

Field studies on the abundance, growth and biofouling of the harvestable red alga *Vertebrata lanosa* (Linnaeus) T.A.Christensen



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Abstract

Macroalgae have an important ecological role as primary producers and habitat engineers for fauna in coastal areas, and many species can also be used for human consumption. Like vegetables, macroalgae contain essential vitamins and minerals, and red algae can also contain large amounts of protein.

Vertebrata lanosa is a small red alga and an obligate epiphyte on seaweed. It grows almost exclusively on knotted wrack, *Ascophyllum nodosum*, which is commonly found in sheltered, upper intertidal habitats. With the exception of the Baltic sea and Greenland, *V. lanosa* is distributed along the coasts of the North Atlantic Ocean. The alga has lately received culinary attention in Scandinavia for its truffle-like taste and has been given the nickname “truffle of the sea”.

This study has focused on distribution, growth and biofouling to gain valuable knowledge related to harvest of *V. lanosa*. 27 locations South of Bergen were included in an abundance study of both *V. lanosa* and its host *A. nodosum*, where physical factors as exposure, geographical orientation, temperature, salinity, inclination and vertical position in the tidal zone were assessed. *V. lanosa* was more abundant in areas of relatively high exposure and inclination and less abundant in more sheltered and flatter areas with large canopies of *A. nodosum*. This is likely due to increased physical impact on *A. nodosum* fronds at exposed sites which results in wounds and scratches. Damaged areas on the fronds of *A. nodosum* have higher settlement and survival of *V. lanosa* spores, likely due to favourable hydrodynamic conditions and limited epidermal shedding in wounded areas which increase the chance of rhizoid anchoring by *V. lanosa*. In total, 19 different epiphytic species were identified growing on *V. lanosa*, and the number and size of epiphytes were substantially higher in November than in February, suggesting that late winter and early spring is the best harvest time to ensure a clean product. For further studies, the growth of *V. lanosa* needs to be assessed in more detail and over longer time periods to gain knowledge on how to harvest the alga sustainably.

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1 Introduction

1.1 Uses of seaweeds

Macroalgae have been used for human consumption for centuries, with the earliest traces from China in the fourth century AD (Yang et al., 2017). Countries in South-east Asia have strong traditions for consuming macroalgae, and are also the main producers of cultivated products, where a large amount of the production is used as food (McHugh, 2003; Buschmann et al., 2017). The remainder of the production is mostly used for extraction of the hydrocolloids alginate, agar and carrageenan which are used as thickening agents in different products (Buschmann et al., 2017). In later years, seaweed consumption has increased in Europe due to import of Asian cuisine like sushi. Although traditions for eating local macroalgae are not as strong as in Asia, some species have been utilized for both human and animal consumption also in Europe, Canada and the USA (Guiry and Morrison, 2013; Rioux et al., 2017). Wild-growing hydrocolloid-rich algae are also harvested for industrial use in these areas.

Of the three major groups of seaweeds (Class Phaeophyceae, Division Chlorophyceae and Division Rhodophyceae), red and brown macroalgae make up the majority of the algae used in production of food, hydrocolloids and fertilisers (Rioux et al., 2017). To prevent depletion of natural resources and to meet market demands, increasing amounts of these algae are now cultivated. In fact, the cultivation of macro algae has been growing exponentially in recent years, and 96 % of the globally harvested macroalgae in 2013 was from aquaculture with an economic value of 6.4 billion US\$ (Rioux et al. 2017).

The nutrient value of macroalgae can be compared to that of terrestrial vegetables, with high amounts of indigestible carbohydrates which contributes to a low-calorie diet, in addition to maintaining a healthy gut microbiota (Rupérez, 2002; Hehemann et al., 2012; Duinker et al., 2016). Furthermore, macroalgae contain a higher amount of trace elements, minerals and vitamins than most terrestrial vegetables, and red algae also have a relatively high protein content compared to both green and brown algae, and conventional vegetables (Morrissey et al. 2001; MacArtain et al., 2007; Smitha et al., 2010). This makes macroalgae a potential food source also in Europe and America, which unlike vegetables do not need large amounts of land, irrigation and fertilisers to grow.

In this study, the main focus will be on the small epiphytic red alga *Vertebrata lanosa* (Linnaeus) T.A.Christensen, which is a relatively new food alga. It has received recent culinary

attention for its truffle-like taste, and has been given the nickname “truffle of the sea” by Nordic chefs. It is small, but has a strong taste and aroma which is well suitable for flavouring.

1.2 The *Ascophyllum nodosum* – *Vertebrata lanosa* host-epiphyte association

Ascophyllum nodosum (Linnaeus) Le Jolis, is a perennial seaweed of the order Fucales common in the North Atlantic Ocean, where it grows on solid substrate like rocks in sheltered intertidal areas. It is a long lived seaweed species of ecological importance, providing shelter for invertebrates and juvenile fish (Schmidt et al., 2011). *A. nodosum* is harvested for the production of seaweed meal which is used in food products, animal feed and fertilizers among other things (Sharp, 1987; Meland and Rebours, 2012; Guiry and Morrison, 2013). The age of an *A. nodosum* individual frond is difficult to tell, as fronds tend to break off over time and new fronds regularly regenerate from the holdfast. It is possible, however, to tell the minimum age of a frond by counting air bladders, as one is formed on each branch every year with the exception of the first 1-2 years (Åberg, 1992). Unbroken fronds can usually reach up to 10-12 years of age, and in extreme cases even up to 20 years (Baardseth, 1970b).

A. nodosum do normally not carry much epiphytes since spores or juveniles of most algal epiphytes are regularly removed over time by the epidermal shedding of *A. nodosum* (Halat et al., 2015), however it commonly hosts the epiphytic brown alga *Pylaiella littoralis* (Pavia et al., 1999; Scrosati and Longtin, 2010). More relevantly for this study, *A. nodosum* hosts the epiphytic red alga *Vertebrata lanosa*, which only habitat is on fronds of *A. nodosum*, and occasionally on wounded parts of *Fucus vesiculosus*, where it attaches by rhizoid penetration (Maggs and Hommersand, 1993).

As *A. nodosum*, *V. lanosa* is common along the Norwegian shore. It was earlier classified to the genus *Polysiphonia*, but is now classified to the genus *Vertebrata*, which constitutes a well-defined clade in the Polysiphonieae-tribe (Díaz et al., 2017). This alga has a repeated pseudodichotomous branching at irregular intervals with corymbose apices, giving it a bush-like structure. The thallus diameter is 3-7.5 cm with a brownish-red colour that differs from the green-brown colour of *A. nodosum* (Maggs and Hommersand, 1993).

The alga is dioecious, and has a triphasic sexual life cycle with a haploid gametophytic stage and a diploid tetrasporophytic stage, where the two stages are morphologically similar (Maggs and Hommersand, 1993). Spermatangia form in tufts at the apices of branches and produce egg-shaped spermatia with a diameter of 3-4 µm. Egg-cell producing carpogonia are formed on short trichoblasts, after fertilization the carpogonium and the surrounding tissue develops to

a cystocarp and releases carpospores that creates new tetrasporophytes (Maggs and Hommersand, 1993). Tetrasporangia are formed in the last two orders of branching. The main period for release of tetraspores in North Wales is in August, according to Pearson and Evans (1990). The reproductive structures die within approximately a month, resulting in loss of biomass (Pearson and Evans, 1990). Cystocarps have been observed during January, April to June and August to October, while spermatangia have been observed in February to July and in December (Maggs and Hommersand, 1993). Another study by Longtin et al. (2009) found that tetraspores and cystocarps were present between July and November and peaked in summer in Nova Scotia. During settlement of tetraspores or carpospores, *V. lanosa* sporelings develop and simultaneously grow erect branches and a primary 40 µm wide rhizoid to anchor itself into the cortex of *A. nodosum*. Subsequently, more rhizoids grow from the basal cells of the erect branches to strengthen the attachment. The adjacent host cells are stretched by the intruding rhizoids and eventually degrade (Garbary et al., 2005).

The reason for the obligate relationship between *V. lanosa* and *A. nodosum* is not yet fully understood, but there have been multiple studies on this unique relationship (Pearson and Evans, 1990; Garbary et al., 2005; Longtin and Scrosati, 2009; Scrosati and Longtin, 2010). A flow tank experiment by Pearson and Evans (1990) examined spore settlement on *A. nodosum* and *F. vesiculosus*, and showed that *V. lanosa* spores had a random settlement pattern on *F. vesiculosus* in contrast to that on *A. nodosum* where settlement mainly occurred in branching axils and damaged spots of the thallus. On both algae, the survival rate of settled *V. lanosa* sporelings were higher in the branching axils and the damaged spots than elsewhere on the thallus. Furthermore, the settlement and survival of sporelings on *F. vesiculosus* was significantly lower than on *A. nodosum*. The reason for the site-specific settlement could be that axils and wounded spots are areas where *A. nodosum* do not shed the outer thallus layer regularly, thus giving more time for *V. lanosa* to anchor its rhizoids through the epidermis layer, which can take up to two months (Rawlence and Taylor, 1970; Pearson and Evans, 1990). Furthermore, Pearson and Evans demonstrated in 1991 that rhizoid growth of *V. lanosa* was stimulated when exposed to exudates from *A. nodosum* and *F. vesiculosus*, thereby boosting the attachment process. Another process that may favour the relationship between the two algae, is *A. nodosum*'s reproduction pattern and shedding of receptacles after the gamete release during spring. The shedding leaves scar sites for *V. lanosa* to settle on, and *V. lanosa* will usually release carpospores in the months following the shedding period (Garbary et al., 1991).

There is a third part in the symbiotic relationship which may favour *V. lanosa*'s obligation to its host. *Mycophycias ascomphylli* is a mutualistic fungus occurring on *A. nodosum* already in its zygote stage where it stimulates growth of its host (Garbary et al., 2005). It seems to interact with both *V. lanosa* and *A. nodosum* by physically occurring in and between *V. lanosa*'s rhizoids and the host's surrounding cells. It has been speculated that this fungus may be a potential pathway for nutrient transfer between *V. lanosa* and *A. nodosum*, and that it also helps to limit tissue damage caused by *V. lanosa*'s rhizoid attachment to their common host (Garbary et al., 2005).

As an epiphyte, *V. lanosa* may have negative impacts on its host. These include shading and damaging of host cells by attachment of rhizoids which may leave *A. nodosum* more vulnerable to pathogens. Damaging of the host's thallus may lead to additional breakage due to mechanical damage from water motion. However, even though *V. lanosa* is usually found attached on damaged areas of *A. nodosum*, it has not been proven that *V. lanosa* was the cause of the damage (Pearson and Evans, 1990). Furthermore, there seem to be no substantial nutrient transmission between the algae (Harlin and Craigie, 1975), so a parasitic relationship does not seem to be a driver of *V. lanosa*'s obligate epiphytism.

There must be other reasons for the obligate epiphytic relationship with *A. nodosum*. In addition to a suitable habitat for settlement, it has been hypothesised that *A. nodosum* provide shelter from radiance and heat in the summer, and protection against frost and wind in the winter (Fralick and Mathieson, 1975). *A. nodosum* is also long lived compared to many other seaweed in the class Fucales, and is believed to live for up 20-40 years (Garbary et al., 2005; Kurr and Davies, 2018). A study by Garbary et al. (2014) found that the growth of *V. lanosa* depends on its host, as the photosynthetic performance of *V. lanosa* significantly decreased when not attached to *A. nodosum* compared to when attached. A third treatment included both species in the same chamber, although not attached to each other. Here, the photosynthetic performance of *V. lanosa* was an intermediate between the two other treatments. The photosynthetic performance of *A. nodosum*, however, was not affected either way.

With its branched structure, *V. lanosa* creates a more complex habitat for fauna and smaller flora than *A. nodosum* would alone (Martin-Smith, 1993). Several epiphytic algae and invertebrates have *V. lanosa* as a habitat. Some mesoherbivores prefer feeding on epiphytic macroalgae rather than *A. nodosum*, but there are also mesoherbivores feeding on both (Pavia

et al., 1999), thus a more complex habitat can attract herbivores that indirectly effects *A. nodosum* negatively.

1.3 Abundance and growth of *Vertebrata lanosa*

V. lanosa is a common epiphyte on *A. nodosum*, and its distribution includes the northern parts of the North Atlantic Ocean, with the exception of Skagerrak and Greenland (Rueness, 1998; Pedersen, 2011). The distribution of *V. lanosa* is limited to that of its host, but is not entirely coinciding with that of *A. nodosum*, which indicates that environmental factors may also limit the distribution of the epiphyte (Fralick and Mathieson, 1975; Garbary and Deckert, 2004).

Its absence in Skagerrak where *A. nodosum* is common is assumed to be due to the low salinity levels caused by the Baltic Current (Åberg, 1992), and similar observations have been done in the tidal pools of Tjongspollen, Hordaland, which is known for low salinity levels (Heggøy, 2001). A study done in New Jersey by Fralick & Mathieson (1975) suggests that *V. lanosa* prefers a salinity range of 25-40 psu for photosynthesis, while 15 psu and below negatively affects the photosynthetic productivity. As a comparison, Åberg (1992) had a mean surface salinity of 20 psu and 25 psu at his two study sites in Skagerrak, which could explain the absence of the alga. However, an ecotype of *V. lanosa* which tolerates brackish water has been recorded in Scotland (Reed, 1983).

Considering this, there might be other environmental factors influencing the distribution of *V. lanosa*, but literature on the subject is sparse. In regards to temperature, *V. lanosa* has a temperature optimum of 22-24 °C for photosynthetic production (Lüning, 1990). In the aspect of vertical preference in the *Ascophyllum*-zone, Longtin et al. (2009) found that *V. lanosa* preferred mid-elevations over low and high elevations in Nova Scotia. However, Fralick and Mathieson (1975), found in Great Bay Estuary, New Hampshire, that *V. lanosa* was restricted to 0.2-1.3 meter above Chart Datum, while *A. nodosum* was extended to 0.0-2.3 meter above Chart Datum. This indicates that it preferred the mid and low elevation, which differs somewhat from the findings of Longtin et al. (2009).

The growth rate of *V. lanosa* and its reaction to loss of biomass is also an area where there is little knowledge. Like *A. nodosum*, it is a perennial alga with apical growth (Fralick and Mathieson, 1975), and it is likely that the growth of *V. lanosa* stagnates during the winter in temperate areas as with most other algae (Mathieson et al., 1976; Stengel and Dring, 1997; Forbord et al., 2012). The only recorded regular biomass loss is due to necrosis of reproductive

structures in autumn, which results in biomass loss during winter months (Pearson and Evans, 1990; Maggs and Hommersand, 1993). Due to the small size and bush-like features of *V. lanosa*, one can easily remove most of the thallus when harvesting, if not the entire thallus. This leaves the oldest part of the thallus left to regrow. It is not yet known whether this will leave *V. lanosa* with low chances of survival, or if this is a common occurrence in nature which it has evolved to withstand.

There seem to be no records of common grazers on this epiphyte, likely because of its tough and rigid structure, although juvenile specimens may be prone to grazing by crustaceans and molluscs commonly found browsing on the surface of *A. nodosum* fronds. A study by Pavia et al. (1999) concluded that macroepiphytes is important as habitat and food for mesoherbivorous crustaceans living on *A. nodosum*, although the study location was in Sweden where *V. lanosa* is absent.

Although there is considerable literature available on the obligate relationship *V. lanosa* has with its host *A. nodosum*, there is little knowledge about the epiphytes occurring on *V. lanosa* itself. This is an interesting topic, as fouling species may influence the taste and quality of *V. lanosa* as a food product. Apart from the parasitic epiphyte *Choreocolax polysiphoniae*, a cushion-like small red alga which almost without exclusion only occurs on *V. lanosa*, there are no other epiphytes on *V. lanosa* described in literature (Callow et al., 1979).

1.4 Scope of study

For harvesters, it is of importance to have knowledge about which areas are likely to have rich abundances of *V. lanosa*, at which rate they grow back after harvesting, and at what time of year the fouling of *V. lanosa* is at its lowest.

In this study, the abundance of *V. lanosa* has been assessed in a local coastal area in relation to physical factors as degree of exposure, substrate, inclination, orientation, height above the lowest astronomical tide (Chart Datum), temperature, and salinity. Locations with various occurrence of *A. nodosum* were chosen to study the abundance of *V. lanosa*. The abundance of *V. lanosa* was also related to the amount of *A. nodosum* present. In addition to the abundance study, a regrowth experiment where marked branches of *A. nodosum* were monitored at two stations from autumn to spring was done, and fouling of *V. lanosa* was assessed at four randomly chosen stations in late autumn and late winter.

Increased knowledge on these topics is essential for potential future commercial harvest of *V. lanosa*. Information on regrowth of the potential food alga is important, as this can advise on how frequent and by which means the alga can be harvested in a sustainable manner. If the alga is slow growing, heavy harvesting may have serious consequences. Furthermore, in relation to human consumption a clean product is important. Therefore, the coverage and abundance of fouling epiphytes on *V. lanosa* was investigated to document which organisms have this alga as a host, and whether there are shifts in abundance and species composition through the season. The study may give an implication on where to harvest, when to harvest and how to harvest the alga to ensure a sustainable practice.

2 Materials and Methods

2.1 Field site

All field work was done in the area surrounding the Marine Biology Station of the University of Bergen at Espegrend (60°16'10.5"N, 5°13'23.3"E), South of Bergen, Norway (Figure 1-5). This is a relatively sheltered inshore archipelagic area which is typical for the west coast of Norway. Abundances of *A. nodosum* and *V. lanosa* were recorded at 27 locations between the 10th of August and the 22nd of September 2017 (Appendix 1). On location 1 and 4, a regrowth experiment of *V. lanosa* was carried out (Figure 3). Furthermore, fouling of *V. lanosa* was recorded on location 1, 2, 11 and 27 (Figure 3, Figure 5).

Sampling locations had to meet certain criteria, and were chosen semi-randomly to secure a certain range of distribution within degree of exposure, inclination, orientation of the locations and substrate of *A. nodosum*. The substrate suitable for *A. nodosum* in the area was either rock or bedrock substrate. All locations were also relatively sheltered, as *A. nodosum* prefers sheltered habitats. With all this in mind, the most important criteria for the sampling locations was that they had to have at least 20 meters of *A. nodosum* growing horizontally along the shore to provide potential habitat for *V. lanosa* to grow. Locations also had to be relatively easily accessible from the marine station, as the boat used for transportation was small with no protection against bad weather and not particularly fast. Furthermore, the inclination had to be no steeper than approximately 45° to avoid unnecessary risks when sampling. In addition, the abundance of *A. nodosum* is less in steep areas. It should, however, be noted that there could be large variations in inclination within sites. Popular swimming sites or areas with high boat

traffic were avoided as these activities could affect the growth and distribution of *A. nodosum* and *V. lanosa* through trampling or increased wave exposure.

