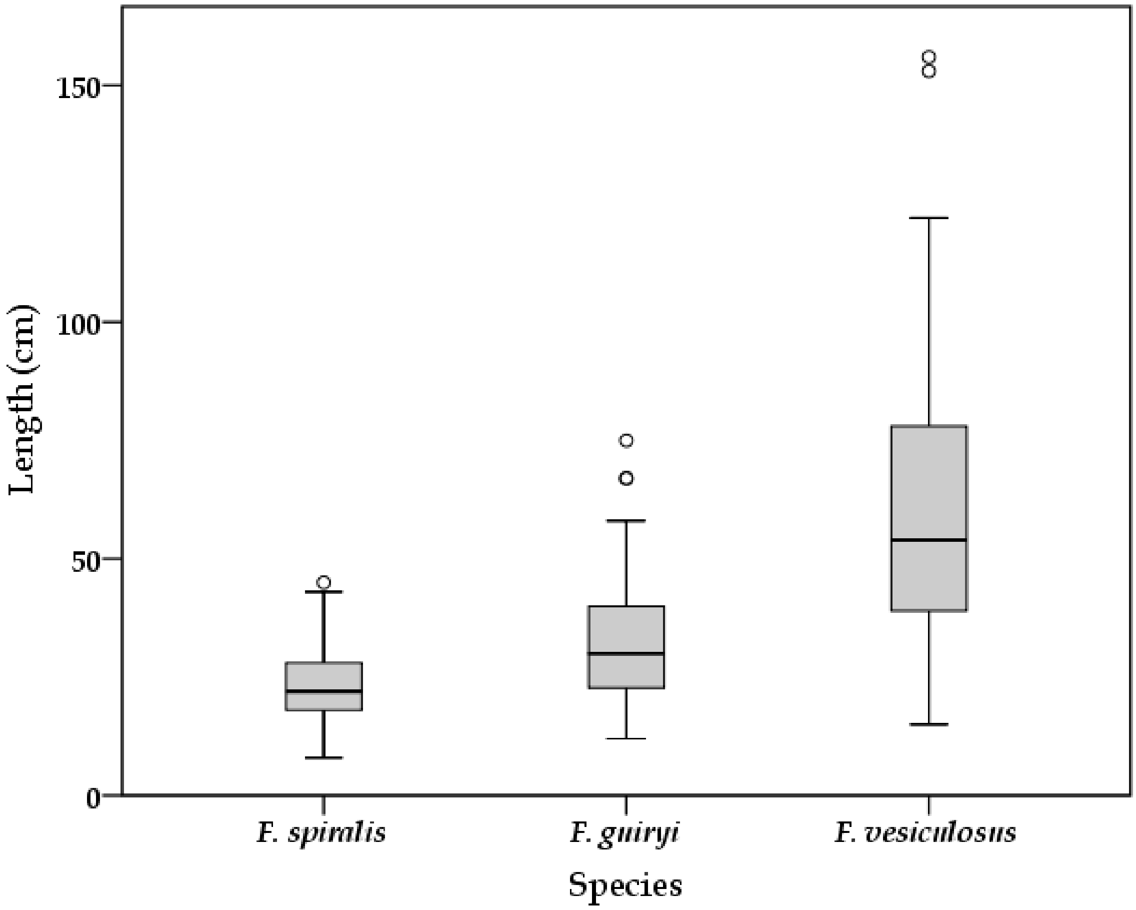

Figure 10. Length of individuals of each species. The descriptor represents the mean values, boxes represent values between 1st and 3rd quartile, error bars represent 95% confidence intervals. *F. spiralis* n = 84, *F. guiryi* n = 112, *F. vesiculosus* n = 196, total N = 392.

There was also a significant difference in bushiness between the species ($F_{2,321}$ = 32.355, p = 0.000). *F. spiralis* individuals, in general, are the bushiest, followed by *F. guiryi* (Figure 11).

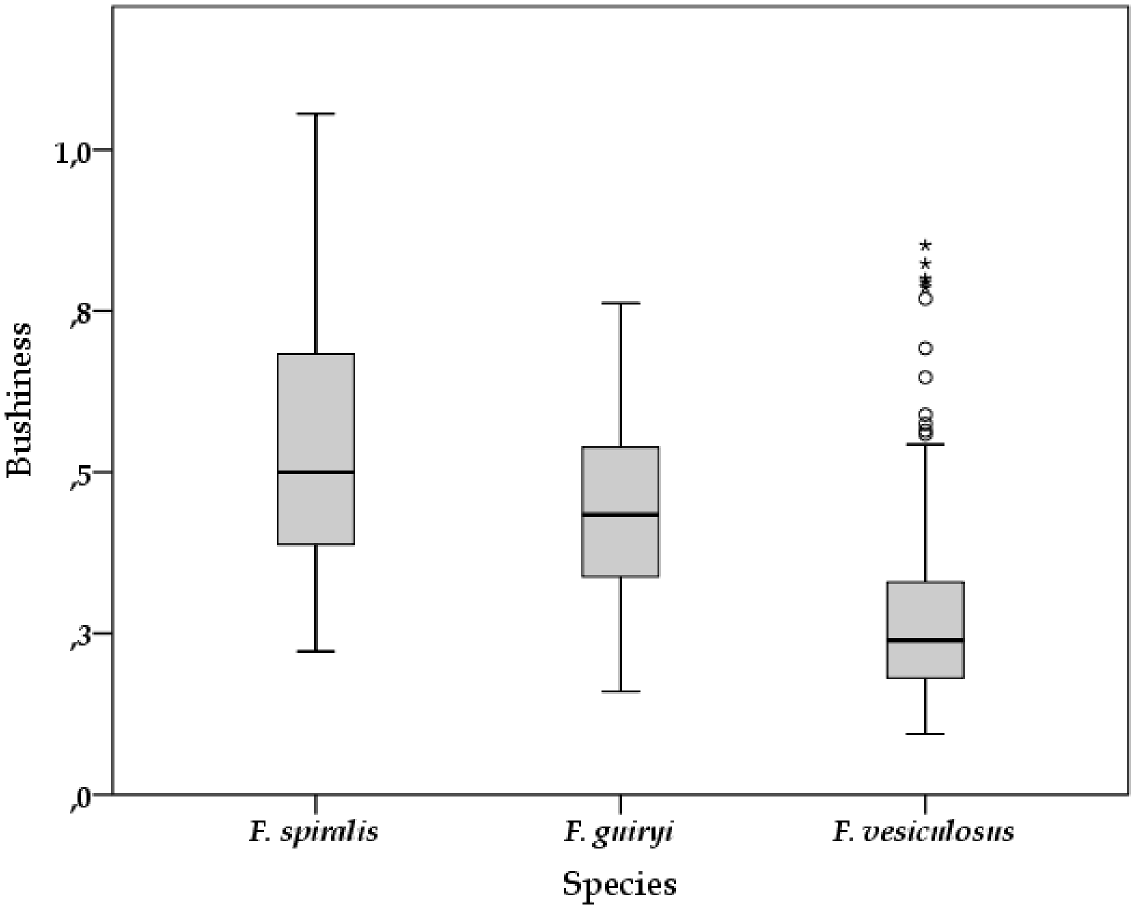

Figure 11. Bushiness (maximum circumference/maximum length) of individuals in each species. The descriptor represents the mean values, boxes represent values between 1st and 3rd quartile, error bars represent 95% confidence intervals. *F. spiralis* n = 63, *F. guiryi* n = 102, *F. vesiculosus* n = 159, total N = 324.

There was a smaller difference in bushiness between *F. spiralis* and *F. guiryi* than that between either compared to *F. vesiculosus* (Table 2). All differences in bushiness were statistically significant.

Table 2. Tukey HSD Post Hoc multiple comparisons based on bushiness, * mean difference is significant at the 0.05 level.

(I) Species	(J) Species	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
F. spiralis	*F. guiryi*	0.118*	0.043	0.017	0.017	0.218
F. guiryi	*F. vesiculosus*	0.178*	0.034	0.000	0.099	0.258
F. vesiculosus	*F. spiralis*	-0.296*	0.040	0.000	-0.389	-0.203

According to One-Way ANOVA there was also a difference in the thallus width between species ($F_{2,\ 383}$ = 3.902, p = 0.021, Figure 12). Tamhane's pairwise comparisons showed that the difference between *F. guiryi* and *F. vesiculosus* was big enough to be significant (Mean difference *F. vesiculosus* - *F. guiryi* = 0.48494, Std. Error = 0.15839, p = 0.007). The average thallus width of *F. spiralis* was 3.8 mm, compared to *F. guiryi,* 3.5 mm, and *F. vesiculosus,* 4.0 mm.