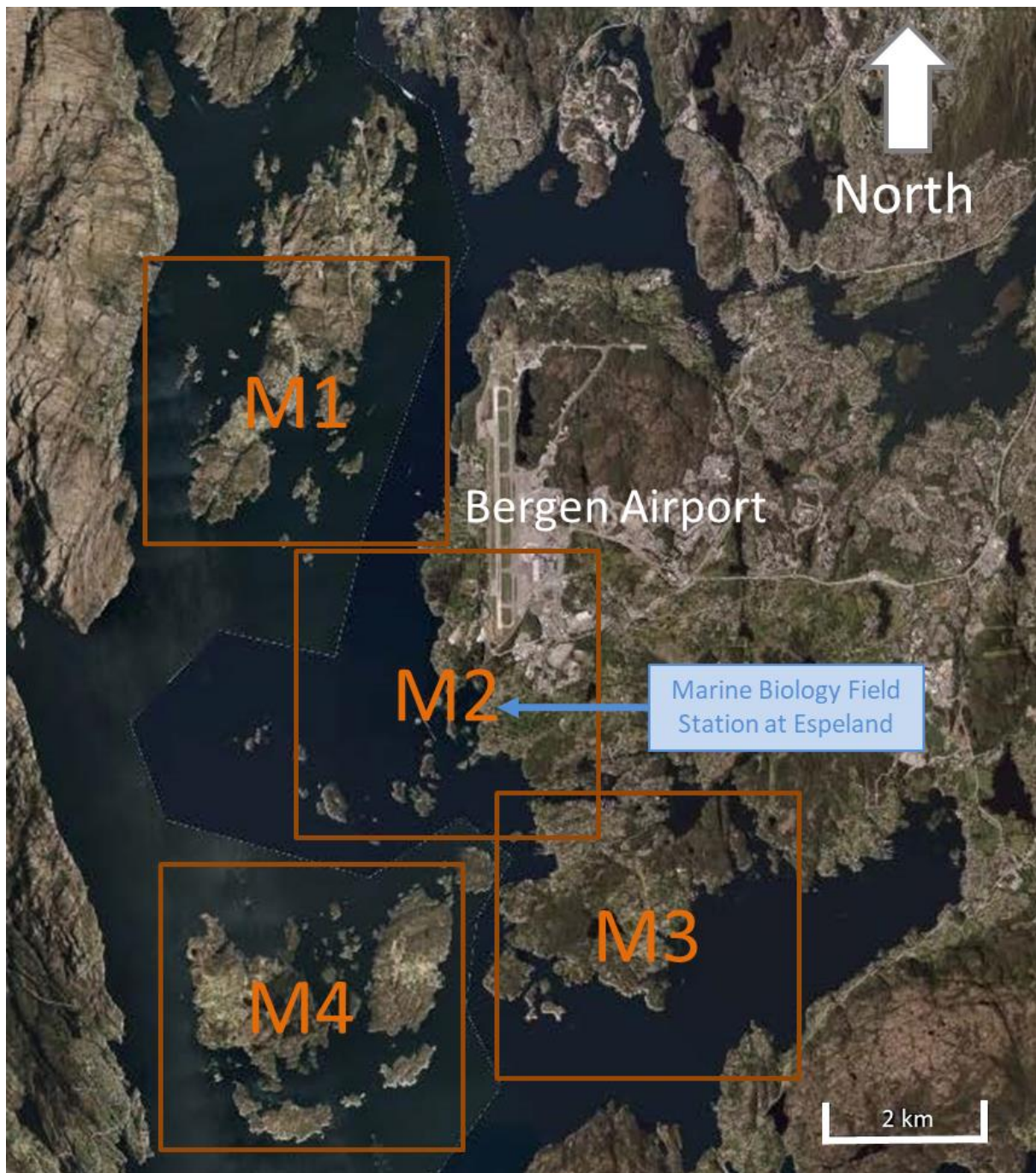


Figure 1. Map overview of the sampling areas South of Bergen, located in Raunefjorden and Fanafjorden. See figure number 2-5 for details.

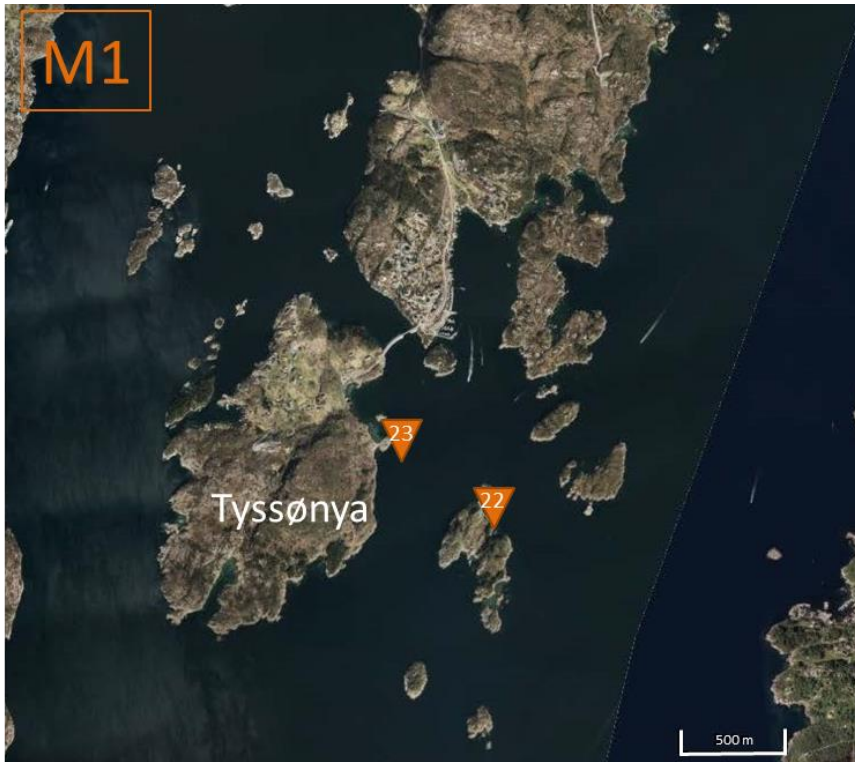


Figure 2. Sampling area number 1: showing sampling location 22 and 23 in the Tyssønya-area. The exact location is at the bottom of triangular icons.



Figure 3. Sampling area number 2: showing sampling location 1-4 and 27. This also includes the growth monitoring locations which are in close proximity to the Marine Biology Field Station at Espeland. *V. lanosa* was harvested at location 1, 2 and 27 for fouling studies, marked with white circles.



Figure 4. Sampling area no. 3, showing sampling location 7, 16 and 17 in Fanafjorden.



Figure 5. Sampling area no. 4, showing location 5, 6, 8-15, 18-21 and 24-27 surrounding Lerøyyna and Bjelkarøyyna. *V. lanosa* was harvested at location 11 for fouling studies, marked with a white circle.

2.2 Field study

2.2.1 Sample square analyses

When a location met the criteria listed earlier, sample square analyses (Salvanes et al., 2018) were done to investigate the abundance of *A. nodosum* and *V. lanosa*. A measuring tape was placed horizontally along the upper extension of the growth zone of *A. nodosum* (hereafter the *Ascophyllum*-zone), parallel to the sea, to define a 20 meter transect (Figure 6). The width of the *Ascophyllum*-zone was measured across every two metres of the transect with a measuring rod, giving a total of 10 cross sections.

The zone was thereafter divided into an upper and a lower part, and a sample square of 50 x 50 cm was placed in the centre of each part, but on different sides of the measuring rod (Figure 7). This resulted in a maximum of 10 x 2 sample square analyses for the 20 m long transect, where the percentage coverage of *A. nodosum* and *V. lanosa* was assessed. If *A. nodosum* did not form a distinct coherent zone in a cross-transect, the distance between the uppermost and lowermost extension of *A. nodosum* patches was measured. If the *Ascophyllum*-zone was 1 m or less across, only one sample square analysis was conducted as the zone width was too short to fit two sample squares. Occasionally cross-transect without *A. nodosum* would appear during the measurements, and this was also recorded.

To more easily get a better overview of the contents of the square, a sample square which was subdivided in 25 smaller squares was placed on top of a regular sample square (Figure 7). The subdivided square made it easier to distinguish the percentage coverage of the two species, as one sub-square represented 4 % of the area of the entire sample square. If the area of *A. nodosum* or *V. lanosa* covered less than one sub-square, an approximation was made by eyesight. When the coverage of *A. nodosum* formed a thick layer, it was searched to expose covered *V. lanosa* specimens.

In each sample square, the thickness of the *A. nodosum* canopy was measured at three different places in the square, and an average was used for the statistical analyses. This was done systematically by measuring the thickness diagonally starting in one corner, measuring the central sub-square and then the other corner of the diagonal. If these sub-squares did not cover *A. nodosum*, other sub-squares containing *A. nodosum* would be randomly chosen. The substratum on which *A. nodosum* was growing was also recorded when doing the measurements, divided into the categories bedrock (massive rock shapes without loose stones or rock) and rocks (loose laying rocks).



Figure 6. A 20 m transect of the *Ascophyllum* zone at location 5.



Figure 7. The two sample squares have been placed in the upper and lower half of one of the 10 cross transects.

2.2.2 Levelling

To be able to compare the vertical location of the measuring squares and the *Ascophyllum*-zone between locations, their height above Chart Datum (the lowest astronomical tide) had to be calculated. For this, a levelling instrument (monocular) was used, and the vertical distance between the water level and levelling instrument was recorded and the time was noted (Figure 8). All the vertical height measurements at the location could thus be correlated to the theoretical low tide available in The Norwegian Mapping Authority's data (Kartverket), thus giving the vertical height of the measurements above Chart Datum.

After measuring the height of the water level, the height of the upper and lower end of the *Ascophyllum*-zone and the two sample squares in each 2 meter-section of the transect was measured (Figure 8). Two persons were necessary to do these measurements, as one had to hold the measuring rod while the other operated the levelling instrument.

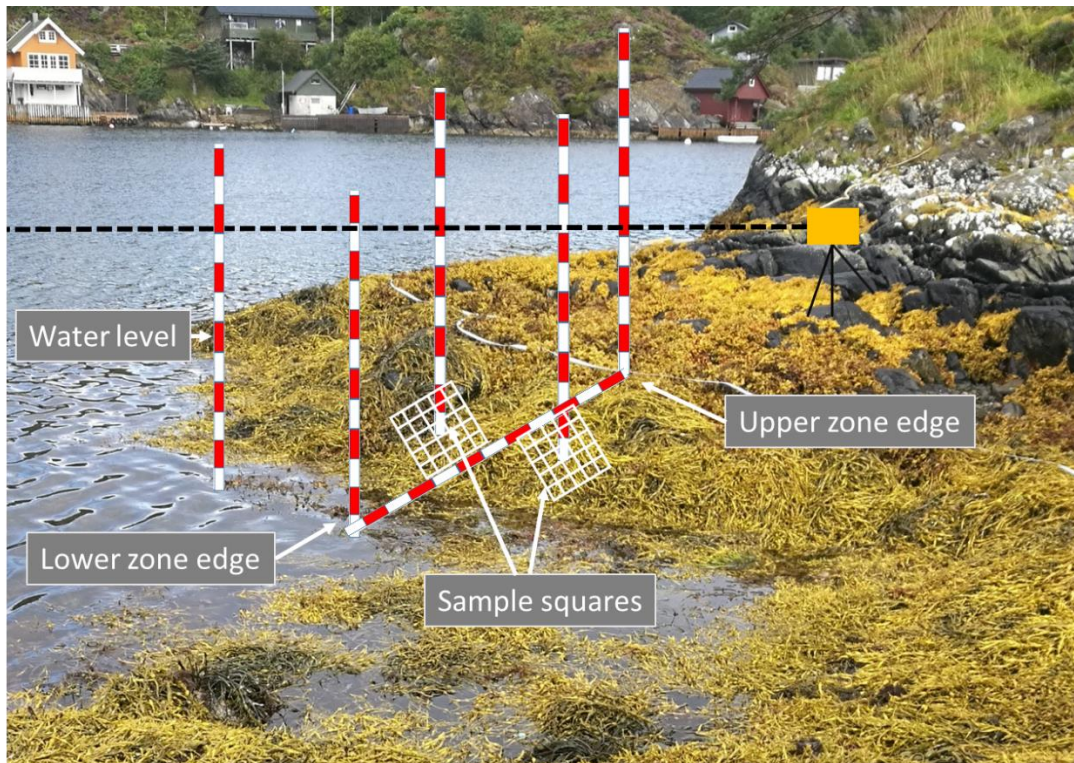


Figure 8. In-field topography measurements. The yellow box to the right is the levelling instrument. The red and white rods are the measuring rod, used to: 1, measure the height of the water at low tide (which was done once before starting other measurements at the location). 2, measure the width of the *Ascophyllum*-zone and place the sample squares. 3, measure the height of the lower and upper zone edge, and the height of the sample squares.

2.2.3 Salinity and temperature measurements

The salinity and temperature were measured at each location on the 9th of October 2017, 4th of February 2018 and the 27th of May 2018 at the water surface (approximately 0.5 m depth) with a WTW LF340 Conductivity Meter. As these two factors fluctuate with changes in season and weather, measurements were done at all locations at the same day to look for relative differences, preferably on days without much precipitation that would affect the salinity.

2.3 Measuring regrowth of *Vertebrata lanosa*

Location 1 and 4 were chosen for studying the regrowth of *V. lanosa* over time due to their close proximity to the marine station. Branches of *A. nodosum* with on-growing *V. lanosa* were marked to make them easily recognisable (Figure 9). There was an equal number of control- and treatment-branches, where the treatment-branches were systematically picked for *V. lanosa* to



Figure 9. Example of a picked branch, where most of the biomass has been removed.

simulate harvesting. A minor part of the *V. lanosa* thallus was left on the branch of *A. nodosum* for potential regrowth. Four of each treatment were marked in August 2017 as a pilot study. The remaining 5 of each treatment were monitored from October 2017, giving nine treatment- and nine control branches in total at the two different locations. The branches were monitored 5 times during the season by photography with a Huawei Honour 8 mobile camera. The camera was placed on a stand to keep a standard 90-degree angle over the grid with 1 cm squares which the branches were photographed on (Figure 9). This was to prevent large differences in angle and distance in the photos which could cause irregularities in the following picture analyses. The part of then branch which was included in the study was from the plastic strip and outwards (blue strip, Figure 9).

The differences in biomass of *V. lanosa* over time were quantified in area (cm²) with the image processing programme ImageJ (Schneider and Rasband, 2012). The programme was calibrated after a known distance in every image, in this case grid. Thereafter, the circumference of the *V. lanosa* specimens growing on each *A. nodosum* branch was outlined in the programme to calculate the total area of *V. lanosa* in the image. This was done twice for each image, to account for any inaccuracies while outlining *V. lanosa* in the images.

2.4 Biofouling

To assess which organisms grew on *V. lanosa*, and if the amount and composition of species varies throughout the season, three branches of *A. nodosum* with *V. lanosa* were collected randomly at four locations of different exposure degree (Location 1, 2, 11 and 27) on the 3rd of November 2017 and the 27th of February 2018. These branches were brought back to the

laboratory and contained in a solution of 4 % formaldehyde buffered with borax. Three subsamples of *V. lanosa* of approximately the same size were picked from each harvested *A. nodosum* branch and studied in a microscope, giving a total of 9 subsamples from each location. The fouling organisms on *V. lanosa* were identified with help from Professor Kjersti Sjøtun (Department of Biological Sciences, University of Bergen), associate professor emeritus Ruth Nielsen (Natural History Museum, Denmark) and Dr. Karl Gunnarsson (Marine and Freshwater Research Institute, Iceland), in addition to the book *Seaweeds of the British Isles, Volume 1 Rhodophyta, Part 3A Ceramiales* (Maggs and Hommersand, 1993) to the lowest taxonomic rank possible, and the amount of fouling was classified to look for differences in amount and composition of fouling. For each subsample, the fouling species were ranked from 0-4 after its level of presence on *V. lanosa* (Table 1) to give an abundance score. The abundance scores were then used to give a perception of the amount of fouling and which species were more common in the samples, hereby called a total abundance score (TAS). Before observing subsamples in the microscope, macroscopic fouling of *V. lanosa* (fouling visible without a microscope) was recorded if present.

Table 1. Ranking system for amount of fouling on subsamples of *V. lanosa* with description of each fouling level.

Fouling level	Description	Value
Extremely dominant	More biomass than that of host	4
Dominant	Covering large parts of host thallus, outweighing other species	3
Common	Occurring multiple times on the host thallus	2
Rare	1-2 specimens in subsample	1
Not present	No visible fouling	0

2.5 Calculations

2.5.1 Cartographic wave-exposure and orientation

A modified version of Baardseth's (1970a) cartographic measuring technique was used to determine a relative exposure degree of the measuring locations. This method has earlier been successfully used by Armitage et al. (2014) in the same area. This was done by placing a protractor on a map (scale 1:500, The Norwegian Mapping Authority, Kartverket) with the measured locality as the centre point. For every 10° around the locality, the distance from the locality to the nearest land or island was measured in mm (Figure 10). The sum of these distances gave the relative exposure degree of the locations, and these were compared between locations.

Figure 10. Measuring relative exposure degree with a modified version of Baardseth's (1970) cartographic method. The yellow lines indicate the distance between the station and the closest landmass, which were measured at a 10° interval. The red is an example of one distance measurement (here 690 mm).

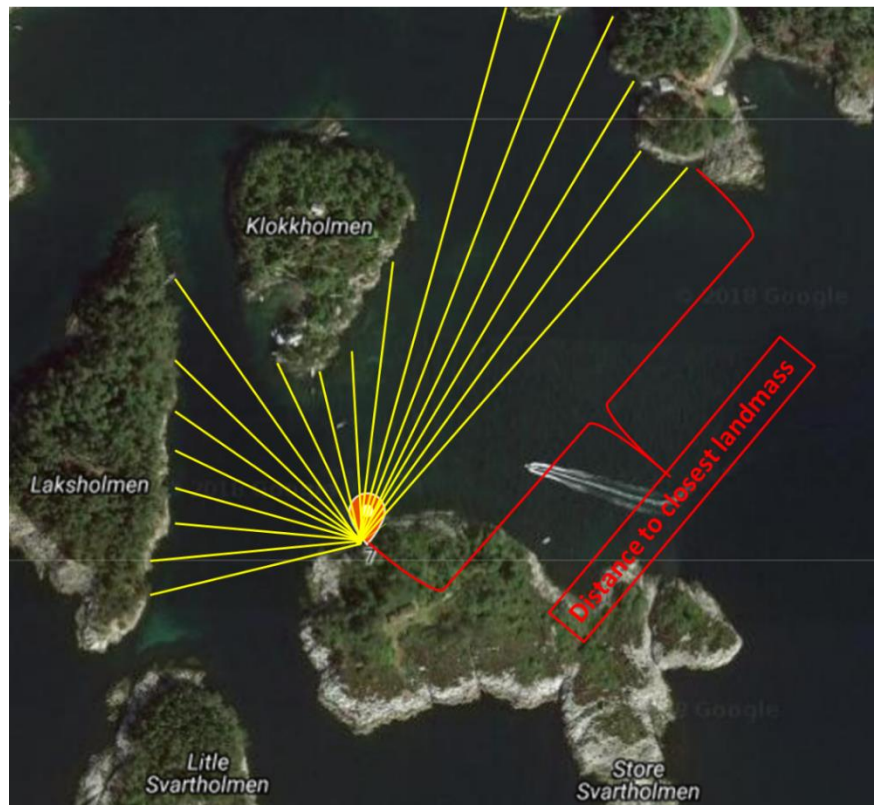


Table 2. Orientation categorised into 360 degrees.

Orientation	Degrees (°)	n
North	315-360, 0-45	8
East	45-135	6
South	135-225	7
West	225-315	6

Orientation of the locations were also found with a cartographic method, where a 360° protractor was placed on the map over each location. The 0 on the protractor was facing towards North on the map, and 180 towards South, and thus the degree of orientation was found by seeing which degree the location was facing out towards. These degrees were subsequently grouped into orientations shown in Table 2.

2.5.2 Topography

To get a common reference point for measurements at all locations, the measured vertical heights of the *Ascophyllum*-zone and the sample squares were adjusted according to Chart Datum, the lowest astronomical tide (Figure 11). This was done by comparing low tide-measurements on site to Chart Datum data for the exact area and time for when the measurements were done supplied by The Norwegian Mapping Authority, Kartverket (www.kartverket.no/sehavniva/).

The vertical height of the upper and lower borders of the *Ascophyllum*-zone was calculated by subtracting height b from height a , as seen in Figure 11. As this vertical height was measured through the horizontally calibrated levelling instrument, it is safe to assume that there is a 90° angle between the vertical height and the distance to the levelling instrument.