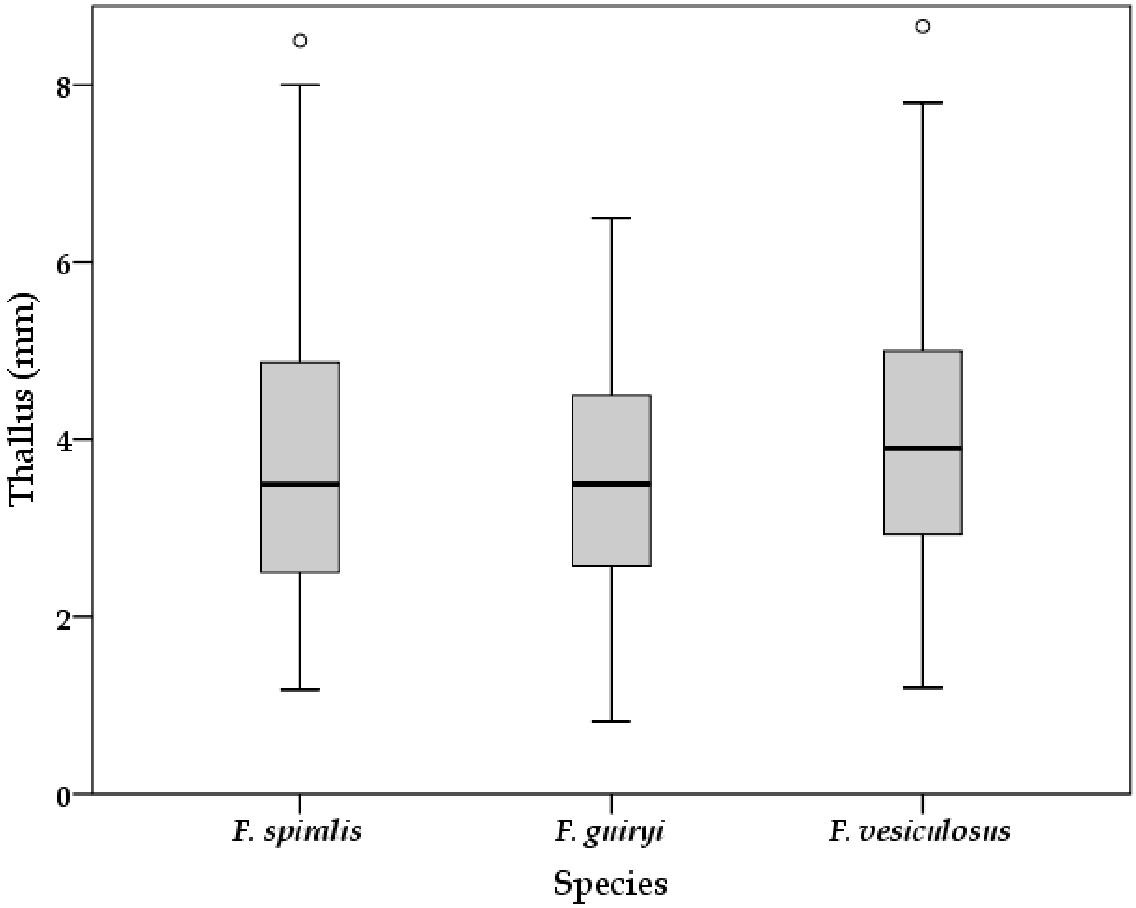

Figure 12. Thallus width of individuals in all three species. The descriptor represents the mean values, boxes represent values between 1st and 3rd quartile, error bars represent 95% confidence intervals. *F. spiralis* n = 84, *F. guiryi* n = 111, *F. vesiculosus* n = 191, total N = 386.

3.3 Zonation patterns

Compared to a previous study by Zardi and colleagues (2011, Table 3), the zonation found on the studied shores varied in the way that there was a clearer zone dedicated solely to *F. guiryi* rather than a zone where all three species would be mixed (Table 4). The zone of *F. spiralis* did not extend to the point where it would have been commonly found on the same zone as *F. vesiculosus*. A clearly defined, most often small ~10–120 cm, zone of *F. spiralis* could be seen nearest the shoreline. After this, a zone with both *F. spiralis* and *F. guiryi* could be determined when moving down along the shore gradient. *F. guiryi* was also sometimes found in the same zone as *F. vesiculosus* and this zone was found to be the largest in many cases. Especially on flat shores the *F. vesiculosus* zone could extend many dozens of meters outwards to sea. In comparison, the *F. guiryi* zone was often a maximum of three meters long depending on the shore slope.

Table 3. For comparison, the zonation of the study species in their southern range according to Zardi et al. 2011.

Zone	**Species**		
A	*F. spiralis*		
B	*F. spiralis*	*F. guiryi*	
C	*F. spiralis*	*F. guiryi*	*F. vesiculosus*
D		*F. guiryi*	*F. vesiculosus*
E			*F. vesiculosus*

Table 4. Zonation of *Fucus* species on studied shores starting from the highest zone on the shore.

Zone	**Species**		
A	*F. spiralis*		
B	*F. spiralis*	*F. guiryi*	
C		*F. guiryi*	
D		*F. guiryi*	*F. vesiculosus*
E			*F. vesiculosus*

3.3 Effect of exposure

Within species, there is a significant difference between the length of *F. spiralis* (One-way ANOVA ($F_{1, 82}$ = 20.501, p = 0.000) and *F. vesiculosus* ($F_{1, 194}$ = 4.692, p = 0.032) individuals found on different shores grouped according to shore shelteredness. There was no significant difference in the length of *F. guiryi* ($F_{1, 110}$ = 0.011, p = 0.916). *F. spiralis* individuals were larger on more exposed shores, whereas *F. vesiculosus* was larger on more sheltered shores. *F. guiryi* individuals were about the same size on both sheltered and exposed shores (Figure 13). According to one-way ANOVA there is a significant difference in the species percentage cover of *F. spiralis* ($F_{1, 83}$ = 14.409, p = 0.000) and *F. vesiculosus* ($F_{1, 199}$ = 4.528, p = 0.035) based on shore shelteredness (Figure 14). The average cover of *F. spiralis* on sheltered shores was 64.84% and on exposed shores 23.40%, while for *F. vesiculosus,* its average coverage on sheltered shores was 55.87%, and exposed shores 42.45%. There was no difference in percentage cover of *F. guiryi* on the different shore types (sheltered 59.98%, exposed 55.82%).

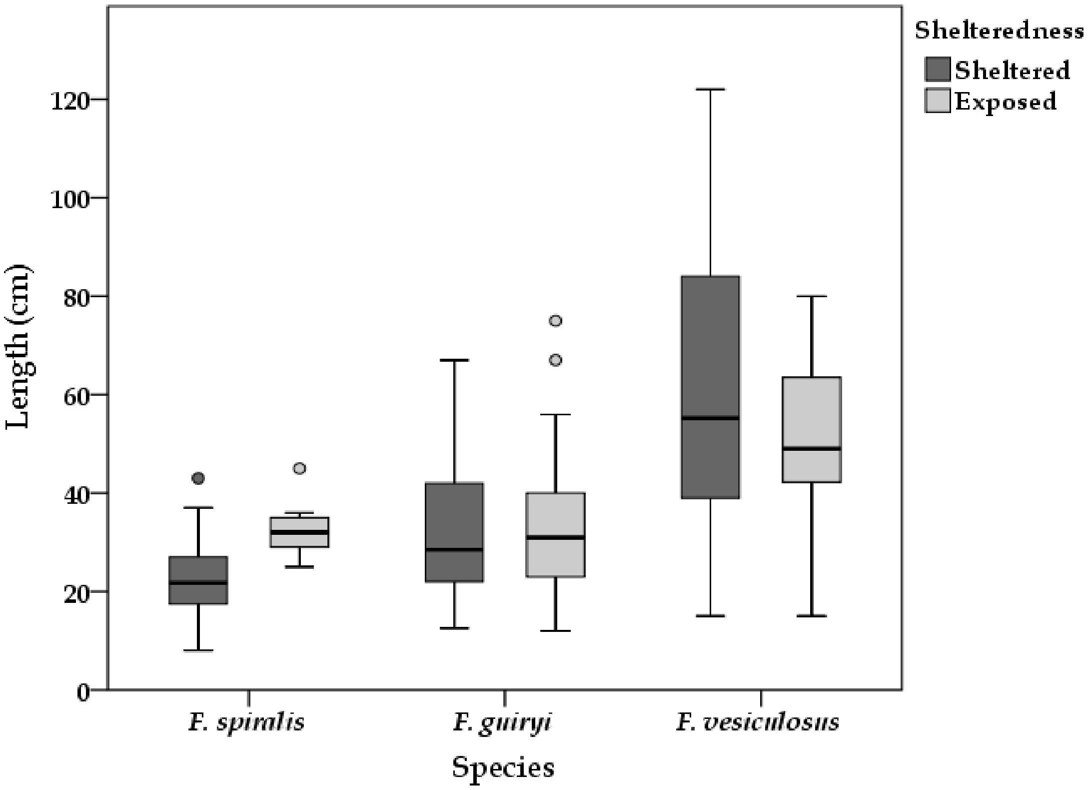

Figure 13. Length of individuals based on shore shelteredness. The descriptor represents the mean values, boxes represent values between 1st and 3rd quartile, error bars represent 95% confidence intervals. *F. spiralis* sheltered n = 74, exposed n = 10, *F. guiryi* sheltered n = 46, exposed n = 66 *F. vesiculosus* sheltered n = 164, exposed n = 33, total N = 393.