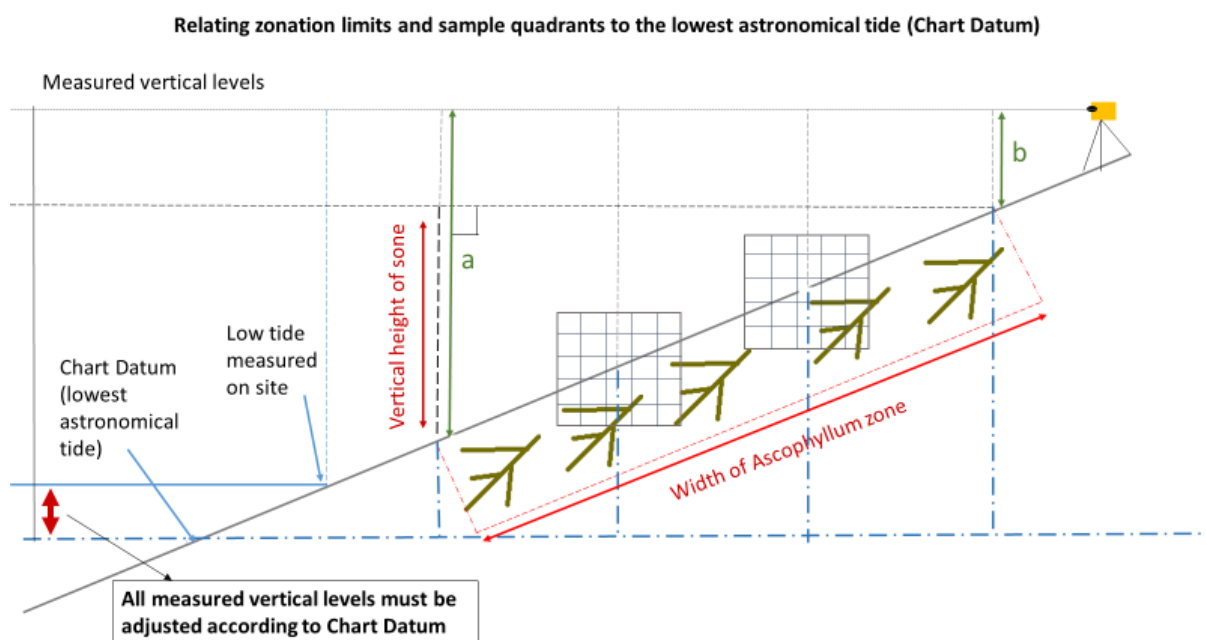


Figure 11. The relation between measured zonation levels and Chart Datum. All vertical levels were later adjusted to the lowest astronomical tide to be able to compare measurements at all locations.

Thus, if the vertical height and width of the *Ascophyllum* zone is known, one can use a simple equation to calculate percentage incline, or grade of the zone:

$$\text{Percentage incline} = 100 * \frac{\text{Vertical height}}{\text{Zone width}}$$

Percentage incline, or grade, is commonly used to describe the inclination of physical structures like roads, rivers and hillsides, and can be presented as a percentage, an angle or a ratio. As seen in Figure 12, a 100 % incline equals 45 ° or a ratio of 1/1.

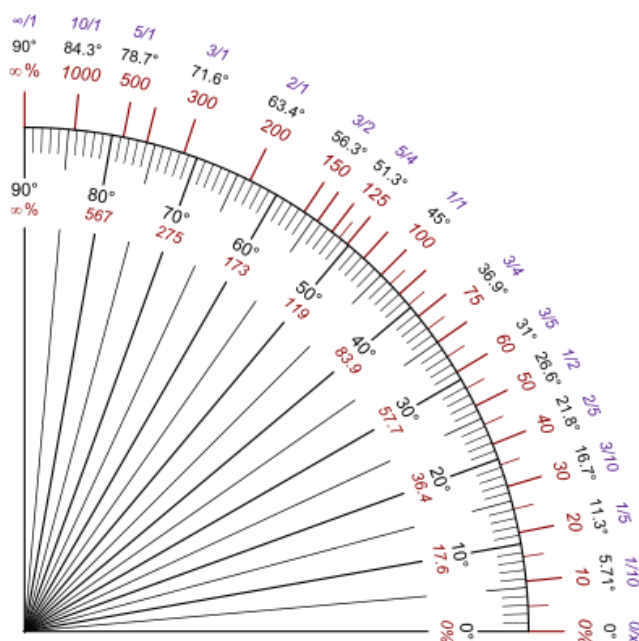


Figure 12. Illustration of degrees, percentage incline and proportions. Created by Toews (2017).

2.6 Statistical analyses

Data records were stored in Microsoft Office Excel 2016. Graphs and statistical analyses were done in the data analysis software R-Studio version 3.4.4 (RStudio Team, 2015). The level of significance for p-values was initially set at $p < 0.05$.

To test for a relationship between inclination and width of the *Ascophyllum*-zone, a log linked general linear model (GLM) with a gaussian family was used. The relationship between exposure and orientation was tested with a linear mixed effect model (LME).

All models which analysed the abundance of *A. nodosum* or *V. lanosa* in relation to abiotic factors (Table 3), were Generalized Linear Mixed Models with a penalized Quasi-likelihood (glmmPQL) and a quasibinomial family (R-package MASS; Venables and Ripley, 2002).

This was firstly because of the nonnormality of the data, due to the abundance being measured in proportion of the sample square, and secondarily because of the involvement of the random effect of location. Proportion or count data is often found in ecological studies and evolution research, and GLMMs is a relatively flexible method to analyse these data (Bolker et al., 2009). The quasibinomial family was assigned to the model because of the proportion data which ranged from 0-1, including values in between the two.

The models were supported with an R^2 -test (or pseudo R^2 -test, for GLMM models). The R^2 coefficient has a value of 0-1 and describes how well the model fit the data - a goodness-of-fit. It is found by dividing the explained variation with the total variation. A R^2 coefficient of 0 indicates that 0 % of variability in the data is described by the model, whilst 1 indicates that 100 % of the variability in the data is described by the model. There are two types of R^2 coefficients: marginal R^2 and conditional R^2 . Marginal R^2 describes the variance explained by fixed factors, whereas conditional R^2 describes the variance explained by both random and fixed factors (Nakagawa and Schielzeth, 2013). This test is a valuable addition to models when handling ecological data, as these often are variable and finding a model with a perfect fit can be difficult.

The factor orientation was organized into the four orientations depending on degrees seen in Table 3. These were made with the help of the R package dplyr (Wickham et al., 2017). When analysing the two categorical factors *substrate* and *orientation*, an additional TukeyHSD-test was performed to look for significant differences between the effect of categories. Collinearity between environmental factors were tested with a Pearson's Product-Moment correlation test. All plots in the study were plotted by means of the R package ggplot2 (Wickham, 2009).

The growth data was analysed with both a linear mixed effect model (LME) and a categorical model to test for significant differences in growth between the two treatments (control and picked). The LME had the best fit (tested with an Akaike information criterion-test, AIC), and was used in the results.

Table 3. Statistical analyses and methods, with response variables in bold, and predictor variables listed below. GLM, General Linear Model; glmmPQL, General Linear Mixed Models with Penalized Quasi-likelihood; LME, Linear Mixed Effect model; TukeyHSD, Tukey's Honest Significant Test. Factors marked with (S) indicates that the factor is common for all measurements at each location, factors marked with (CS) indicate that the factor is common for both measurements in each cross section of the transect. Unmarked factors are unique for each sample quadrant.

Response and predictor variables	Statistical methods
Exposure vs Orientation	LME
Inclination vs Zone-width	GLM
A. nodosum abundance	
Exposure (S)	glmmPQL + R^2
Temperature (S)	glmmPQL + R^2
Salinity (S)	glmmPQL + R^2

Inclination (CS)	glmmPQL + R ²
Zone width (CS)	glmmPQL + R ²
Height above Chart Datum	glmmPQL + R ²
Substrate	glmmPQL + R ² + TukeyHSD
Bedrock vs rock	
Orientation (S)	glmmPQL + R ² + TukeyHSD
East vs North	
East vs South	
East vs West	
North vs South	
North vs West	
South vs West	

***V. lanosa* abundance**

Exposure (S)	glmmPQL + R ²
Temperature (S)	glmmPQL + R ²
Salinity (S)	glmmPQL + R ²
Inclination (CS)	glmmPQL + R ²
Zone width (CS)	glmmPQL + R ²
Volume of <i>A. nodosum</i>	glmmPQL + R ²
Height above Chart Datum	glmmPQL + R ²
Substrate	glmmPQL + R ² + TukeyHSD
Bedrock vs rock	
Orientation (S)	glmmPQL + R ² + TukeyHSD
East vs North	
East vs South	
East vs West	
North vs South	
North vs West	
South vs West	

3 Results

3.1 Physical factors

At the 27 study sites, the most abundant substrate was bedrock (325 grids) and stones (212 grids), followed by rocks (48 grids) and a mix of bedrock and stone (10 grids). While 15 of the stations had a mix of substrates, 10 were solely bedrock and two consisted of stone substrate. The cartographic wave exposure values ranged from 33-692, and the majority of stations were on the sheltered side of this range, as 16 out of 27 stations were below the mean value of 327.4 (Appendix 2).

Of the 27 locations, 8 faced North, 7 faced South, 6 faced East and 6 faced West. As seen in Figure 13, all four orientations had locations with a relatively broad range of relative exposure degrees. However, East oriented sites were on average somewhat more exposed than the other sites. The orientation of the sites was significantly associated with exposure ($p < 0.001$), and there were significant differences between several orientations (Table 4). The East- and West-orientated sites had exposure degrees within similar ranges and were not significantly different, as was also the case for South- and West-orientated sites. However, there was a significant difference in cartographic wave exposure between all other orientations (Table 4).

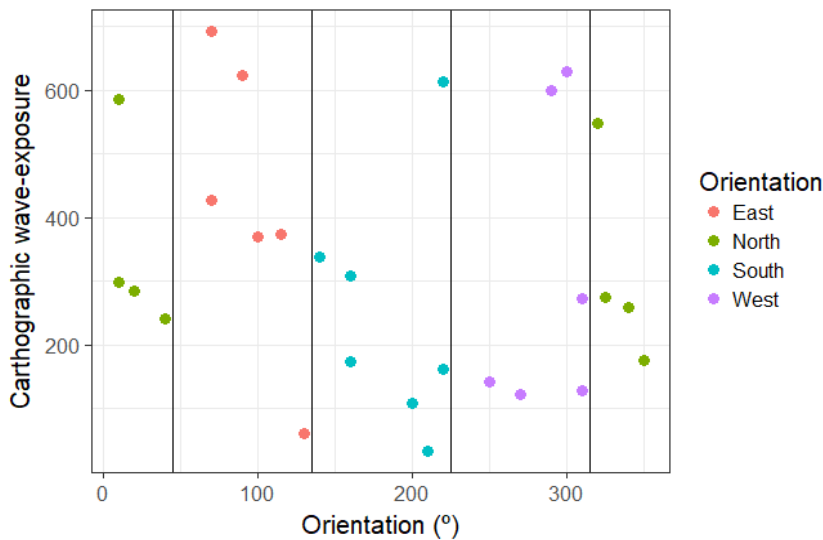


Figure 13. Scatterplot with the cartographic wave exposure of the sites facing in the orientations East (n=8), North (n=8), South (n=7) and West (n=6). The orientations are grouped by degrees, where East lays within 45-135°, North lays within 315-360° and 0-45°, South lays within 135-225°, and West lays within 225-315°.

Table 4. Variation of cartographic wave exposure between orientations analysed with a linear mixed effect model and a TukeyHSD-test.

Orientations	P-value
East - North	0.0085
East - South	<.0001
East - West	0.2174
North - South	0.0085
North - West	0.0003
South - West	0.2174

At each station, inclination was measured in the 10 cross sections of the transect and is presented here as percentage incline. The inclination could vary to a large degree within stations due to change in topography or due to rocks and stones (Appendix 3). The width of the *Ascophyllum*-zone was both visibly and statistically affected by the inclination of the sites, as there was a large negative correlation between the two factors (Appendix 4). The belt widened with lower inclination, as there was more habitat available within *A. nodosum*'s preferred range of physical conditions in the tidal zone. The relationship was somewhat curved and thus analysed by a GLM-model with a Gaussian family which was log-linked as seen fitted in Figure 14. One data point showed a negative increase percentage, as the slope of the *Ascophyllum*-zone was in fact facing towards land and not the sea. This is the outlier to the far left with a value of -14% (Figure 14).

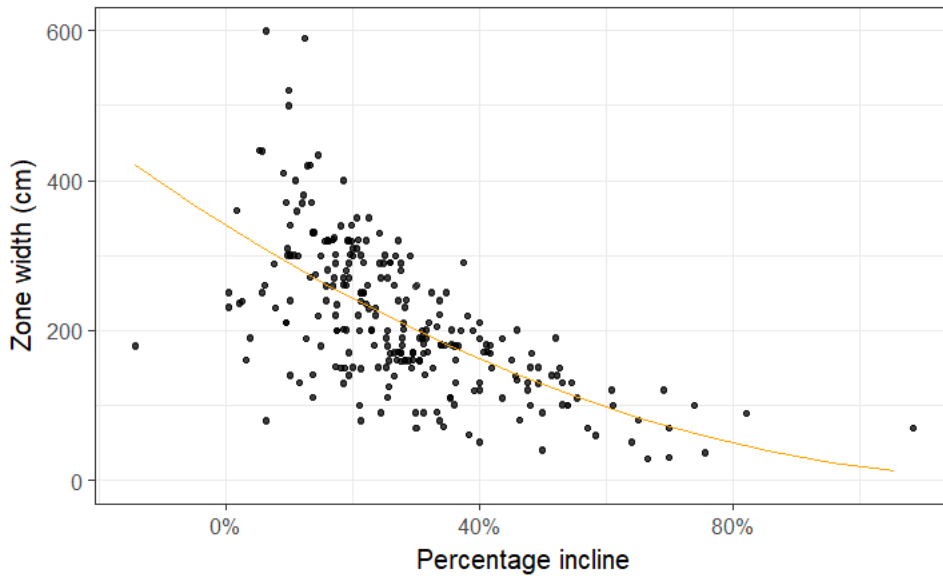


Figure 14. Zone width (cm) of *Ascophyllum*-zones measured at all stations (n=270) versus the inclination (percentage incline) of the zone. The orange line corresponds to a fitted log-linked generalized linear model with a Gaussian family ($p < 0.001$).

One could see a local pattern in the salinity and temperature measurements, as stations situated close together would usually share similar measures. There was a relative difference in both salinity and temperature between groups of stations. The differences in salinity among stations were relatively small, the maximum difference being 4.7 psu between least and most saline location at the same day. Neither was the temperature differences between stations substantial, the maximum difference being 2.6 °C. There was a large positive correlation between salinity and temperature (Appendix 4), which is likely to be due to the relatively similar temperature and salinity levels at stations that were situated close together.

3.2 Abundance of *Ascophyllum nodosum* and *Vertebrata lanosa*

The sample squares were in the range of -24 to 104 cm above Chart Datum with an average of 42 cm (Figure 15). The abundance and thickness of *A. nodosum* measured with sample squares varied between the 27 sites (Appendix 3). At some sites, *A. nodosum* formed dense mats covering the substrate. At others, it grew in patches with either bare substrate or *Fucus* spp disrupting the *A. nodosum*-coverage. The coverage in the sample squares ranged from 0-100 %, with an average of 75 % (n=508).

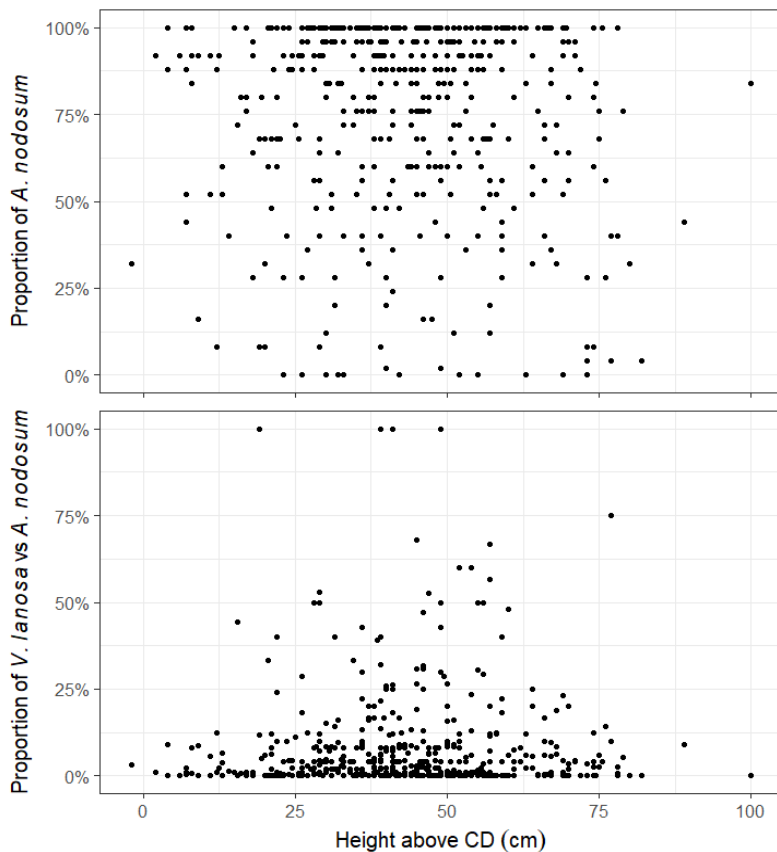


Figure 15. Above: The proportion of *A. nodosum* (%) above Chart Datum (cm). Below: Proportion of *V. lanosa* vs *A. nodosum* (%) above Chart Datum (cm).

Sample squares with *V. lanosa* present ranged from -2 to 89 cm above Chart Datum, although most seem to be centred in the mid-range of the *Ascophyllum*-zone (Figure 15). The abundance of *V. lanosa* in individual sample squares varied between 0 % to 68 %, with an average cover of 5 % (n=508) (Appendix 3). When describing the abundance of *V. lanosa* in this section, a proportion of *V. lanosa* versus *A. nodosum* ($V. lanosa / A. nodosum$) is used, as this accounts for the amount of habitat which is available for *V. lanosa* to grow in each measurement.

Table 6. The statistical analyses used to test the abundance of *A. nodosum* and *V. lanosa*. Response variables are in bold with their predictor variables below. Statistical methods: GLM, General Linear Model; glmmPQL, General Linear Mixed Models with Penalized Quasi-likelihood; LME, Linear Mixed Effect model; TukeyHSD, Tukey’s Honest Significant Test; R2m, marginal R²; R2c: conditional R². Significant p-values are in bold. Factors marked with (S) indicates that the factor is common for all measurements at each station, factors marked with (CS) indicate that the factor is common for both measurements in each cross section of the transect.