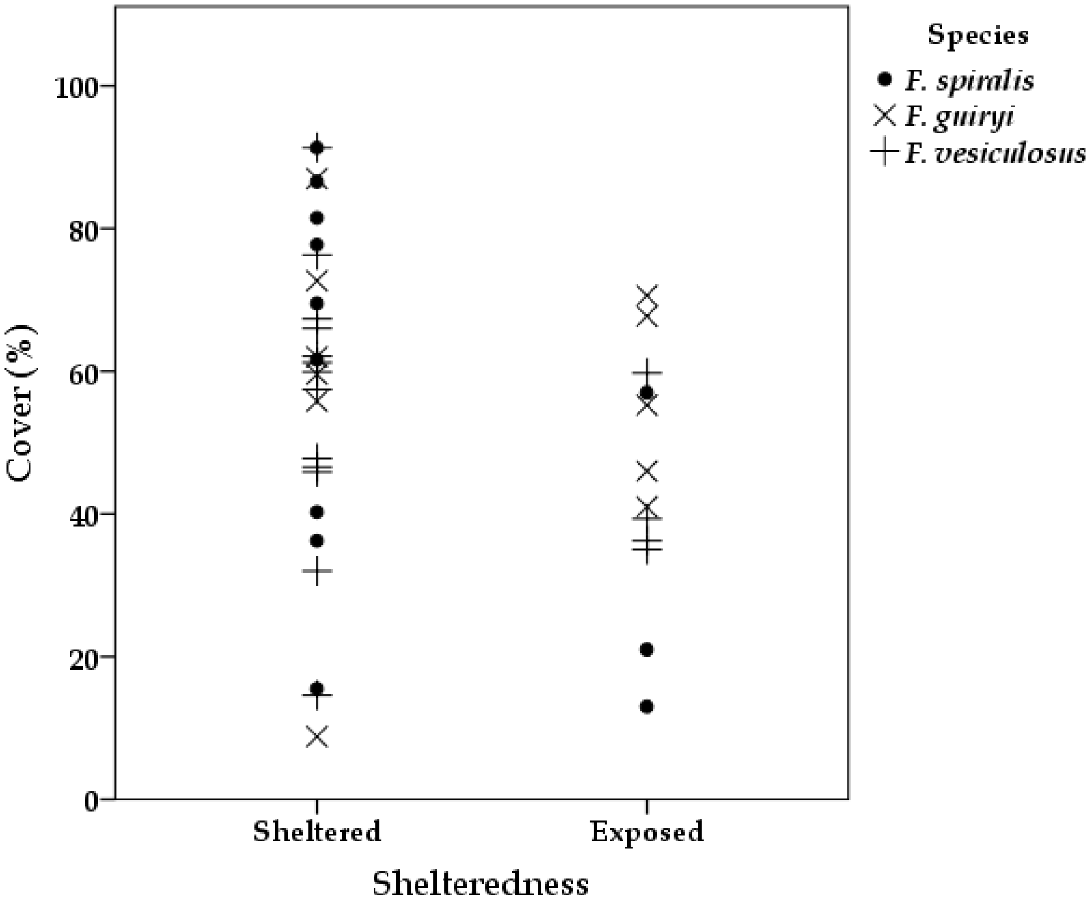

Figure 14. Species cover percentages on eighteen studied shores based on shelteredness. Each mark denotes the average percentage cover of one species from one shore. *F. spiralis* sheltered n = 9, exposed n = 3, *F. guiryi* sheltered n = 6, exposed n = 5, *F. vesiculosus* sheltered n = 13, exposed n = 4, total N = 40.

3.4 Principal Component Analysis

A Principal Component Analysis was done using the shore variables aspect, substrate, slope, shelteredness and percentage cover of each species to visualize the similarities among shores based on the multivariate data. The variables were first normalized to make the shore variables and the species coverages comparable. According to the PCA analysis, the main difference was a split between the shores that have *F. guiryi* and those that do not and shores with steeper slopes (Figure 15). There seemed to be a possible correlation between *F. guiryi* and *F. spiralis* percentage covers based on the PCA. However, there was no significant correlation between the percentage covers of *F. guiryi* and *F. spiralis* according to Pearson correlation (r = -0.358, p = 0,487).

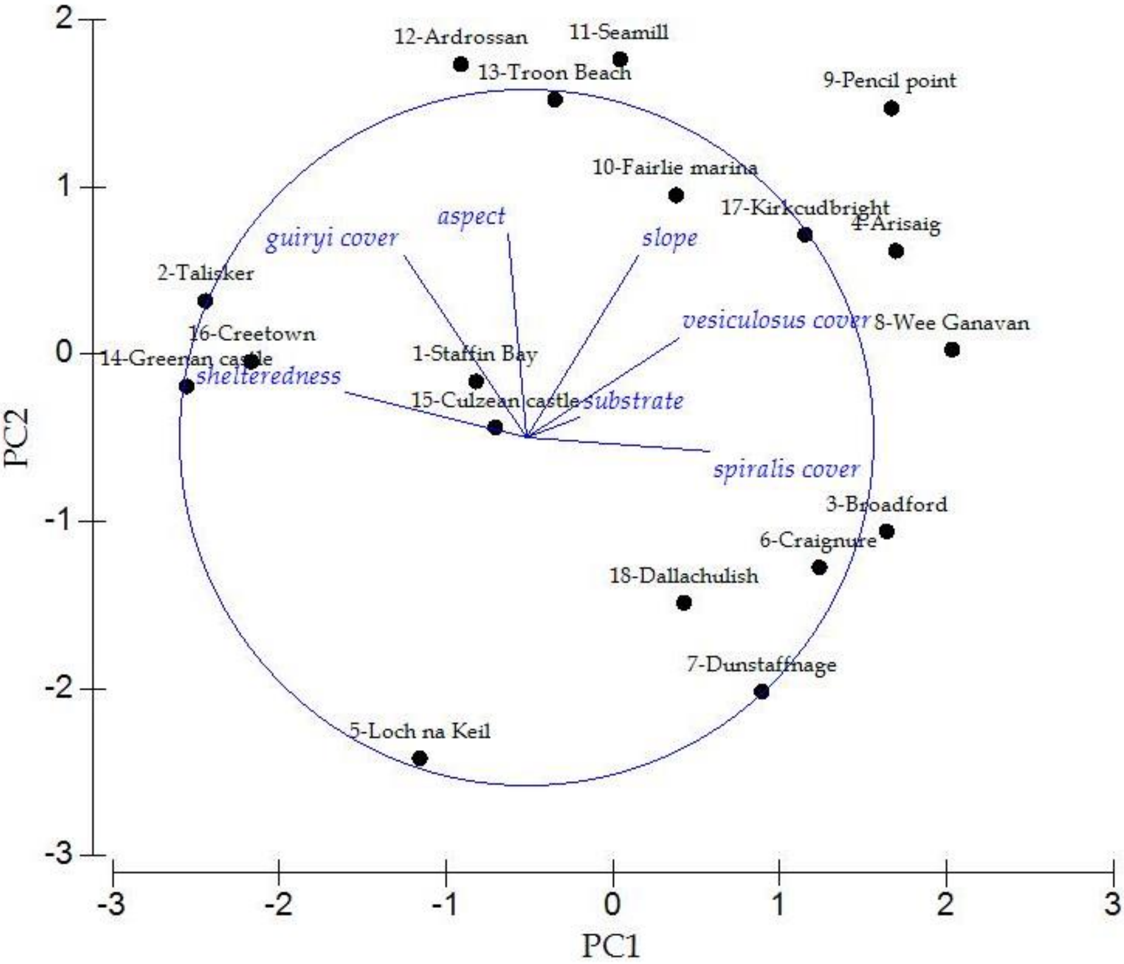

Figure 15. Principal Component Analysis with factors aspect, substrate, slope, shelteredness and percentage coverage of each species.

4 DISCUSSION AND CONCLUSIONS

4.1 Determinants of *Fucus* species distributions

I investigated the distribution and abundance of three species of fucoid algae on the west coast of Scotland. Recognition of a new species, *Fucus guiryi* which was earlier thought to be a variety of *F. spiralis*, had raised questions about the extent of its distribution and abundance in relation to co-occurring *F. spiralis* and *F. vesiculosus*. Because we must first know the distribution of organisms in order to understand potential threats of climate change on biological communities, it is important to document distributions and identify the environmental factors that could limit their distribution. *F. vesiculosus* was measured in this study in addition to *F. guiryi* and *F. spiralis* because it was uncertain how abundant *F. guiryi* would be in this range and an additional species ensured enough data for analysis. It is also very closely related and could provide information about the effect of shelteredness. Fortunately, it was found on all shores and so provided a good range for the comparison of size and abundance. The biggest interest, however, was between the difference of *F. guiryi* and *F. spiralis.* On over half of the shores studied only one of these species was found.

Like other *Fucus* species, the studied species are perennial and thus maintain the same geographical distribution and zonation on the shore throughout the year for several years (Schiel and Foster 2006). In a bigger, time frame, they exhibit migration to new habitats, such as a long-term movement to cooler habitats as the seas warm (Stenseth et al. 2002, Meehl 2005, Chen et al. 2011). However, there are many factors that determine the distribution and zonation of these species, such as physiological tolerances and requirements. Biological interactions, such as herbivory and competition can affect species distributions as well (Lubchenco 1983, Engkvist et al. 2000). On rocky shores, the combination of these factors leads to the zonation patterns observed, where the three species have their own, quite clearly defined zones. Previous studies of rocky shore communities have led to the development of general guidelines, such as the Ballantine scale (1961). It can be used when comparing different shores and the multiple factors that influence species zonation.