Response and predictor variables	Statistical method	p-value	R2m	R2c
Exposure vs Orientation	LME	<0.001	0.064	1.000
Inclination vs Zone-width	GLM	<0.001	(multiple)	(adjusted)
<i>A. nodosum</i> abundance				
Exposure (S)	glmmPQL	0.1261	0.053	0.483
Temperature (S)	glmmPQL	0.6159	0.020	0.489

Salinity (S)	glmmPQL	0.7767	0.002	0.485
Inclination (CS)	glmmPQL	0.0290	0.039	0.466
Zone width (CS)	glmmPQL	<0.001	0.222	0.629
Height above Chart Datum	glmmPQL	0.6028		
Substrate	glmmPQL + TukeyHSD		0.020	0.486
Bedrock vs rock		0.2554		
Orientation (S)	glmmPQL + TukeyHSD		0.024	0.155
East vs North		0.4350		
East vs South		0.4220		
East vs West		0.8428		
North vs South		0.9998		
North vs West		0.9144		
South vs West		0.8950		
<i>V. lanosa</i> abundance				
Exposure (S)	glmmPQL	<0.001	0.316	0.658
Temperature (S)	glmmPQL	0.0406	0.155	0.690
Salinity (S)	glmmPQL	0.0341	0.133	0.696
Inclination (CS)	glmmPQL	<0.001	0.089	0.742
Zone width (CS)	glmmPQL	<0.001	0.161	0.759
Zone layer (upper/lower)	glmmPQL	0.0704	0.027	0.717
Volume of <i>A. nodosum</i>	glmmPQL	<0.001	0.320	0.841
Height above Chart Datum	glmmPQL	0.9231		
Substrate	glmmPQL + TukeyHSD		0.316	0.658
Bedrock vs rock		0.0544		
Orientation (S)	glmmPQL + TukeyHSD		0.005	0.100
East vs North		1.0000		
East vs South		0.9083		
East vs West		0.9988		
North vs South		0.8748		
North vs West		0.9977		
South vs West		0.9538		

Cartographic wave exposure

Typically, the more sheltered sites would have a denser cover of *A. nodosum*, and more exposed sites would have less, often patchy coverage. However, the effect of exposure was not significant on the cover of *A. nodosum* (Table 6). There was a significant positive effect of cartographic wave exposure on the abundance of *V. lanosa* (Table 6). The relationship was tested with a quasibinomial glmmPQL-model which is fitted in Figure 16. These findings suggest that *V. lanosa* prefers more exposed areas.

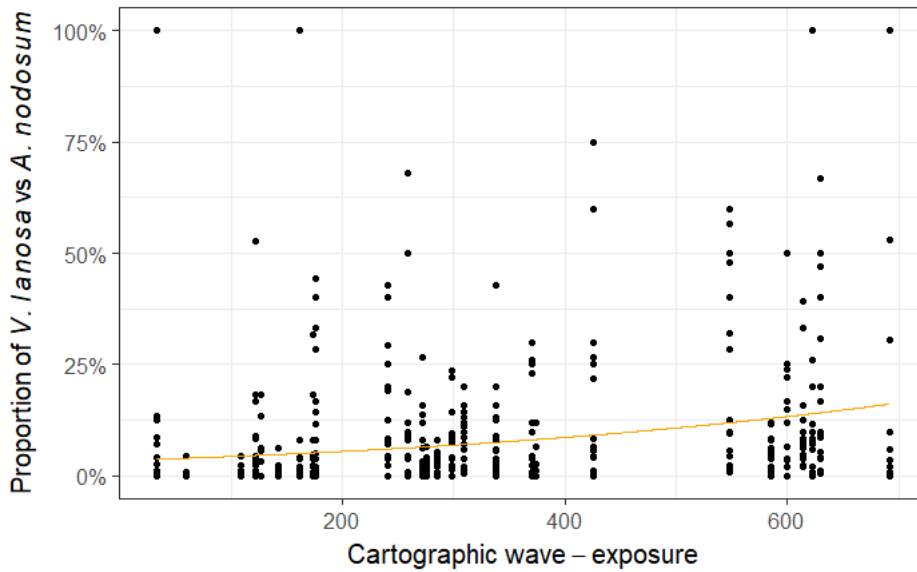


Figure 16. Abundance of *V. lanosa* in proportion to *A. nodosum* versus cartographic wave exposure ($p < 0.001$). The orange line corresponds to the fitted generalized linear model.

Substrate

Substrate had no significant effect on the abundance of *A. nodosum* or the abundance of *V. lanosa* (Table 6). The two algae do not seem to have a preference between bedrock and rocks.

Inclination

The inclination of the zone had a significant effect on the abundance of *V. lanosa* and *A. nodosum* (Table 6). As for exposure, increased inclination had a negative effect on the abundance of *A. nodosum* and a positive effect on *V. lanosa* (Table 6, Figure 17). A possible correlation between exposure degree and inclination was tested, but the coefficient value was small ($r = 0.1442$, Appendix 4), and suggesting the two were not correlated.

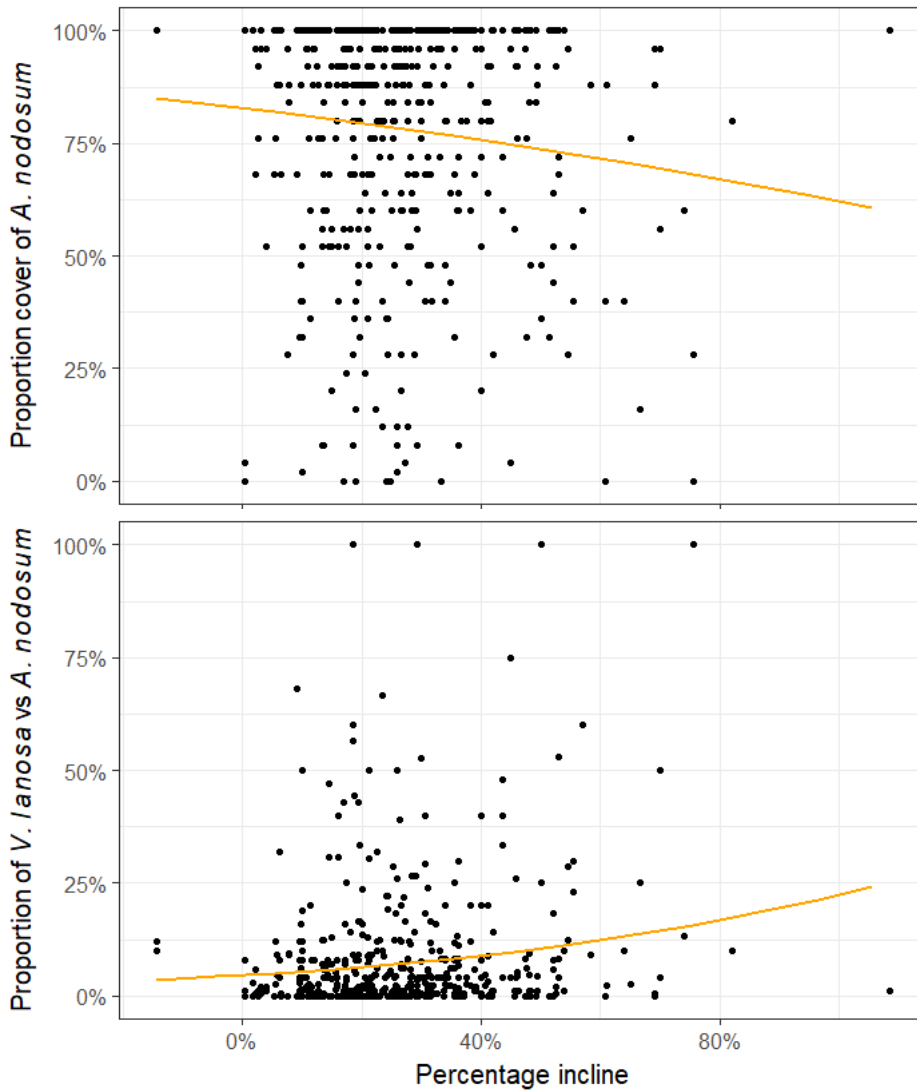


Figure 17. Above: Abundance of *A. nodosum* versus inclination of the tidal zone. Below: Abundance of *V. lanosa* in proportion to *A. nodosum* versus incline measured in incline percentage. 100% incline equals an incline of 45°. Both scatterplots are fitted with the respective generalized linear mixed models with a Penalized Quasi-Likelihood (orange).

Orientation

No significant differences were found regarding the abundance of either *A. nodosum* or *V. lanosa* between sites of different orientations (Table 6).

Temperature and salinity

Neither salinity nor temperature had a significant effect on the abundance of *A. nodosum*, but a slightly significant correlation between abundance of *V. lanosa* and temperature and salinity was found (Table 6). In both cases a higher abundance was associated with lower values of salinity and temperature. Both the salinity and temperature-model had large degrees of variation which is unexplained by the model (r^2 coefficients of 0.13 and 0.16, respectively).

Width of *Ascophyllum*-zone

There was a strong significant effect between the width of the *Ascophyllum*-zone and the abundance of the two species (Table 6). The width (n=270) ranged from 0 to 600 cm, and the amount of *A. nodosum* present in the sample square naturally increased with the width of the zone. The effect was positive on the abundance of *A. nodosum* and negative on the abundance of *V. lanosa* (Figure 18). This means that, even though there is potentially more habitat available for *V. lanosa* in form of *A. nodosum*, there is a negative effect on the abundance of *V. lanosa*, suggesting there is other factors influencing the abundance than presence of *A. nodosum*. The zone-width was negatively correlated with incline to a large degree (Appendix 4), which means that increased inclination would lead to shorter zone widths in most cases.

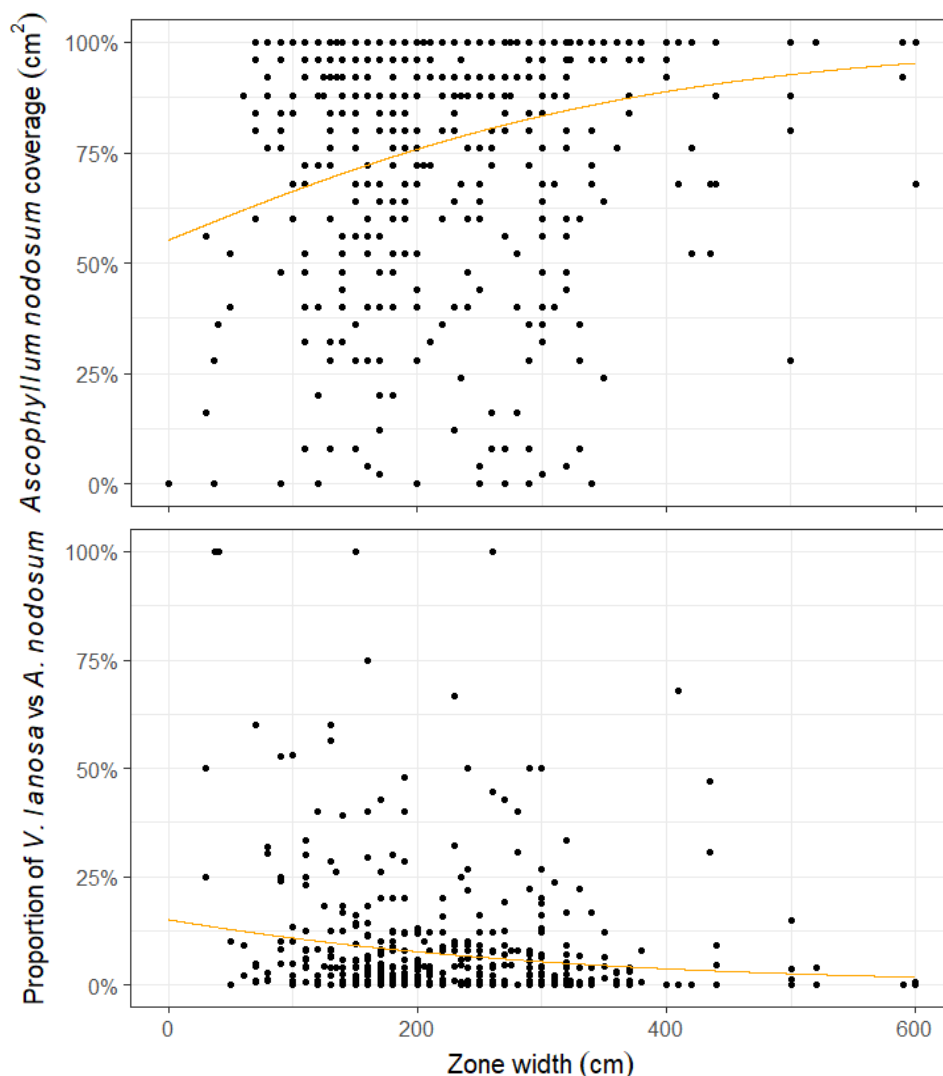


Figure 18. Above: *A. nodosum* coverage versus width of the *Ascophyllum*-zone (cm). Below: Proportion of *V. lanosa* versus *A. nodosum* with width of *Ascophyllum*-zone (cm). Both plots fitted with a glmmPQL model.

Thickness of *Ascophyllum nodosum*

The thickness of *A. nodosum* in the sample squares ranged from 0 to 12.67 cm, with an average of 5.18 cm (Appendix 3). By using the measured thickness and area of *A. nodosum* in the sample squares, the volume was calculated. The volume ranged from 0 to 31.675 cm³ with an average of 10.71 cm³. The abundance of *V. lanosa* significantly decreased (Table 6) with larger volumes of *A. nodosum*. In Figure 19, one can see that a 100 % *V. lanosa*/*A. nodosum* cover in sample squares was measured four times in the study. In all four measurements, the *A. nodosum* volume was below 5 cm³. Additionally, the volume was not correlated with any of the physical factors (Appendix 4).

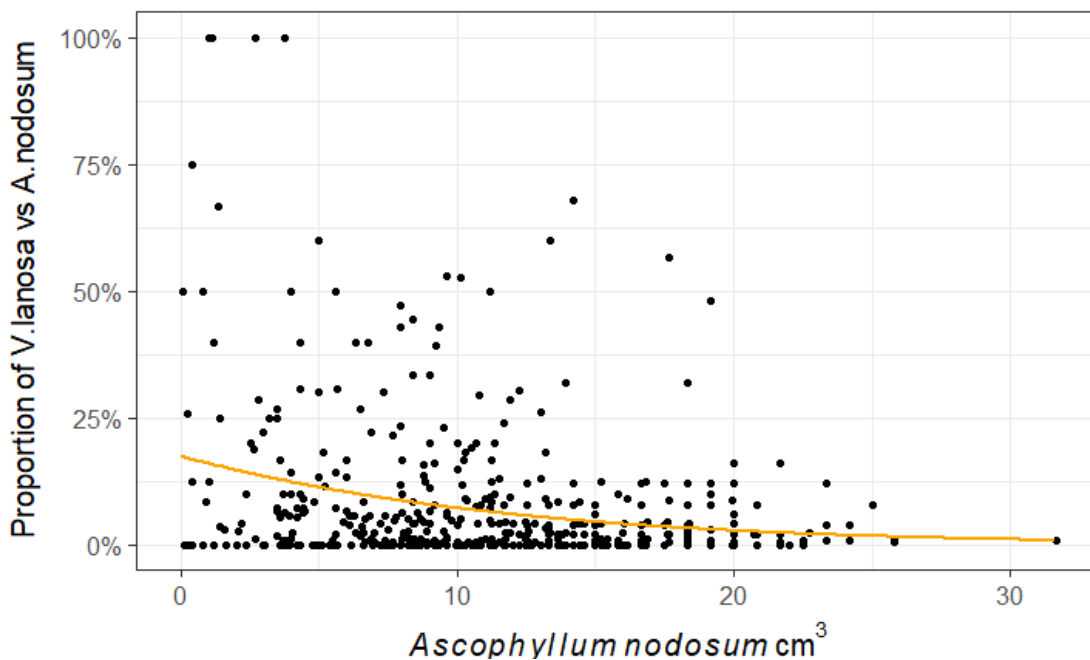


Figure 19. The proportion of *V. lanosa* versus *A. nodosum* in sample squares versus volume of *A. nodosum* (cm³) in sample squares.

3.3 Regrowth of *Vertebrata lanosa*

The biomass of *V. lanosa* (measured in area) was monitored 5 times from August 2017 to April 2018. Loss of sample material occurred during the period, as some branches or marks disappeared for unknown reasons. In total, 9 of 36 of the marked *A. nodosum* branches included in the growth-study disappeared during the winter months between November and March. Of these, 3 were control-branches and 1 picked-branch at Station 1, and 3 were control-branches and 2 picked-branches at Station 4. Other branches were found at some monitoring days and not others, as the marks could be somewhat challenging to locate when covered with seaweed. Furthermore, a few of the monitored *A. nodosum* branches had parts torn off during the winter period, perhaps due to rough weather. Because of this, what was left of the respective *A.*

nodosum thallus' at the last monitoring had to be traced backwards in all the pictures taken before parts of the branches were removed. Only the part of the frond that was left at the end was included in the area measurements in ImageJ. This ensured that only the parts of the thallus with specimens of *V. lanosa* which made it through the study were used for statistical analysis.

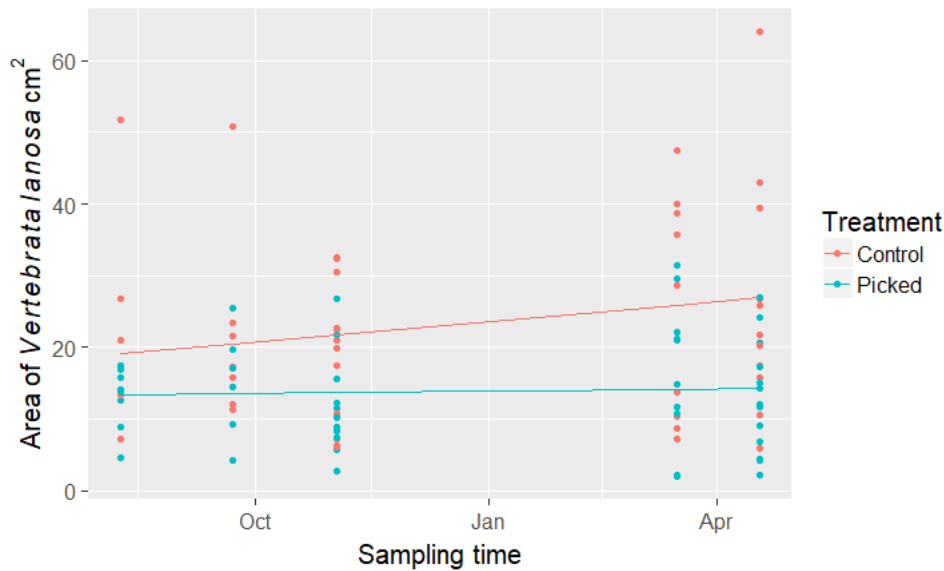


Figure 20. Biomass of *V. lanosa* (cm^2) of both control and picked treatments, measured from November 2017 - April 2018.

Table 7. P-values from the linear mixed effect model with the area of *V. lanosa* as response variable. Significant values are in **bold**.

Factors	p-values
Treatment	0.0029
Time	0.0507
Treatment:Time	0.1019

While some of the *V. lanosa* individuals showed biomass loss during winter and gain during spring, others had a more random or stagnant biomass development (Appendix 4). As seen in Table 7, there was a significant effect of treatment on the biomass of *V. lanosa* measured in area. The treatment factor explains the difference in biomass between the control treatments, which were left untouched during the study, and the picked treatment, where large amounts of biomass was removed at the start of the study. Thus, the significant effect of treatment was expected in the study, as there was a major difference in biomass between the two treatments from the beginning of the experiment. The effect of time was almost significant for the study period (Table 7), and there seems to be a slight positive growth-trend in the control treatment (Figure 20). However, there are large varieties in the data as seen in Figure 20. The effect of treatment on biomass over time was non-significant (Table 7), indicating that there was no significant difference in the increase or decrease of biomass between the control and picked treatment over time. Thus, there are no indications that the harvesting experiment had significant effect on the growth of *V. lanosa*. This was tested with both categorical and linear models, which gave similar results. A linear

mixed effect model is fitted to the data in Figure 20. Through observation in microscope, there seemed to be new apical growth in spring. However, this growth was not substantial enough to make a statistically significant differentiation for the study period as there was much variation between specimens.

3.4 Fouling of *Vertebrata lanosa*

All the samples of *V. lanosa* collected at both sampling dates were fouled to some degree by epiphytic taxa. The largest amount of fouling was found in November 2017, where the total abundance score (TAS) was larger than the fouling in late February 2018 (Table 8). The size of the fouling taxa was also larger in November, as 22 of 36 subsamples had macroscopic fouling (fouling observable without microscope) compared to 11 of 36 in February.