4.2 Differences in size and morphology between species

I hypothesized that there would likely be significant differences in the size and morphology of all three species. I expected that more similarities would most likely be found between *F. spiralis* and *F. guiryi* due to their recent separation (Zardi et al. 2011). *F. vesiculosus* was easily identified. Because the species are in their fertile stage during the summer months, it was also possible to distinguish *F. guiryi* from *F. spiralis*, by examining the presence or absence of the receptacle sterile rim. However, when this feature was not present, it was harder to distinguish the two species. Since some individuals were not easy to distinguish, it is possible that they were either immature individuals (lacking receptacles) or hybrids of *F. spiralis* and *F. guiryi.* Regardless, there also was a statistically significant difference in length between the three species with *F. spiralis* being the shortest, *F. vesiculosus* longest, and *F. guiryi* in between.

The difference in the length of individuals between species is most likely a result of their vertical distribution on the shore. Species and individuals in deeper water need to be longer in order to reach the sunlight they need to photosynthesize. Zardi et al. (2011) found the average length of *F. spiralis* to be 25.29 cm, *F. guiryi* 34.11 cm, and *F. vesiculosus* 43.48 cm. These are consistent with the results found in this study, apart from having some very long *F. vesiculosus* individuals from sheltered shores. The differences between species could either be due to genetic constraints and be inherent to the species or they could be a result of phenotypic plasticity. Both responses are very likely and have been observed in *Fucus* species (Norton 1991, Chapman 1995, Kalvas and Kautsky 1998). One experiment to further disentangle this relationship would be to test the limits of the plasticity of the species. This could be done for example by exposing them to varying degrees of wave forces in a more controlled environment.

F. spiralis individuals were found to be the bushiest of all three species. Bushiness describes the relationship between circumference and height. *F. spiralis* might benefit from being bushy because of its position on the upper shore, near the shoreline. Since species living on the upper shore are frequently exposed to air and thus prone to desiccation, morphologies that help retain moisture are expected to be beneficial. A bushier design maintains moisture in the most efficient way. The ratio of evaporating surface area to the volume of organs is what primarily determines the rate of evaporation (Dromgoole 1980). Bushy plants also have the benefit of fronds overlapping during low tide, reducing evaporation (Norton 1991). Overlapping may also protect inner fronds from exposure damage (Norton 1991). The most efficient parts of a *Fucus spiralis* to take up nutrients are the tips of its fronds (Topinka Bigelow 1978), so it is also most likely beneficial to have an abundance of these structures. *F. guiryi* showed a smaller difference in bushiness to *F. spiralis* than either species did to *F. vesiculosus*, which was the least bushy of the three species. Very long *F. vesiculosus* individuals would need to grow to a very large size to obtain the same degree of bushiness as *F. spiralis*. This could increase the chance of dislodgement, especially on more exposed shores.

F. vesiculosus was found to have, on average, the largest thallus. A larger thallus is most likely needed for structural support and so would be beneficial for *F. vesiculosus* individuals, which can grow up to over a meter long. The longest individual found in this study was 156 cm. The second widest thallus was found from *F. spiralis.* In addition to providing structural support, larger thallus thickness decreases the rate of desiccation (Bell 1995), which could be related to desiccation stress of the high shore dwelling *F. spiralis*. Perhaps because *F. guiryi* experiences smaller stress compared to *F. spiralis* and *F. vesiculosus* from both of these factors (structural support and desiccation) it exhibits the smallest thallus width of the three species.

4.3 Zonation patterns and geographical distribution

Zardi et al. (2011) defined *Fucus* zones based on biological criteria i.e. morphotype presence, for these species at the southern end of their distribution. However, it was not known if the species show similar zonation in the north. The shores studied in this thesis were divided into similar zones, but I did not find a zone where all three species were present in sympatry. Even when some of the species were not found from a particular shore, the same general zonation pattern was observed. Clear zonation was found despite the fact that there can be hybridization between the species when they are in sympatry (Zardi et al. 2011). In my study, some species that were assumed to inhabit zones A to C were also found further away from the shoreline. These anomalies could be caused by elevation due to higher ground or large boulders along the measured transect.

The differences between the zonation of this study and that of Zardi (2011) could be due to slightly different methods employed. Possibly the scale at which the samples were collected in this study was more dispersed and thus the 50 x 50 cm quadrats did not catch the overlap of all the species. Though this is unlikely since it was not found in a single quadrat on any of the shores. More overlap found by Zardi and colleagues could point to less competition, which facilitates the overlap of species. It is possible that competition is harsher in a cooler climate which facilitates the growth of *F. guiryi* in a multitude of locations. This could lead to a clearer separation of zones because the species are excluding one another. A warming climate might force *F. guiryi* to reside in cooler upwelling areas like in its more southern habitats, and lead to a change in competition.