A range of different organisms was found fouling *V. lanosa*, including algae species belonging to Rhodophyta, Phaeophyceae, Chlorophyta and Cyanophyta. Species of Rotifera, Tunicata, Polychaeta, Bivalvia and Hydrozoa were also present in samples. Some of the algae were difficult to identify to species, as some of them were in their juvenile stages and their traits diverged somewhat from their adult traits normally used to identify algae. Therefore, the algae were identified to the closest taxonomical level possible. In total, 19 different species were identified.

The epiphyte *Chorecolax polysiphoniae*, commonly found on *V. lanosa*, was recorded in some of the samples but not included in the abundance count because it was omitted in the first sampling. Microplastics were present in three of the 36 subsamples from the second sampling, but was not recorded in the first sampling.

Table 8. Summarized total abundance score (abundance of each fouling species rated from 0-4 in each subsample) of fouling organisms on *V. lanosa* at the four sampling locations at both sampling dates.

Sampling date	03.11.2017	27.02.2018	Cartographic wave exposure
Station 1	162	88	275
Station 2	164	54	370
Station 11	122	52	548
Station 27	83	49	614
Total	531	243	-

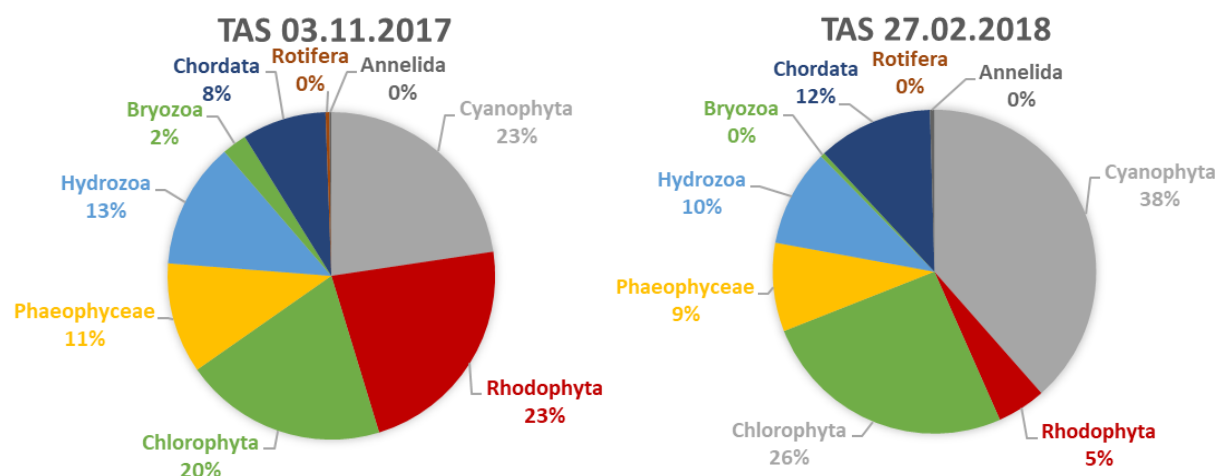


Figure 21. The composition of the main groups of fouling taxa at the two sampling dates presented in pie charts. TAS = Total Abundance Score.

Although there was a general reduction of fouling organisms in February compared to November, the amount of fouling varied between different sites as seen in Table 8, and also somewhat within sites. The more exposed sites seem to have less fouling than the more sheltered sites (Table 8), but the number of stations were too few to draw any firm conclusions. *Dermocarpa sp.* and another cyanobacteria of the order Oscillatoriales were present in most of the samples (Figure 22), and were also the most abundant fouling taxa (Figure 21). Other common fouling taxa were a brown alga of the order Spachelariales, the green alga *Cladophora sp.*, the hydrozoa *Laomedea flexuosa*, and a small tunicate, as seen in Table 9.

The abundance of red algae was larger in samples from November than February. In terms of composition, the brown and green algae seem to be approximately equally abundant at both sampling dates, whereas cyanophytes were more abundant compared to other groups in February (Figure 21). The animal groups do also seem to have approximately the same abundance at both sampling dates.

Table 9. Overview of organisms growing on *V. lanosa* and their total abundance score (TAS) from all samples at both sampling dates.

Higher grouping	Species (or closest identification)	TAS 03.11.2017	TAS 27.02.2018	Total TAS
Cyanophyta	Oscillatoriales	62	38	100
	<i>Dermocarpa sp.</i>	58	49	107
Rhodophyta	<i>Bonnemaisonia hamifera</i>	47	0	47
	Ceramiales indet..	23	17	40
	<i>Ceramium sp.</i>	32	2	34
	<i>Dasysiphonia japonica</i>	1	0	1

	Juvenile Stylonemataceae	17	9	26
Chlorophyta	<i>Chaetomorpha ligustica</i>	26	6	32
	<i>Cladophora</i> sp.	50	37	87
	<i>Pseudendoclonium dynamenae</i>	15	9	24
	<i>Ulva compressa</i>	15	6	21
Phaeophyceae	<i>Dictyota dichotoma</i>	7	3	10
	Spachelariales sp.	51	17	68
Hydrozoa	<i>Laomedea flexuosa</i>	39	22	61
	<i>Dynamena pumila</i>	27	0	27
Bryozoa	<i>Electra pilosa</i>	13	1	14
Chordata	Small tunicate	44	26	70
Rotifera	Rotifers	2	0	2
Annelida	<i>Spirobis</i> sp.	1	1	2

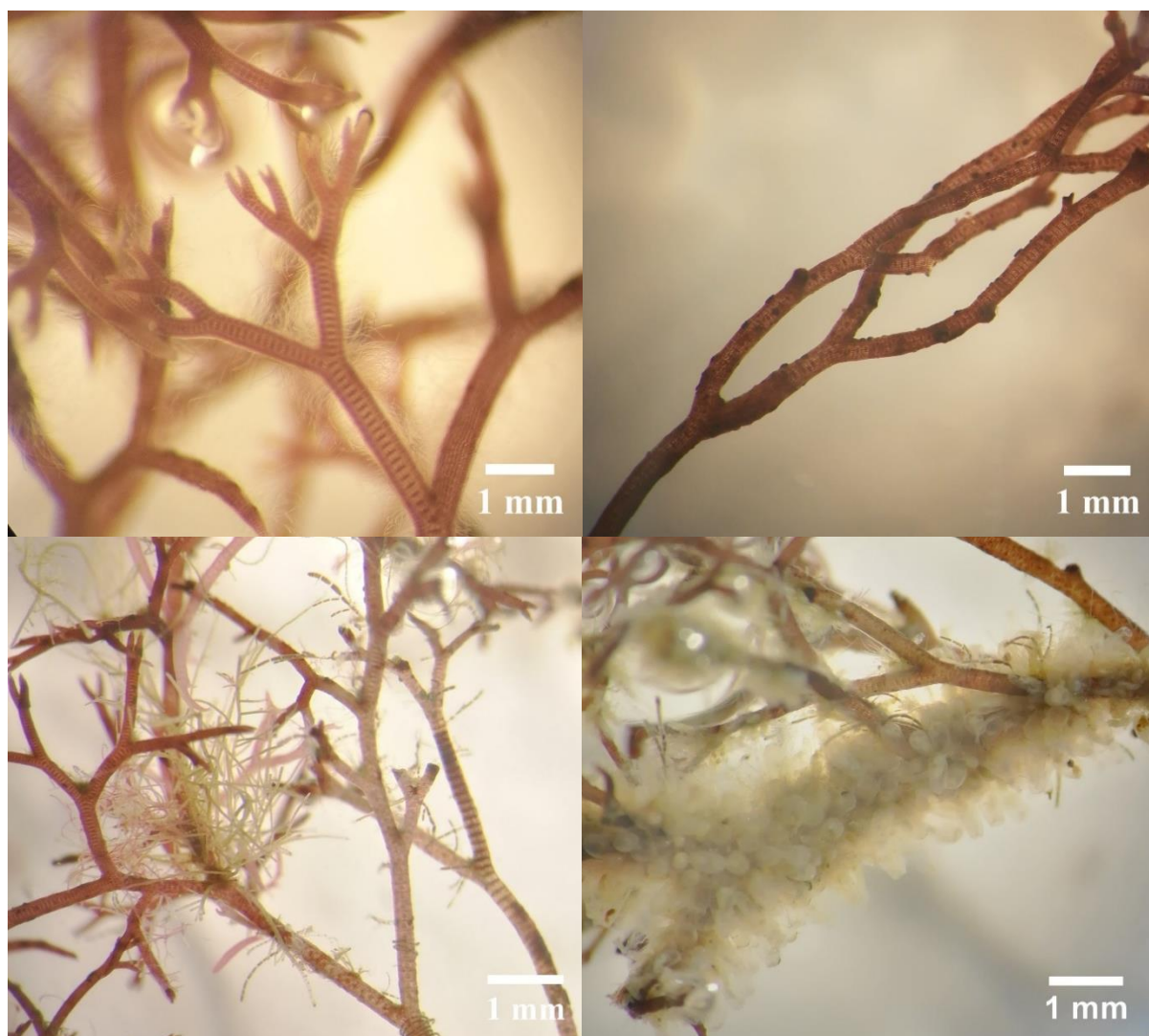


Figure 22. Top left: Cyanobacteria of the order Oscillatoriales attached to *V. lanosa*. Top right: *Dermocarpa* sp. (small, black lumps) attached to *V. lanosa*. Bottom left: *V. lanosa* with Spachelariales sp. and *Ceramium* sp. (pink). Bottom right: *V. lanosa* strongly overgrown with small tunicates.

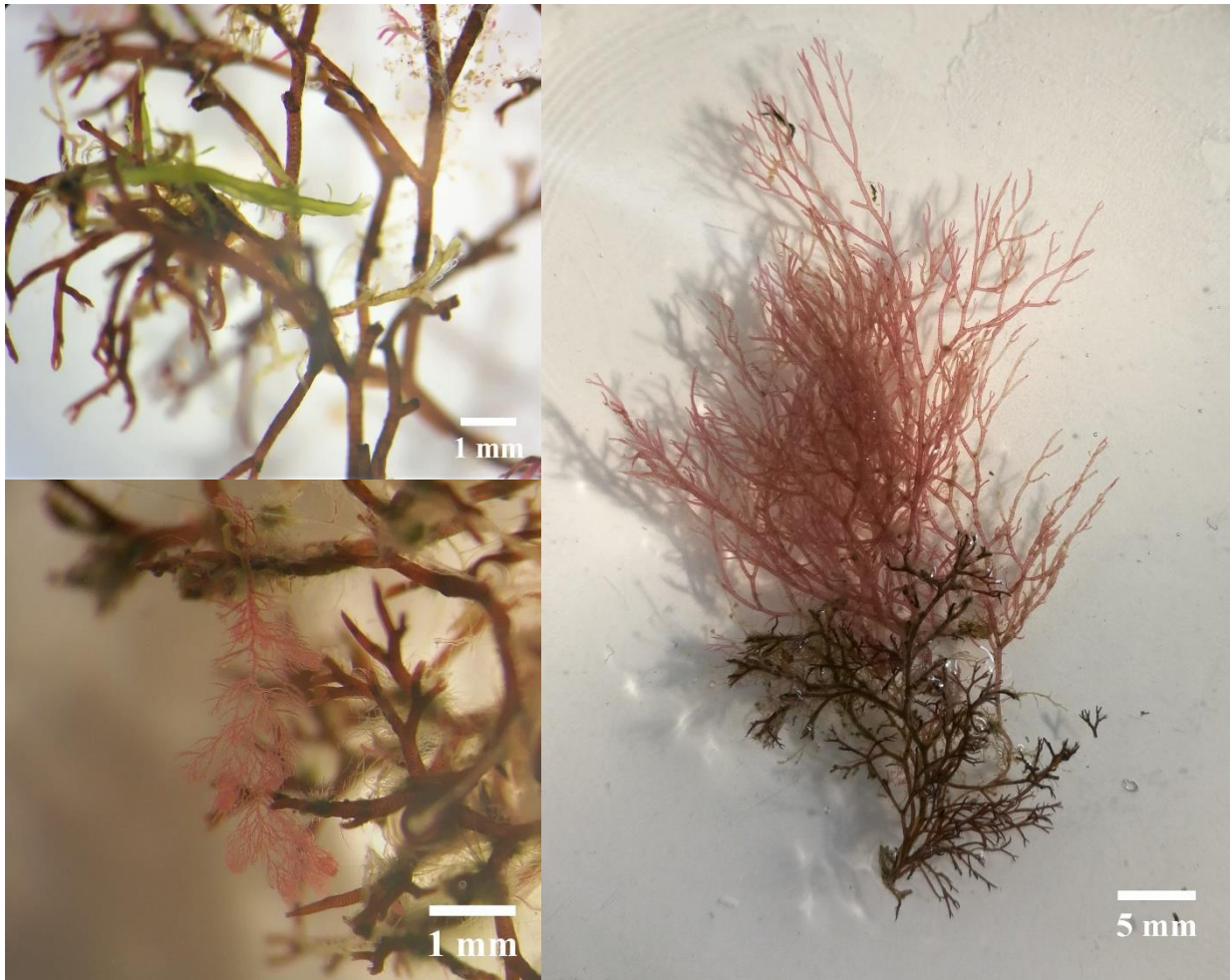


Figure 23. Top left: *V. lanosa* with *Ulva compressa* and hydroids. Bottom left: *Dasysiphonia japonica* growing on *V. lanosa*. Right: Large *Ceramium* sp. growing on *V. lanosa*.

4 Discussion

Vertebrata lanosa, or so called “Truffle of the sea”, has drawn attention in later years for being a new, local food product with an appealing taste (Viestad, 2016). This study is the first to assess growth and quality of *V. lanosa* for human consumption, and has obtained valuable information for future harvesting of this alga as a valuable food product. Several factors have been mapped that influences the alga’s habitat, distribution and quality. This information is not only important for fundamental research purposes, but also as background information related to harvesting of the alga.

4.1 Uncertainties of the results

The abundance of *A. nodosum* and *V. lanosa* was assessed with sample square analysis. This method is not the most precise method of measuring percentage coverage, but it is time efficient and relatively constant when done consistently by the same person, as in this study. Still, it is easier to take accurate measurements by eyesight when there are smaller amounts of algae in the sample squares (Meese and Tomich, 1992). Hence, the uncertainty in the measurements

may be higher with larger quantities of algae in the sample squares. This provides a justification for interpreting the p-values from the statistical testing in a conservative way.

Since the sample squares were consistently put in the centre of the upper- and lower half of the *Ascophyllum*-zone, there were no samples from the outer edges or the exact middle of the zone, unless when the zone was as short as 1 meter. This way of measuring could prevent gathering valuable information on the coverage of *V. lanosa* in the centre and outskirts of the *Ascophyllum*-zone at each site. However, the data shows a range of heights above Chart Datum preferred by *V. lanosa* within the range of the vertical heights of the *Ascophyllum*-zone, which is valuable information.

A levelling instrument was used to measure the average inclination of the *Ascophyllum*-zone. However, not all sites were as straight and standardized as the calculated average inclination. Rocks of different sizes affected the topography and thus the degree of inclination and exposure on the algae, and the bedrock was also of irregular shapes at some of the stations. Therefore, some of the inclination measurements can be inaccurate.

Cartographic wave exposure is a simple and cost-efficient way to theoretically calculate the exposure degree of locations. However, this method does not take weather and water motion created by marine traffic into consideration, and these elements may also influence wave exposure at sites. To reduce the error from wave exposure by marine traffic, locations close to frequently used shipping and ferry routes were avoided. Nevertheless, the likeliness of boat traffic passing the sampling locations is relatively high, as private leisure boats are common in the area. The results of this could be that some locations were more wave exposed than the cartographic wave-exposure suggests, especially during the summer, which is the peak time for leisure boat activity. However, compared to wave motion produced by natural causes, the wave motion from marine traffic in these areas is weaker and seasonal and will probably have limited effect on the abundance of the algae.

Salinity and temperature were measured at all stations three times during the study period. Naturally, the values obtained from these measurements must be considered as point measurements, as they cannot describe the full fluctuation of the salinity and temperature during a season, or even a day. Therefore, the main purpose of the measurements was to see if there were major differences between the stations. Both increased salinity and temperature had a somewhat negative significant effect on the abundance of *V. lanosa*. The statistical analyses could be biased due to the clustering of stations, which is an incentive to interpret the relatively high significant p-values in a conservative manner. Furthermore, previous studies have found that lower salinity levels had a negative effect on the photosynthetic productivity and abundance of *V. lanosa*, and there is an absence of the alga in low salinity areas (Fralick and Mathieson 1975; Åberg, 1992; Heggøy, 2001). However, there was a narrow range in both salinity and temperature in the investigated area in the current study, and all measurements were well within both algae's optimum ranges (Fralick and Mathieson, 1975; Halat et al.,

2015). This could indicate that other factors which accidentally covaries with salinity and temperature affects the results. Salinity and temperature therefore most likely did not have a substantial effect on the abundance of the alga.

There were relatively few locations in each orientation category, and no clear effect of orientation on the abundance of the algae. Factors that could give an effect on the algae could be increased desiccation due to sun exposure on South-orientated sites or higher risk of wind and exposure from West-orientated sites. However, if there was a small effect of orientation, it was most likely overpowered by other factors like exposure or inclination.

During the regrowth-experiment, 9 of 36 branches were lost during the study, and others were not found at certain sampling dates but reoccurred at later sampling dates, leaving holes in the data. Yet, most of the branches were present throughout the study, and even though there are occasional growth data missing, the general growth trend is still intact. Future studies should, however, consider the high loss rates that can occur during a year, as the dislodgement of branches is a relatively normal occurrence in the *A. nodosum* alga, and new fronds will usually continue to originate from the holdfast after others break off (Åberg, 1992).

Analysing growth of *V. lanosa* with the image analysing programme ImageJ may not have been precise enough to demonstrate the biomass changes, as ImageJ only does two-dimensional measurements and *V. lanosa* has a bush like three-dimensional structure. This method would have been more efficient on algae with a flat structure. However, one would probably be able to see a general growth trend in the experiment if it was substantial. Furthermore, a potential error source in the regrowth-experiment could be the positioning of the *A. nodosum*-branches when photographing them. Although the same part of the branch was always photographed, there was no simple way to make sure the branch faced the same direction during each monitoring, thus measurements may have variations based on which side of the specimens were photographed, as parts of *V. lanosa* could unintentionally be covered. The thallus of *V. lanosa* was easily distinguishable and rather easy to outline in ImageJ, as even though parts of it was covered by *A. nodosum*, the outline of *V. lanosa* could still be distinguished. Nevertheless, this could lead to slight under- or overestimation of biomass.

Grazing by mesoherbivores and human disturbance could also influence the growth of *V. lanosa*, but this is not assessed in this study. The only potential grazer observed were amphipods inhabiting the thallus of *V. lanosa*. Whether the amphipods were using *V. lanosa* just as shelter or also as food is unclear, as there are no studies that mention grazing of the alga. Grazing on *A. nodosum* could potentially also have a positive effect on the abundance of *V. lanosa*, as it can leave grazing wounds for *V. lanosa* spores to settle (Longtin and Scrosati, 2009).

With respect to the fouling study, one limitation with the method used for examining fouling species in the lab, was that the size of the subsamples taken from collected samples of *V. lanosa* were measured on eyesight. Approximately the same amount of *V. lanosa* was collected for

each subsample, but the exact amount was not measured. This could lead to some uncertainty in the data, as larger samples of *V. lanosa* have a larger chance of containing more fouling species than smaller samples. Therefore, no statistical analyses were used to compare the fouling between samples and sample dates. For further studies, a potential way to standardize this method could be to consistently weigh subsamples. However, one should keep in mind that the fouling organisms also will contribute to the weight, and that the bush-like thallus of *V. lanosa* can hold relatively large amounts of water (personal observation) which might affect the weight.

4.2 Abundance of *Vertebrata lanosa*

This study showed that the abundance of *V. lanosa* was affected by several environmental factors. One of the main factors positively affecting the abundance, was the exposure of the locations, i.e. the stronger the exposure, the higher abundance of *V. lanosa*. This is likely due to *A. nodosum* being more prone to damage in areas with more wave-exposure, as the waves will beat the branches against hard substrate which causes cuts and scrapes, and can eventually cause tearing of branches. Wound areas on *A. nodosum* is the preferred area for settlement of *V. lanosa* spores, possibly due to favourable hydrodynamic conditions and lack of epidermal-shedding (Pearson and Evans, 1990). Higher frequencies of wounds on *A. nodosum* generate more area for *V. lanosa* spores to successfully settle (Pearson and Evans, 1990; Levin and Mathieson, 1991; Longtin and Scrosati, 2009).

Increased inclination and a narrow zone width, which are correlated factors, affected the abundance of *V. lanosa* positively. One reason for this could be that it is more difficult for *A. nodosum* to grow dense mats in steep areas than in flat ones, and that steeper locations give less available habitat within its preferred vertical range in the tidal zone. This makes *A. nodosum* more exposed to desiccation and waves, which causes more thallus damage. This can be a potential reason for the positive effect of increased inclination on the abundance of *V. lanosa*, as this again makes it easier for spores to settle on wounded parts of *A. nodosum*.

There was a strong negative effect of *A. nodosum* canopy-thickness (volume) on the abundance of *V. lanosa*. This was an interesting finding, as one could expect more *V. lanosa* where its habitat was more abundant. One reason for this is that in a dense canopy of *A. nodosum*, the many fronds may act as a defence against exposure and thereby shield each other from wave exposure. This again will lead to less wounded areas on *A. nodosum* for *V. lanosa* spores to settle on, and it seems that it is the availability of settlement areas on *A. nodosum* that is the main factor influencing the abundance of *V. lanosa* and not the availability of *A. nodosum* itself. Another reason for *V. lanosa* not growing as well in thicker mats of *A. nodosum* could be shading, as the irradiance is reduced by a hundredfold within the canopy of *A. nodosum* compared to in the periphery (Longtin et al., 2009), and *V. lanosa* has a relatively high light requirement (Fralick and Mathieson, 1975).

Previous studies found that *V. lanosa* was restricted to a zone of 0.2-1.3 m above Chart Datum, whereas *A. nodosum* stretched to 0.0-2.3 m above Chart Datum in New Hampshire (Fralick and Mathieson, 1975). This suggests that *V. lanosa* prefers the low middle range of the *Ascophyllum*-zone, perhaps due to the increased impact of physical factors like grazing, desiccation, radiation and extreme temperatures in the upper intertidal zone. Somewhat similar tendencies were also found in this study, where the coverage of *V. lanosa* peaked at the mid-range of the *Ascophyllum*-zone. Although, the height range of the *Ascophyllum*-zone was considerably shorter than in New Hampshire, ranging from approximately -0.2-1.0 m above Chart Datum. This is natural, as the vertical difference between low and high tide in northern North America is larger than in the area surrounding Espegrend where this study was done (Stephenson and Stephenson, 1954).

By combining these results, one could expect to find more *V. lanosa* in the most exposed areas where *A. nodosum* grows, and the abundance is likely to be higher in steep areas with short *Ascophyllum*-zones and thinner canopies of *A. nodosum*. There is also a larger chance of finding *V. lanosa* in the lower half of the *Ascophyllum*-zone. These findings are valuable in relation to harvest of *V. lanosa*. Biological factors like grazing on *A. nodosum* could also affect the abundance of *V. lanosa*, either negatively as juvenile specimens are removed by grazers, or positively as grazing wounds on *A. nodosum* could lead to suitable areas for settlement of *V. lanosa*. This has not been assessed in the study. Also, one should keep in mind that the geographical extent of this study was a relatively small area South of Bergen and only represents a certain range of habitat suitable for the two algae. Still, the archipelago habitats included in this study are common along the Norwegian coastline and the results is most likely applicable to most of the Norwegian coast if habitats are within the preferred range of physical and biological factors for both algae.

4.3 Regrowth of *Vertebrata lanosa*

Unfortunately, the regrowth experiment did not bring forward major new knowledge, partly due to methods used and partly due to timing of the experiment. The observed algae regrowth was relatively low and no effect of the treatment or time was detected. This may be due to the experiment being done during the winter period when low growth is expected in most algae due to low temperature and light conditions (Mathieson et al., 1976; Stengel and Dring, 1997; Forbord et al., 2012). Yet, as there was no visible trend for loss of biomass during the study, one can conclude that the *V. lanosa* that was exposed for the picked treatment was rather resilient, as there were no detectable mortalities of any specimens. A full year study, or even a study during spring and early summer could perhaps reveal more information about the growth and regrowth of *V. lanosa*.

4.4 Fouling of *Vertebrata lanosa*

As with many other macroalgae, the fouling of *V. lanosa* seems to vary by season, and is higher during autumn than in spring (Saunders & Metaxas, 2008; Førde et al., 2016). More biofouling

was found on *V. lanosa* than originally anticipated. This was an interesting biological observation, which shows that *V. lanosa* does not have the same efficient anti-fouling abilities as *A. nodosum* which uses epidermal shedding as a fouling defence (Halat et al., 2015). It is also a notable observation regarding the quality of *V. lanosa* as a food alga, as a clean product at harvest is preferred for consumption. The amount of fouling present on the thallus of *V. lanosa* was in most cases only visible through microscopy. With simple eye inspection *V. lanosa* often appears bare and clean, but this is seldom the case.

There was a substantial reduction in rhodophytes over the winter, which may suggest that several of the red algae are seasonal and disappears during the winter months, or that the number of juvenile algae, which have a higher mortality than adult algae, was high (Vadas et al., 1992). The cyanobacteria *Dermocarpa* sp. and one of the order Oscillatoriales were the most abundant fouling species and were found throughout the year. As they do not grow as voluminous as many of the fouling algae and invertebrates, they may not negatively affect its host to the same degree as larger species, which may be why they are so abundant. Other algae species seemed to use *V. lanosa* purely as a random holdfast to grow, like the *Ceramium* sp. in Figure 23, which had outgrown *V. lanosa* completely. Larger epiphytes are likely to have a larger negative effect on *V. lanosa*, as they can cause more shading, more momentum during wave motion (and thus breakage), and damage of *V. lanosa* tissue at their holdfast-area.

4.5 Conclusion and implications for further research

The main driver affecting the abundance of *V. lanosa* seems to be the availability of easy settlement areas on *A. nodosum*. Damage of *A. nodosum* fronds is usually associated with wave-exposure, which is possibly why we find more *V. lanosa* in exposed areas. Furthermore, there was a significant seasonal difference in the amount of biofouling on *V. lanosa*, showing more biofouling during autumn than early spring, which implies that the best harvesting time is during spring and not autumn. Thallus reduction by harvesting did not seem to have a clear effect on the growth of *V. lanosa*. As this study is the first to assess growth and quality of *V. lanosa* in perspective to harvest, it will hopefully be of use for potential further studies of this interesting alga. An important topic which is left unanswered in this study, is how the harvest of *V. lanosa* affects the growth and survival of the alga. Further studies with more optimized biomass measurement methods and longer study periods might be able to enlighten this subject, which is essential to provide guidelines for sustainable harvest. Furthermore, an extended year-round study of seasonal fouling of *V. lanosa* which also includes exposure degree as a factor could obtain valuable information on whether exposure affects the amount of fouling on the alga, and give more accurate details on when the fouling of *V. lanosa* is at its minimum.

When harvesting, one should initially search for areas with relatively high salinity levels. In Norway that usually implies to coastal areas west of Skagerrak, in localities where the salinity level is not substantially affected by freshwater input as e.g. larger fjord systems often are. Furthermore, the more exposed areas where *A. nodosum* is present seem to be hotspots for *V.*

lanosa, which also seem to be the case for locations with high inclination. Thus, sheltered, flat areas with large canopies of *A. nodosum* are seldom good areas to harvest *V. lanosa*. In a larger geographical perspective, areas with larger tidal differences would be preferable, as they will have a wider range of preferable vertical heights above Chart Datum for *V. lanosa* to grow, and thus likely more of the alga, perhaps not in proportion to *A. nodosum*, but in total biomass per area. To avoid large amounts of fouling on *V. lanosa*, harvesting should be done in late winter and perhaps early spring, and be avoided in late summer and autumn when there seems to be substantially more fouling on the alga. Finally, since the knowledge of regrowth after harvest is limited, one should be careful of removing too much of the alga, and harvested areas should be left to recover for at least a year.

5 References

- Armitage, C. S., Sjøtun, K. and Jensen, K. H. (2014) ‘Correlative evidence for competition between *Fucus serratus* and the introduced chlorophyte *Codium fragile* subsp. *fragile* on the southwest coast of Norway’, *Botanica Marina*, 57(2), pp. 85–97. doi: 10.1515/bot-2013-0087.
- Baardseth, E. (1970a) ‘A square-scanning, two-stage sampling method of estimating seaweed quantities’, *Norwegian Institute of Seaweed Research*. Trondheim, Norway, 33, pp. 1–40.
- Baardseth, E. (1970b) ‘Synopsis of biological data on knobbed wrack *Ascophyllum nodosum*’, *FAO Fisheries Synopsis*, 38(1), p. 44. Available at: <http://www.fao.org/docrep/017/b0672e/b0672e.pdf>.
- Bolker, B. M. *et al.* (2009) ‘Generalized linear mixed models: a practical guide for ecology and evolution’, *Trends in Ecology and Evolution*, 24(3), pp. 127–135. doi: 10.1016/j.tree.2008.10.008.
- Buschmann, A. H. *et al.* (2017) ‘Seaweed production: overview of the global state of exploitation, farming and emerging research activity’, *European Journal of Phycology*. Taylor & Francis, 52(4), pp. 391–406. doi: 10.1080/09670262.2017.1365175.
- Callow, J. A., Callow, M. E. and Evans, L. V. (1979) ‘Nutritional studies on the parasitic red alga *Choreocolax Polysiphoniae*’, *New Phytologist*, 83, pp. 451–462.
- Díaz, P. *et al.* (2017) ‘The genera *Melanothamnus* Bornet & Falkenberg and *Vertebrata* S.F. Gray constitute well-defined clades of the red algal tribe Polysiphonieae (Rhodomelaceae, Ceramiales)’, *European Journal of Phycology*, 52(1), pp. 1–30.
- Duinker, A. *et al.* (2016) ‘Potential risks posed by macroalgae for application as feed and food – A Norwegian perspective’, *Report from NIFES (National Institute of Nutrition and Seafood Research, Norway) 17 June 2016*, p. 24. doi: 10.13140/RG.2.2.27781.55524.
- Forbord, S. *et al.* (2012) ‘Development of *Saccharina latissima* (Phaeophyceae) kelp hatcheries with year-round production of zoospores and juvenile sporophytes on culture ropes for kelp aquaculture’, *Journal of Applied Phycology*, 24(3), pp. 393–399. doi:

10.1007/s10811-011-9784-y.

Førde, H. *et al.* (2016) 'Development of bryozoan fouling on cultivated kelp (*Saccharina latissima*) in Norway', *Journal of Applied Phycology*, 28(2), pp. 1225–1234. doi: 10.1007/s10811-015-0606-5.

Fralick, R. A. and Mathieson, A. C. (1975) 'Physiological ecology of four *Polysiphonia* species (Rhodophyta, Ceramiales)', *Marine Biology*, 29(1), pp. 29–36. doi: 10.1007/BF00395524.

Garbary, D., Burke, J. and Lining, T. (1991) 'The Ascophyllum/Polysiphonia/Mycosphaerella symbiosis. II. Aspects of the ecology and distribution of *Polysiphonia lanosa* in Nova Scotia', *Botanica Marina*, 34(5), pp. 391–402.

Garbary, D. J. and Deckert, R. J. (2004) 'Three Part Harmony --- *Ascophyllum* and Its Symbionts', in Seckbach, J. (ed.) *Symbiosis: Mechanisms and Model Systems*. Dordrecht: Springer Netherlands, pp. 309–321. doi: 10.1007/0-306-48173-1_19.

Garbary, D. J., Deckert, R. J. and Hubbard, C. B. (2005) '*Ascophyllum* and Its Symbionts. VIII. Interactions Among *Ascophyllum nodosum* (Phaeophyceae), *Mycophycias ascophylli* (Ascomycetes) and *Elachista fucicola* (Phaeophyceae)', *Algae*, 20(4), pp. 363–368. doi: 10.4490/ALGAE.2005.20.4.363.

Garbary, D. J., Miller, A. G. and Scrosati, R. A. (2014) '*Ascophyllum nodosum* and its symbionts: XI. The epiphyte *Vertebrata lanosa* performs better photosynthetically when attached to *Ascophyllum* than when alone', *Algae*, 29(4), pp. 321–331. doi: 10.4490/algae.2014.29.4.321.

Guiry MD, Morrison L (2013) 'The sustainable harvesting of *Ascophyllum nodosum* (Fucaceae, Phaeophyceae) in Ireland, with notes on the collection and use of some other brown algae.' *J Appl Phycol* 25:1823–1830. doi: 10.1007/s10811-013-0027-2

Halat, L. *et al.* (2015) 'Epidermal shedding in *Ascophyllum nodosum* (Phaeophyceae): seasonality, productivity and relationship to harvesting', *Phycologia*, 54(6), pp. 599–608. doi: 10.2216/15-32.1.

Harlin, M. M. and Craigie, J. S. (1975) 'The Distribution of Photosynthate in *Ascophyllum Nodosum* As It Relates To Epiphytic *Polysiphonia Lanosa*', *Journal of Phycology*, pp. 109–113. doi: 10.1111/j.1529-8817.1975.tb02756.x.

Heggøy, E. (2001) 'Algevegetasjonen i Tjongspollen, Bømlo, Hordaland', *Cand.scient. thesis, University of Bergen*, p. 102 + 15.

Hehemann, J.-H. *et al.* (2012) 'Bacteria of the human gut microbiome catabolize red seaweed glycans with carbohydrate-active enzyme updates from extrinsic microbes', *Proceedings of the National Academy of Sciences*, 109(48), pp. 19786–19791. doi: 10.1073/pnas.1211002109.

Kurr, M. and Davies, A. J. (2018) 'Sex-specific reproductive trade-offs in the gregarious fucoid macroalga *Ascophyllum nodosum*', *European Journal of Phycology*. Taylor & Francis, 53(1), pp. 1–13. doi: 10.1080/09670262.2017.1328746.

Levin, P. S. and Mathieson, A. C. (1991) 'Variation in a host epiphyte relationship along a wave exposure gradient.', *Mar.Ecol.Progr.Ser.*, 77, pp. 271–278. doi: 10.3354/meps077271.

Longtin, C. M. *et al.* (2009) 'Distribution of algal epiphytes across environmental gradients at

- different scales: Intertidal elevation, host canopies, and host fronds', *Journal of Phycology*, 45(4), pp. 820–827. doi: 10.1111/j.1529-8817.2009.00710.x.
- Longtin, C. M. and Scrosati, R. A. (2009) 'Role of surface wounds and brown algal epiphytes in the colonization of *Ascophyllum nodosum* (phaeophyceae) fronds by *Vertebrata lanosa* (Rhodophyta)', *Journal of Phycology*, 45(3), pp. 535–539. doi: 10.1111/j.1529-8817.2009.00672.x.
- Lüning, K. (1990) 'Seaweeds'. Hamburg: John Wiley & Sons Ltd., pp. 332–339.
- MacArtain, P. *et al.* (2007) 'Nutritional Value of Edible Seaweeds', *Nutrition Reviews*, 65(12), pp. 535–543. doi: 10.1301/nr.2007.dec.535.
- Maggs, C. A. and Hommersand, M. H. (1993) 'Volume 1 Rhodophyta - Part 3A Ceramiales', in *Seaweeds of the British Isles*. London, pp. 346–349. doi: 10.1017/CBO9781107415324.004.
- Martin-Smith, K. M. (1993) 'Abundance of mobile epifauna: The role of habitat complexity and predation by fishes', *Journal of Experimental Marine Biology and Ecology*, 174(2), pp. 243–260. doi: 10.1016/0022-0981(93)90020-O.
- Mathieson, A. C. *et al.* (1976) 'Seasonal growth and reproduction of estuarine fucoid algae in New England', *Journal of Experimental Marine Biology and Ecology*, 25(3), pp. 273–284. doi: 10.1016/0022-0981(76)90129-5.
- McHugh, D. J. (2003) 'A guide to the seaweed industry', *FAO FISHERIES TECHNICAL PAPER*, 441. doi: ISBN 92-5-104958-0.
- Meese, R. J. and Tomich, P. A. (1992) 'Dots on the rocks: a comparison of percent cover estimation methods', *Journal of Experimental Marine Biology and Ecology*, 165(1), pp. 59–73. doi: 10.1016/0022-0981(92)90289-M.
- Meland, M. and Rebours, C. (2012) *The Norwegian Seaweed Industry -*, *Bioforsk*. AGROCAMPUS df. : pp.11.
- Morrissey, J., Kraan, S. and Guiry, M. D. (2001) *A Guide to Commercially Important Seaweeds on the Irish Coast*. Dublin: Irish Sea Fisheries Board.
- Nakagawa, S. and Schielzeth, H. (2013) 'A general and simple method for obtaining R² from generalized linear mixed-effects models', *Methods in Ecology and Evolution*, 4(2), pp. 133–142. doi: 10.1111/j.2041-210x.2012.00261.x.
- Pavia, H., Carr, H. and Åberg, P. (1999) 'Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae', *Journal of Experimental Marine Biology and Ecology*, 236(1), pp. 15–32. doi: 10.1016/S0022-0981(98)00191-9.
- Pearson, G. A. and Evans, L. V. (1990) 'Settlement and Survival of *Polysiphonia Lanosa* (Ceramiales) Spores on *Ascophyllum nodosum* and *Fucus vesiculosus* (Fucales)', *Journal of Phycology*, (26), pp. 597–603.
- Pearson, G. A. and Evans, L. V. (1991) 'Stimulation of secondary rhizoid production in *Polysiphonia lanosa* by brown algal tissues and exudates', *British Phycological Journal*, 26, pp. 93–94.
- Pedersen, P. M. (2011) *Grønlands havalger*. Forlaget Epsilon, Copenhagen, Denmark.