Climate change most likely drives the distribution of species towards the north and even changes the exposure of some shores. So, we might expect a shift in the species zonation on a shore level, as well as larger changes in their distribution from shore to shore. From the distributional map, we can see that around Ayr more shores with just *F. guiryi* and *F vesiculosus* were sampled. In comparison to shores around Oban and the Isle of Skye where shores with just *F. spiralis* and *F vesiculosus* were more common. Though there might be some geographical separation between *F. spiralis* and *F. guiryi* it could also be due to the shelteredness of the studied shores. It is clear that both species can be found both in the southern and northern parts of the western coast of Scotland. This could indicate that there is no clear distinction to cooler water and warm water dwelling species as can be found in Portugal. There *F. guiryi* can exclusively be found in cold water upwelling areas (Lourenço et al. 2016).

4.4 Effect of shore shelteredness to the size and abundance of species

When comparing shores expected to experience different degrees of exposure due to wave action and desiccation, *F. vesiculosus* was statistically longer and had a higher percentage cover on more sheltered shores. It could be that *F. vesiculosus* prefers more sheltered shores than does *F. guiryi* which did not show a significant difference in either variable based on shore exposure. These patterns suggest that possibly *F. guiryi* has no preference or even favors exposed shores. Longer *F. spiralis* individuals were found on more exposed shores, but its percentage cover was higher on exposed ones. It was expected that all species would be longer on sheltered shores, as indicated by previous research (Lewis 1968, Menge 1976). This could be because *F. spiralis,* as a high shore dwelling species, does not suffer as much from wave exposure as do the other species. Being able to withstand wave action might allow it to escape competition with the other species, giving it an opportunity to grow larger. A wider exploration of different types of shores could further explain this speculation. For example, the shores studied could be divided into shelteredness categories beforehand in order to get a wide range of different types of shores, including more replicate shores of each substrate and steepness.

Using the multivariate data set of shore characteristics and the percentage coverage of the three different *Fucus* species in a PCA, the different shores were grouped primarily based on percentage coverage of *F. spiralis* or *F. guiryi*. Shores where no *F. spiralis* was found, shores 3, 4, 6, and 7, are slightly grouped on the right side of the PCA graph. This could be due to competition between the two species as they were also found to solely habit some shores with the exclusion of the other species. We can see that Loch na Keil, shore number 5, is separate due to only *F. vesiculosus* having been measured on this shore. The sites in the upper right corner also form a group of shores with slope category 3. Pencil point falls into this group in the PCA even though it is a category 2 shore. This could indicate that some other shared variable between Pencil point and the other shores is also important. The other shores with slope categories 1 and 2, seem to be divided mainly based on the coverage of *F. guiryi* and *F. spiralis*. It is possible that there are too few shores categorized as exposed to see a clear effect of shelteredness.

4.5 Improvements

In this study, the shores were generally distributed based on a subjective evaluation of shelteredness, including the geographical location of the shore. However, a more detailed and structured approach, perhaps including quantitative data of wave strength, would allow a more direct evaluation of the hypothesis that exposure influences the *Fucus* distribution patterns. This study gives a general direction of the possible effects of shelteredness. However, it cannot be stated what effect specific individual factors have on the study species. Since the shores were chosen based on general exposure from maps beforehand there are still many variables that were uncontrolled. This could be avoided if there was more time to collect detailed data beforehand on the shores in order to group them. In comparison to grouping them after the data collection, as was done here. This caused there to be much fewer exposed shores than sheltered.

A larger amount of transects on each shore would ensure a larger sample and thus a more accurate representation of the individuals on each shore. In this case, there wasn’t enough personnel to collect more than two transects at a time. So, either more people collecting the samples or more time to go back to the same shore more than once would be a valuable addition to the data collection. The placement of transects and the quadrats that it contains varies from shore to shore based on a subjective evaluation of the slope before it was measured. This means that it is difficult to exactly replicate the transects on a different shore in a way that would be statistically comparable.

4.6 Conclusions and future prospects

In conclusion, all three species are significantly different in size as well as morphology, and it is possible to distinguish them from one another in the field. However, some challenges will arise, especially with hybridized individuals. The zonation patterns found in the species' southern range are reflected in their northern distribution along the west coast of Scotland. However, some differences were found in the classification of these zones. The species also exhibited different sizes and abundances based on shore shelteredness. *F. vesiculosus* preferred sheltered shores, whilst *F. guiryi* and *F. spiralis* showed no clear preference.

Though these results, for the most part followed what was predicted, there were also some surprising results that would be interesting to disentangle in the future. For example: Why some *F. guiryi* individuals have a sterile receptacle rim and others do not? There could be a separation between different populations. Though there was large variation in thallus width, the average of all species was remarkably similar. This is surprising since *F. vesiculosus* can grow to be at least six times the size of an *F. spiralis* individual. Also, why *F. spiralis* seems to grow larger on more exposed shores, counter to the hypothesis would need to be further studied. *F. spiralis var. platycarpus* was noted to also have been found on the east coast of Scotland and the Islands of Orkney and Shetland. So, it would be valuable to also collect additional data from these areas.

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