- Rawlence, D. J. and Taylor, A. R. A. (1970) 'The rhizoids of *Polysiphonia lanosa*', *Canadian Journal of Botany*, 48(3), pp. 607–611. Available at: <https://doi.org/10.1139/b70-083>.
- Reed, R. H. (1983) 'The osmotic responses of *Polysiphonia lanosa* (L.) Tandy from marine and estuarine sites: Evidence for incomplete recovery of turgor', *Journal of Experimental Marine Biology and Ecology*, 68(2), pp. 169–193. doi: 10.1016/0022-0981(83)90158-2.
- Rioux, L., Beaulieu, L. and Turgeon, S. L. (2017) 'Food Hydrocolloids Seaweeds : A traditional ingredients for new gastronomic sensation', *Food hydrocolloids*. Elsevier Ltd, 68, pp. 255–265. doi: 10.1016/j.foodhyd.2017.02.005.
- RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL: <http://www.rstudio.com/>
- Rueness, J. (1998) *Alger i Farger*. Oslo: Almater Forlag.
- Rupérez, P. (2002) 'Mineral content of edible marine seaweeds', *Food Chemistry*, 79(1), pp. 23–26. doi: 10.1016/S0308-8146(02)00171-1.
- Salvanes, A. G. V. *et al.* (2018) *Marine Ecological Field Methods*. West Sussex: John Wiley & Sons Ltd.
- Saunders, M. and Metaxas, A. (2008) 'High recruitment of the introduced bryozoan *Membranipora membranacea* is associated with kelp bed defoliation in Nova Scotia, Canada', *Marine Ecology Progress Series*, 369, pp. 139–151. doi: 10.3354/meps07669.
- Schmidt, A. L. *et al.* (2011) 'Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats', *Marine Ecology Progress Series*, 437, pp. 51–68. doi: 10.3354/meps09276.
- Schneider, C. A.; Rasband, W. S. & Eliceiri, K. W. (2012), "NIH Image to ImageJ: 25 years of image analysis", *Nature methods* 9(7): 671-675, PMID 22930834 (on Google Scholar).
- Scrosati, R. A. and Longtin, C. M. (2010) 'Research note: Field evaluation of epiphyte recruitment (*Vertebrata lanosa*, Rhodophyta) in different microsite types on host fronds (*Ascophyllum nodosum*, Phaeophyceae)', *Phycological Research*, 58(2), pp. 138–142. doi: 10.1111/j.1440-1835.2010.00571.x.
- Sharp G (1987) *Ascophyllum nodosum* and its harvesting in Eastern Canada. In: Case studies of seven commercial seaweed resources, Issues 281-282. Food & Agriculture Org., 1987, pp 3–5
- Smitha, J. L., Summers, G. and Wong, R. (2010) 'Nutrient and heavy metal content of edible seaweeds in New Zealand', *New Zealand Journal of Crop and Horticultural Science*, 38(1), pp. 19–28. doi: 10.1080/01140671003619290.
- Stengel, D. and Dring, M. (1997) 'Morphology and in situ growth rates of plants of *Ascophyllum nodosum* (phaeophyta) from different shore levels and responses of plants to vertical transplantation', *European Journal of Phycology*, 32(2), pp. 193–202. doi: 10.1080/09670269710001737129.
- Stephenson, T. A. and Stephenson, A. (1954) 'Life Between Tide-Marks in North America : IIIB . Nova Scotia and Prince Edward Island : The Geographical Features of the Region Author (s): T . A . Stephenson and Anne Stephenson Stable URL : <http://www.jstor.org/stable/2256978> . TIDE-MARKS IN NORTH AM', *Journal of Ecology*, 42(1), pp. 46–70.

- Toews, M. W. (2017) *Slope quadrant.svg*. Available at: https://commons.wikimedia.org/wiki/File:Slope_quadrant.svg (Accessed: 28 May 2018).
- Vadas, R. L., Johnson, J. S. and Norton, T. A. (1992) 'Recruitment and mortality of early post-settlement stages of benthic algae', *British Phycological Journal*, 27(3), pp. 331–351. doi: 10.1080/00071619200650291.
- Venables, W. N. and Ripley, B. D. (2002) 'Modern Applied Statistics with S. Fourth Edition'. New York: Springer. doi: ISBN 0-387-95457-0.
- Viestad, A. (2016) *Norges ukjente delikatesser: Tang som smaker trøfler, og gress med kanel- og vaniljesmak*, *Dagbladet*. Available at: <https://www.dagbladet.no/mat/norges-ukjente-delikatesser--tang-som-smaker-trofler-og-gress-med-kanel--og-vaniljesmak/60344771>.
- Wickham, H. (2009) 'ggplot2: Elegant Graphics for Data Analysis'. New York: Springer-Verlag.
- Wickham, H. et al. (2017) 'dplyr: A Grammar of Data Manipulation'. R package version 0.7.4, URL: <https://cran.r-project.org/package=dplyr>.
- Yang, L. E., Lu, Q. Q. and Brodie, J. (2017) 'A review of the bladed Bangiales (Rhodophyta) in China: history, culture and taxonomy', *European Journal of Phycology*. Taylor & Francis, 52(3), pp. 251–263. doi: 10.1080/09670262.2017.1309689.
- Åberg, P. (1992) 'A Demographic Study of Two Populations of the Seaweed *Ascophyllum Nodosum*', *Ecology*, 73(4), pp. 1473–1487. doi: 10.2307/1940691.

6 Appendices

Appendix 1

Overview of the 27 sampling stations, with area description, coordinates and sampling dates.

Station	Description	GPS	Date of measurement
1	Nordre Steinskjeret	60.2688597, 5.2188744	22.09.2017
2	Kuholmen	60.260656, 5.207237	10.08.2017
3	Nordre Egdholmen	60.264592, 5.212678	10.08.2017
4	Skogsholmen	60.2707726, 5.214878	14.08.2017
5	Grønningen (wall)	60.228350, 5.180169	21.08.2017
6	Kubholmen	60.229005, 5.177616	21.08.2017
7	Store Svartholmen	60.239903, 5.245101	22.08.2017
8	Lerøyna, bay in Fuglevika	60.227799, 5.185919	23.08.2017
9	Lerøyna, South	60.226034, 5.185584	23.08.2017
10	Bay North on Buarøyna	60.224088, 5.190833	24.08.2017
11	Buarøyna North	60.225157, 5.198484	24.08.2017
12	Bjelkarøyna North	60.250321, 5.214518	25.08.2017
13	Islet north of Bjelkarøyna	60.249954, 5.211632	25.08.2017
14	Bjelkarøy-Buarøyna	60.233101, 5.219464	05.09.2017
15	South-East on Bjelkarøy	60.234623, 5.217886	06.09.2017
16	Mørkevågen, ytre	60.257619, 5.282060	07.09.2017
17	Mørkevågen, indre	60.258126, 5.281650	07.09.2017
18	South-West on Littlekinna	60.250976, 5.219690	08.09.2017
19	East on Lerøyna, backside of island	60.236013, 5.194839	10.09.2017
20	Bjelkarøy-Buarøyna	60.231870, 5.215819	18.09.2017
21	Bjelkarøy-Buarøyna	60.231336, 5.214452	18.09.2017
22	Alvøyna north	60.293612, 5.174675	19.09.2017
23	Tyssøyna east	60.296010, 5.166925	19.09.2017
24	Skurvholmen	60.228327, 5.194504	20.09.2017
25	Beleholmen west	60.229542, 5.196101	20.09.2017
26	Landbeleholmen west	60.231267, 5.194887	21.09.2017
27	Ospøyna west	60.257726, 5.190621	21.09.2017

Appendix 2

Degree of orientation, exposure, salinity and temperature for all stations. Salinity and temperature values are averages of the three measurements at each station.

Station	Orientation °	Exposure	Salinity (psu)	Temperature °C
1	325	275	30.0	10.9
2	100	370	29.9	10.3
3	90	622	29.9	10.4
4	115	374	30.0	10.4
5	350	176	29.3	10.1
6	40	241	28.9	10.1
7	340	259	28.6	9.9
8	160	174	28.8	10.3
9	220	161	28.8	10.2
10	250	142	28.8	10.0
11	320	548	29.0	9.9
12	20	285	29.8	10.5
13	160	309	29.9	10.4
14	300	629	29.1	10.0
15	140	338	29.1	9.8
16	70	692	27.7	10.1
17	70	426	27.8	10.0
18	200	109	29.7	10.6
19	210	33	29.4	10.8
20	10	585	28.8	9.9
21	290	599	29.0	10.0
22	10	298	30.0	10.2
23	310	127	30.0	9.9
24	310	272	29.0	10.0
25	270	122	28.9	10.1
26	130	60	29.0	10.2
27	220	614	29.8	10.4

Appendix 3

Collection of raw data: Sampling station, date, proportion of *A. nodosum* in sample squares, proportion of *V. lanosa* in sample squares, substrate type, zone width of transects, the percentage increase of transects, thickness of *A. nodosum* and height of sample squares above Chart Datum.

St.	Date	<i>A. nodosum</i> proportion	<i>V. lanosa</i> proportion	Substrate	Zone- width (cm)	Zone inclination (%)	<i>A. nodosum</i> thickness (cm)	Height above CD
1	22/09/2017	1	0.04	Stone	300	17%	6	18.5
1	22/09/2017	0.92	0	Stone	320	16%	2.67	29.5
1	22/09/2017	0.96	0.01	Stone	340	18%	4.67	31.5
1	22/09/2017	1	0	Stone	260	16%	4.33	18.5
1	22/09/2017	0.84	0	Stone	370	14%	5	18.5
1	22/09/2017	0.76	0.02	Stone	360	11%	5	22.5
1	22/09/2017	1	0.01	Stone	370	9%	5.33	18.5
1	22/09/2017	0.6	0.04	Stone	330	14%	2.33	20.5
1	22/09/2017	0.96	0.04	Stone	300	11%	8.33	14.5
1	22/09/2017	1	0.005	Stone	160	3%	8.67	12.5
1	22/09/2017	0.96	0.04	Stone	300	17%	6	6.5
1	22/09/2017	1	0	Stone	320	16%	5	46.5
1	22/09/2017	0.68	0.005	Stone	340	18%	4.33	-0.5
1	22/09/2017	1	0.02	Stone	260	16%	5	23.5
1	22/09/2017	1	0.04	Stone	370	14%	5	18
1	22/09/2017	1	0.01	Stone	360	11%	6.33	9
1	22/09/2017	1	0.03	Stone	370	9%	7.33	9.5
1	22/09/2017	1	0.005	Stone	330	14%	4.33	13.5
1	22/09/2017	1	0.02	Stone	300	11%	7.33	4.5
1	22/09/2017	0.96	0.02	Stone	160	3%	5.67	8.5
2	10/08/2017	0.52	0.12	Bedrock	110	55%	7.33	36
2	10/08/2017	1	0.1	Bedrock	100	54%	6.33	13
2	10/08/2017	1	0.04	Bedrock	135	46%	7.33	29
2	10/08/2017	0.88	0.02	Bedrock	190	28%	10.33	7
2	10/08/2017	0.56	0	Bedrock	320	17%	8	26
2	10/08/2017	0.72	0.03	Bedrock	205	33%	4.67	19
2	10/08/2017	0.24	0.06	Bedrock	235	17%	2.33	8
2	10/08/2017	0.96	0	Bedrock	323	17%	8.33	23
2	10/08/2017	0.96	0	Bedrock	235	22%	6.67	18
2	10/08/2017	1	0	Bedrock	300	20%	7.67	13
2	10/08/2017	0.4	0.12	Bedrock	110	55%	7.33	3
2	10/08/2017	NA	NA	Bedrock	NA	54%	NA	NA
2	10/08/2017	0.92	0.24	Bedrock	135	46%	5.67	8
2	10/08/2017	1	0.12	Bedrock	190	28%	7.33	8
2	10/08/2017	1	0.01	Bedrock	320	17%	7.33	22
2	10/08/2017	1	0.1	Bedrock	205	33%	6.33	19
2	10/08/2017	0.88	0	Bedrock	235	17%	10	18
2	10/08/2017	1	0.01	Bedrock	323	17%	7.67	8
2	10/08/2017	0.88	0.04	Bedrock	235	22%	8	15
2	10/08/2017	0.84	0.02	Bedrock	300	20%	5.67	6

3	10/08/2017	0.28	0.28	Bedrock	37	76%	5.33	23
3	10/08/2017	0	0	Bedrock	0	NA	0	NA
3	10/08/2017	0.12	0	Bedrock	170	26%	4	25
3	10/08/2017	1	0.005	Bedrock	200	18%	8.67	-19
3	10/08/2017	0.96	0.005	Bedrock	235	2%	7	14
3	10/08/2017	0.4	0.04	Bedrock	240	10%	3.67	3
3	10/08/2017	0	0	Bedrock	0	NA	0	NA
3	10/08/2017	0.96	0.08	Bedrock	90	33%	6	24
3	10/08/2017	1	0.02	Bedrock	200	36%	8.33	19
3	10/08/2017	0.2	0.04	Bedrock	170	26%	5	31
3	10/08/2017	0	0	Bedrock	37	76%	0	NA
3	10/08/2017	0	0	Bedrock	0	NA	0	NA
3	10/08/2017	0.02	0.005	Bedrock	170	26%	5	14
3	10/08/2017	0.52	0.005	Bedrock	200	18%	8.33	-19
3	10/08/2017	0.68	0.04	Bedrock	235	2%	5.67	-6
3	10/08/2017	1	0.08	Bedrock	240	10%	4.33	22
3	10/08/2017	0	0	Bedrock	0	NA	0	NA
3	10/08/2017	0	0	Bedrock	90	33%	0	NA
3	10/08/2017	0.68	0.08	Bedrock	200	36%	4.67	-7
3	10/08/2017	0.28	0.02	Bedrock	170	26%	5	14
4	14/08/2017	0.08	0	Stone	130	36%	2	-13
4	14/08/2017	1	0.12	Stone	250	6%	7.67	-12
4	14/08/2017	0.92	0.01	Stone	240	3%	7.33	-4
4	14/08/2017	0.68	0	Stone	440	5%	9.33	5
4	14/08/2017	0.96	0	Stone	400	11%	4.67	16
4	14/08/2017	1	0	Stone	500	10%	6.33	15
4	14/08/2017	0.76	0.02	Stone	190	13%	4.67	13
4	14/08/2017	0	0	Stone	0	NA	0	NA
4	14/08/2017	0	0	Stone	0	NA	0	NA
4	14/08/2017	0	0	Stone	0	NA	0	NA
4	14/08/2017	0.6	0.04	Stone	130	36%	6	-20
4	14/08/2017	0.76	0.02	Stone	250	6%	4.67	42
4	14/08/2017	0.76	0	Stone	240	3%	4.33	-16
4	14/08/2017	1	0	Stone	440	5%	4.67	15
4	14/08/2017	0.92	0	Stone	400	11%	6	5
4	14/08/2017	0.88	0.01	Stone	500	10%	8.33	17
4	14/08/2017	0.88	0.01	Stone	190	13%	7	7
4	14/08/2017	0	0	Stone	0	NA	0	NA
4	14/08/2017	0	0	Stone	0	NA	0	NA
4	14/08/2017	0	0	Stone	0	NA	0	NA
5	21/08/2017	0.72	0	Bedrock	120	40%	6.67	19.5
5	21/08/2017	0.68	0.005	Bedrock	160	29%	4.33	12.5
5	21/08/2017	0.92	0.02	Bedrock	160	26%	5.33	17.5
5	21/08/2017	1	0.005	Bedrock	190	32%	5.33	28.5
5	21/08/2017	0.84	0.24	Bedrock	190	25%	5.67	11.5
5	21/08/2017	0.84	0	Bedrock	170	29%	4	36.5
5	21/08/2017	1	0	Bedrock	130	40%	5.67	21.5
5	21/08/2017	0.92	0	Bedrock	260	19%	8.67	-8.5

5	21/08/2017	0.96	0.16	Bedrock	320	20%	4.67	1.5
5	21/08/2017	1	0.005	Bedrock	320	19%	6.33	18.5
5	21/08/2017	0.2	0.08	Bedrock	120	40%	2.33	-6.5
5	21/08/2017	0.28	0.04	Bedrock	160	29%	5.67	-6.5
5	21/08/2017	0.96	0.01	Bedrock	160	26%	4	6.5
5	21/08/2017	0.68	0.08	Bedrock	190	32%	6	2.5
5	21/08/2017	1	0.01	Bedrock	190	25%	6	0.5
5	21/08/2017	1	0.04	Bedrock	170	29%	7.33	7.5
5	21/08/2017	1	0.08	Bedrock	130	40%	6.67	10.5
5	21/08/2017	0.72	0.32	Bedrock	260	19%	4.67	-22.5
5	21/08/2017	0.6	0.2	Bedrock	320	20%	6	-17.5
5	21/08/2017	0.8	0.04	Bedrock	320	19%	3.33	-18.5
6	21/08/2017	0.68	0.2	Bedrock	160	31%	6.33	24
6	21/08/2017	0.56	0.24	Bedrock	170	19%	6.67	4
6	21/08/2017	1	0.08	Bedrock	280	19%	5.33	1
6	21/08/2017	0.4	0.01	Bedrock	180	34%	7	46
6	21/08/2017	0	0	Bedrock	0	NA	0	NA
6	21/08/2017	0.32	0.08	Bedrock	110	35%	4.33	32
6	21/08/2017	0	0	Stone	0	NA	0	NA
6	21/08/2017	0.84	0.16	Stone	270	24%	5	13
6	21/08/2017	1	0.04	Stone	240	34%	4	21
6	21/08/2017	0.08	0.01	Stone	270	13%	5	42
6	21/08/2017	0.4	0.16	Bedrock	160	31%	6.33	7
6	21/08/2017	1	0.08	Bedrock	170	19%	7.33	-11
6	21/08/2017	0.16	0	Bedrock	280	19%	2	-23
6	21/08/2017	0.8	0.16	Bedrock	180	34%	5	18
6	21/08/2017	0	0	Bedrock	0	NA	0	NA
6	21/08/2017	0.96	0.08	Bedrock	110	35%	4.67	18
6	21/08/2017	0	0	Stone	0	NA	0	NA
6	21/08/2017	0.88	0.04	Stone	270	24%	5.33	7
6	21/08/2017	1	0	Stone	240	34%	4.33	1
6	21/08/2017	0.56	0.04	Stone	270	13%	4	25
7	22/08/2017	1	0.68	Stone	410	9%	5.67	22
7	22/08/2017	0.96	0.005	Stone	380	12%	8.33	-5
7	22/08/2017	0.88	0.04	Stone	275	14%	5.67	20
7	22/08/2017	0.4	0.2	Bedrock	300	10%	4	32
7	22/08/2017	1	0.04	Stone	260	6%	5.67	36
7	22/08/2017	1	0.04	Stone	140	14%	6.67	15
7	22/08/2017	1	0.08	Stone	230	0%	5.67	20
7	22/08/2017	0.88	0.04	Stone	440	6%	7.67	1
7	22/08/2017	1	0.1	Stone	180	-14%	7.67	13
7	22/08/2017	0	0	Stone	0	NA	0	NA
7	22/08/2017	0.68	0	Stone	410	9%	5	-1
7	22/08/2017	1	0.08	Stone	380	12%	8.33	13
7	22/08/2017	1	0.08	Stone	275	14%	10	12
7	22/08/2017	0.32	0.06	Bedrock	300	10%	3.33	45
7	22/08/2017	1	0.08	Stone	260	6%	6.67	18
7	22/08/2017	1	0.04	Stone	140	14%	6	0

7	22/08/2017	1	0.01	Stone	230	0%	6	15
7	22/08/2017	0.88	0.08	Stone	440	6%	6	20
7	22/08/2017	1	0.12	Stone	180	-14%	6.67	34
7	22/08/2017	0	0	Stone	0	NA	0	NA
8	23/08/2017	0.88	0.02	Bedrock	60	38%	6.33	-7
8	23/08/2017	0.84	0.04	Bedrock	90	24%	5.33	4
8	23/08/2017	0.92	0.02	Stone	210	32%	6.33	-7
8	23/08/2017	1	0	Stone	150	21%	8.67	22
8	23/08/2017	0.84	0	Stone	170	29%	5	18
8	23/08/2017	0.8	0	Bedrock	180	37%	5.33	39
8	23/08/2017	1	0.08	Stone	250	21%	7.67	27
8	23/08/2017	0.88	0.16	Stone	125	26%	4.67	6
8	23/08/2017	0.84	0.04	Bedrock	100	48%	4.67	-5
8	23/08/2017	0.88	0.28	Stone	80	6%	6.33	11
8	23/08/2017	NA	NA	NA	60	38%	NA	NA
8	23/08/2017	NA	NA	NA	90	24%	NA	NA
8	23/08/2017	0.92	0.005	Stone	210	32%	7.67	6
8	23/08/2017	1	0.04	Stone	150	21%	7.33	-2
8	23/08/2017	0.96	0.005	Stone	170	29%	5.33	21
8	23/08/2017	1	0.005	Bedrock	180	37%	8	30
8	23/08/2017	0.68	0.005	Stone	250	21%	2.17	22
8	23/08/2017	0.92	0.04	Stone	125	26%	4.67	-6
8	23/08/2017	NA	NA	Stone	100	48%	NA	NA
8	23/08/2017	NA	NA	Stone	80	6%	NA	NA
9	23/08/2017	1	0.08	Rock	240	16%	6	11
9	23/08/2017	0.52	0	Stone	420	13%	3.67	36
9	23/08/2017	0.68	0	Stone	600	6%	6.67	23
9	23/08/2017	1	0	Stone	590	12%	8	28
9	23/08/2017	1	0	Bedrock	520	10%	8.67	33
9	23/08/2017	0.88	0	Stone	370	12%	4.67	24
9	23/08/2017	0.76	0	Stone	200	19%	7	22
9	23/08/2017	0.76	0.005	Stone	260	18%	4.5	13
9	23/08/2017	0.64	0.01	Stone	150	24%	6	33
9	23/08/2017	0.96	0.01	Bedrock	120	39%	6.33	23
9	23/08/2017	0.92	0	Stone	240	16%	3.33	-11
9	23/08/2017	0.76	0	Stone	420	13%	6.67	14
9	23/08/2017	1	0.005	Stone	600	6%	2.67	7
9	23/08/2017	0.92	0	Stone	590	12%	6	30
9	23/08/2017	1	0.04	Bedrock	520	10%	9.67	12
9	23/08/2017	0.96	0	Stone	370	12%	6	13
9	23/08/2017	0.28	0	Stone	200	19%	7	-4
9	23/08/2017	0.08	0.08	Stone	260	18%	5	-3
9	23/08/2017	0.96	0.04	Bedrock	150	24%	6	8
9	23/08/2017	0.96	0.02	Bedrock	120	39%	7.33	8
10	24/08/2017	0.76	0	Rock	150	25%	4	-8
10	24/08/2017	0.8	0	Rock	320	16%	8	2
10	24/08/2017	0.88	0	Bedrock	120	69%	3	27
10	24/08/2017	1	0.005	Rock	270	26%	4	-21

10	24/08/2017		1	0	Bedrock	300	25%	6.33	7
10	24/08/2017		1	0	Bedrock	200	37%	7	8
10	24/08/2017		1	0	Bedrock	340	20%	6.33	0
10	24/08/2017		0.08	0	Bedrock	330	14%	6	28
10	24/08/2017		1	0	Bedrock	210	28%	8	15
10	24/08/2017		0.64	0.04	Stone/bedrock	250	35%	5.33	2
10	24/08/2017		0.8	0	Rock	150	25%	5	1
10	24/08/2017		0.88	0	Bedrock	320	16%	7.33	-1
10	24/08/2017		0.96	0.005	Bedrock	120	69%	4.33	-9
10	24/08/2017		0.8	0.005	Rock	270	26%	5.33	-29
10	24/08/2017		0.6	0.005	Bedrock	300	25%	2.5	-23
10	24/08/2017		1	0.005	Bedrock	200	37%	6	-17
10	24/08/2017		0.8	0.01	Bedrock	340	20%	4.33	-15
10	24/08/2017		1	0	Bedrock	330	14%	5.67	5
10	24/08/2017		1	0.02	Bedrock	210	28%	5.33	-10
10	24/08/2017		0.44	0.01	Bedrock	250	35%	3.67	-38
11	24/08/2017		0.44	0.01	Bedrock	200	28%	6	18
11	24/08/2017		0.96	0.01	Bedrock	1990	4%	5.67	39
11	24/08/2017		0.96	0.12	Bedrock	130	55%	7	28
11	24/08/2017		1	0.48	Bedrock	190	44%	7.67	30
11	24/08/2017		0.56	0.28	Bedrock	30	70%	8	-2
11	24/08/2017		1	0.32	Bedrock	230	23%	7.33	9
11	24/08/2017		0.84	0.08	Bedrock	150	48%	5.33	37
11	24/08/2017		0.92	0.04	Bedrock	180	26%	3.67	41
11	24/08/2017		0.8	0.48	Bedrock	130	18%	6.67	24
11	24/08/2017		0	0	Bedrock	290	25%	0	12
11	24/08/2017		1	0.02	Bedrock	200	28%	7.33	-9
11	24/08/2017		0.52	0.01	Bedrock	1990	4%	2.67	1
11	24/08/2017		0.28	0.08	Bedrock	130	55%	4	-4
11	24/08/2017		0.6	0.24	Bedrock	190	44%	4.5	-8
11	24/08/2017	NA		NA	Bedrock	30	70%	NA	NA
11	24/08/2017		0.8	0.08	Bedrock	230	23%	4	-8
11	24/08/2017		1	0.01	Bedrock	150	48%	7.67	20
11	24/08/2017		0.96	0.12	Bedrock	180	26%	3.67	-3
11	24/08/2017		0.92	0.52	Bedrock	130	18%	7.67	27
11	24/08/2017		0.72	0.04	Bedrock	290	25%	4.33	3
12	25/08/2017		0.92	0.04	Bedrock	200	46%	6.33	40
12	25/08/2017		0.96	0	Bedrock	200	32%	6.33	32
12	25/08/2017		1	0	Bedrock	170	42%	9	21
12	25/08/2017		1	0.01	Bedrock	170	48%	9.67	26
12	25/08/2017		1	0	Bedrock	360	2%	6.67	13
12	25/08/2017		1	0.02	Bedrock	130	12%	8	-8
12	25/08/2017		0.2	0	Stone	180	15%	4	11
12	25/08/2017		0.88	0	Bedrock	310	21%	6.33	26
12	25/08/2017		0.56	0	Bedrock	140	46%	5.67	37
12	25/08/2017		0.8	0	Bedrock	180	42%	3.67	-12
12	25/08/2017		0.76	0.04	Bedrock	200	46%	5.33	24
12	25/08/2017		1	0.01	Bedrock	200	32%	9.33	20

12	25/08/2017	1	0.01	Bedrock	170	42%	7.33	22
12	25/08/2017	0.48	0	Bedrock	170	48%	6	2
12	25/08/2017	1	0.03	Bedrock	360	2%	7.67	18
12	25/08/2017	1	0.08	Bedrock	130	12%	6	18
12	25/08/2017	0.52	0.02	Stone	180	15%	4.67	-16
12	25/08/2017	1	0.02	Bedrock	310	21%	6.67	5
12	25/08/2017	1	0.01	Bedrock	140	46%	4.67	12
12	25/08/2017	0.92	0.005	Bedrock	180	42%	5	-21
13	25/08/2017	0.92	0.12	Bedrock	300	15%	5	22
13	25/08/2017	0.8	0.16	Bedrock	180	41%	5.33	38
13	25/08/2017	1	0.04	Bedrock	170	32%	5	42
13	25/08/2017	0.28	0.04	Bedrock	150	42%	8	44
13	25/08/2017	1	0.04	Bedrock	160	36%	7	25
13	25/08/2017	1	0.12	Bedrock	220	38%	8	25
13	25/08/2017	1	0.0058	Bedrock	250	32%	10.33	46
13	25/08/2017	0.68	0.04	Bedrock	200	39%	4.33	28
13	25/08/2017	0.4	0.005	Bedrock	310	10%	4	18
13	25/08/2017	1	0.04	Bedrock	250	22%	6.67	14
13	25/08/2017	0.56	0.04	Bedrock	300	15%	3	9
13	25/08/2017	0.92	0.08	Bedrock	180	41%	7.67	18
13	25/08/2017	0.4	0.04	Bedrock	170	32%	4.33	34
13	25/08/2017	1	0.01	Bedrock	150	42%	6	25
13	25/08/2017	0.72	0.08	Bedrock	160	36%	5	-7
13	25/08/2017	0.6	0.12	Bedrock	220	38%	6	6
13	25/08/2017	1	0.16	Bedrock	250	32%	8	5
13	25/08/2017	1	0.01	Bedrock	200	39%	12.67	-2
13	25/08/2017	1	0.01	Bedrock	310	10%	10.33	11
13	25/08/2017	0.92	0.02	Bedrock	250	22%	7.67	32
14	05/09/2017	0.52	0.16	Bedrock	435	14%	4.33	6
14	05/09/2017	0.76	0.04	Bedrock	320	16%	4.33	39
14	05/09/2017	0.92	0.08	Bedrock	220	24%	8.67	4
14	05/09/2017	1	0.01	Bedrock	250	22%	5	-4
14	05/09/2017	0.48	0.24	Stone	240	21%	4.67	16
14	05/09/2017	0.96	0.04	Stone	150	17%	6.67	-1
14	05/09/2017	0.4	0.16	Stone	280	16%	4.33	19
14	05/09/2017	0.44	0.04	Bedrock	320	19%	4	49
14	05/09/2017	0.8	0.16	Bedrock	190	40%	5.67	-3
14	05/09/2017	0.4	0.04	Bedrock	230	23%	4	37
14	05/09/2017	0.68	0.32	Bedrock	435	14%	4.67	6
14	05/09/2017	0.76	0.01	Bedrock	320	16%	4.33	5
14	05/09/2017	0.8	0.01	Bedrock	220	24%	4	7
14	05/09/2017	0.88	0.08	Bedrock	250	22%	5	10
14	05/09/2017	0.88	0.08	Stone	240	21%	6	-4
14	05/09/2017	1	0.04	Stone	150	17%	6	-7
14	05/09/2017	0.52	0.16	Stone	280	16%	3.33	5
14	05/09/2017	0.48	0.08	Bedrock	320	19%	5	2
14	05/09/2017	1	0.005	Bedrock	190	40%	5	-17
14	05/09/2017	0.12	0.08	Bedrock	230	23%	4.5	17

15	06/09/2017		0.68	0.04	Bedrock	110	14%	4.33	-6
15	06/09/2017		0	0	Bedrock	270	17%	0	28
15	06/09/2017		0.36	0.00005	Rock	300	11%	3.33	8
15	06/09/2017		0.52	0.03	Bedrock	160	28%	4.67	19
15	06/09/2017		0.92	0.12	Bedrock	200	21%	5.67	1
15	06/09/2017		0.92	0.01	Bedrock	270	19%	3	-43
15	06/09/2017		1	0.04	Bedrock	210	10%	5	-7
15	06/09/2017		0.92	0	Bedrock	300	21%	4.33	-39
15	06/09/2017		0.88	0.14	Stone	220	17%	4	5
15	06/09/2017		1	0.04	Rock	340	10%	5.33	-8
15	06/09/2017		0.08	0.01	Bedrock	110	14%	2	-33
15	06/09/2017		0.56	0.24	Bedrock	270	17%	5.67	4
15	06/09/2017		0.6	0.12	Bedrock	300	11%	6	19
15	06/09/2017		0.72	0.02	Bedrock	160	28%	7	-1
15	06/09/2017		0.52	0.01	Bedrock	200	21%	5	0
15	06/09/2017		0.88	0.08	Bedrock	270	19%	4.67	-41
15	06/09/2017		0.32	0.01	Bedrock	210	10%	2	-47
15	06/09/2017		0.76	0.02	Bedrock	300	21%	4.33	-12
15	06/09/2017		1	0.08	Rock	220	17%	5	-37
15	06/09/2017		1	0.01	Bedrock	340	10%	4.67	-28
16	07/09/2017	NA	NA		Bedrock	100	53%	NA	NA
16	07/09/2017	NA	NA		Bedrock	40	50%	NA	NA
16	07/09/2017	NA	NA		Bedrock	80	21%	NA	NA
16	07/09/2017	NA	NA		Bedrock	90	82%	NA	NA
16	07/09/2017		0.68	0.04	Bedrock	190	31%	4	19
16	07/09/2017		0.56	0.02	Rock	160	29%	4.67	23
16	07/09/2017		1	0	Bedrock	220	34%	7.33	7
16	07/09/2017		0.76	0.005	Bedrock	180	23%	4.67	0
16	07/09/2017		0.32	0	Bedrock	140	51%	4.5	33
16	07/09/2017	NA	NA		Bedrock	70	109%	NA	NA
16	07/09/2017		0.68	0.36	Bedrock	100	53%	5.67	-18
16	07/09/2017		0.36	0.44	Bedrock	40	50%	3	-6
16	07/09/2017		0.92	0.28	Bedrock	80	21%	5.33	8
16	07/09/2017		0.8	0.08	Bedrock	90	82%	5.67	3
16	07/09/2017		1	0	Rock	190	31%	4.67	20
16	07/09/2017		0.92	0.02	Rock	160	29%	6	-21
16	07/09/2017		1	0.01	Bedrock	220	34%	6	7
16	07/09/2017		1	0.01	Bedrock	180	23%	6.33	-13
16	07/09/2017		1	0	Bedrock	140	51%	5.67	-26
16	07/09/2017		1	0.01	Bedrock	70	109%	5.33	-25
17	07/09/2017		0.68	0.04	Bedrock	150	19%	3.67	38
17	07/09/2017		0.96	0.04	Bedrock	160	45%	6.67	34
17	07/09/2017		1	0.06	Bedrock	240	27%	8	26
17	07/09/2017		0.6	0.16	Stone	240	28%	2.33	13
17	07/09/2017		0.96	0.04	Stone	150	33%	5	22
17	07/09/2017		1	0	Stone	170	31%	3	41
17	07/09/2017		0.6	0.04	Stone	160	27%	3	10
17	07/09/2017		0.72	0.06	Stone	180	36%	3.67	14

17	07/09/2017	NA	NA	Stone	90	50%	NA	NA	
17	07/09/2017	NA	NA	Stone	70	57%	NA	NA	
17	07/09/2017		0.36	0.02	Bedrock	150	19%	4	30
17	07/09/2017		0.04	0.03	Bedrock	160	45%	4	40
17	07/09/2017		0.92	0.2	Bedrock	240	27%	3.33	2
17	07/09/2017		0.92	0.01	Stone	240	28%	3.67	-19
17	07/09/2017		1	0.005	Stone	150	33%	4	5
17	07/09/2017		0.88	0.04	Stone	170	31%	4	11
17	07/09/2017		0.88	0.005	Stone	160	27%	4.33	17
17	07/09/2017		0.6	0.18	Bedrock	180	36%	3.33	12
17	07/09/2017		0.48	0.12	Bedrock	90	50%	2.67	3
17	07/09/2017		0.6	0.36	Bedrock	70	57%	3.33	15
18	08/09/2017		1	0	Bedrock	420	13%	6.33	-4
18	08/09/2017		1	0	Bedrock	400	19%	4.67	20
18	08/09/2017		1	0	Bedrock	270	19%	3.67	-23
18	08/09/2017		0.88	0	Bedrock	220	15%	7	10
18	08/09/2017		0.84	0	Bedrock	130	49%	8	-5
18	08/09/2017		0.92	0.04	Bedrock	150	49%	8	-10
18	08/09/2017		1	0.01	Bedrock	100	54%	6	-34
18	08/09/2017		0	0	Bedrock	120	61%	0	6
18	08/09/2017		0.88	0.02	Bedrock	100	61%	5.33	-6
18	08/09/2017		0.76	0	Bedrock	320	22%	5.33	-11
18	08/09/2017		1	0	Bedrock	420	13%	4.33	-18
18	08/09/2017		1	0	Bedrock	400	19%	6	2
18	08/09/2017		1	0	Bedrock	270	19%	5	-45
18	08/09/2017		1	0	Bedrock	220	15%	8	-6
18	08/09/2017		1	0	Bedrock	130	49%	8.33	-14
18	08/09/2017		0.88	0.01	Bedrock	150	49%	5.67	-42
18	08/09/2017	NA	NA	Bedrock	100	54%	NA	NA	
18	08/09/2017		0.4	0	Bedrock	120	61%	2.33	-16
18	08/09/2017	NA	NA	Bedrock	100	61%	NA	NA	
18	08/09/2017		1	0.01	Bedrock	320	22%	6	-23
19	10/09/2017		0.48	0.02	Stone	110	25%	6	0
19	10/09/2017		0.6	0.08	Bedrock	100	36%	4	-6
19	10/09/2017		0.52	0	Bedrock	200	23%	4.33	-29
19	10/09/2017		0	0	Stone	200	19%	0	-12
19	10/09/2017		1	0	Stone	170	27%	4.67	-15
19	10/09/2017		0.88	0	Stone	320	21%	5.33	-3
19	10/09/2017		1	0.01	Bedrock	150	29%	6	9
19	10/09/2017		0.36	0.01	Stone	220	21%	2.33	-15
19	10/09/2017		0.84	0.005	Stone	70	30%	3.33	-34
19	10/09/2017		0.76	0.02	Bedrock	80	65%	5	-1
19	10/09/2017		0.92	0.005	Stone/bedrock	110	25%	4	-14
19	10/09/2017	NA	NA	NA	100	36%	NA	NA	
19	10/09/2017		0.96	0.12	Rock	200	23%	6.33	-15
19	10/09/2017		0.4	0.005	Stone	200	19%	2.67	-28
19	10/09/2017		0.88	0.01	Stone	170	27%	5	-30
19	10/09/2017		0.56	0.04	Stone	320	21%	3.17	-13

19	10/09/2017		0.08		0.16	Stone/bedrock	150		29%		5.67		-3
19	10/09/2017		0.92		0.08	Stone	220		21%		4.5		-33
19	10/09/2017	NA		NA		NA	70		30%	NA		NA	
19	10/09/2017	NA		NA		NA	80		65%	NA		NA	
20	18/09/2017		0.92		0.005	Bedrock	150		53%		3.33		6
20	18/09/2017	NA		NA		Bedrock	80		46%	NA			13
20	18/09/2017	NA		NA		Bedrock	70		34%	NA			11
20	18/09/2017		0.76		0	Bedrock	130		48%		4.67		27
20	18/09/2017		0.88		0.01	Bedrock	200		31%		5.33		29
20	18/09/2017		0.52		0.06	Bedrock	160		28%		4		19
20	18/09/2017		1		0.06	Bedrock	110		35%		6		16
20	18/09/2017		1		0.08	Stone/bedrock	250		21%		5.33		4
20	18/09/2017		1		0.08	Stone/bedrock	210		10%		4.67		2
20	18/09/2017		0.72		0.06	Bedrock	130		53%		4.67		30
20	18/09/2017		1		0.02	Bedrock	150		53%		5.67		1
20	18/09/2017		1		0.01	Bedrock	80		46%		3.67	NA	
20	18/09/2017		0.8		0.04	Bedrock	70		34%		4.33	NA	
20	18/09/2017		0.32		0.02	Bedrock	130		48%		4.67		-1
20	18/09/2017		0.72		0.04	Bedrock	200		31%		2.33		3
20	18/09/2017		0.96		0.04	Bedrock	160		28%		4.67		-12
20	18/09/2017		1		0.08	Bedrock	110		35%		5		1
20	18/09/2017		1		0.08	Rock	250		21%		6.67		-10
20	18/09/2017		1		0.12	Stone	210		10%		7		-9
20	18/09/2017		1		0.04	Bedrock	130		53%		6		23
21	18/09/2017		0.6		0.04	Bedrock	330		14%		4		8
21	18/09/2017		0.36		0.08	Bedrock	290		24%		7.67		19
21	18/09/2017		0.04		0	Bedrock	320		27%		1		33
21	18/09/2017		0.96		0.02	Bedrock	290		26%		5.67		30
21	18/09/2017	NA		NA		Bedrock	90		31%	NA		NA	
21	18/09/2017	NA		NA		Bedrock	30		67%	NA		NA	
21	18/09/2017		0.02		0.01	Bedrock	300		10%		1		9
21	18/09/2017		0.8		0.12	Bedrock	500	NA			5		-10
21	18/09/2017		0		0	Bedrock	250		0%		0		23
21	18/09/2017		0.72		0.12	Bedrock	340	NA			5.67		26
21	18/09/2017		1		0.04	Bedrock	330		14%		5		1
21	18/09/2017		0		0	Bedrock	290		24%		0		12
21	18/09/2017		0.96		0.16	Bedrock	320		27%		3.33		-3
21	18/09/2017		0.08		0.04	Bedrock	290		26%		4		-11
21	18/09/2017		1		0.24	Bedrock	90		31%		4.67		-18
21	18/09/2017		0.16		0.04	Bedrock	30		67%		3.5		6
21	18/09/2017		1		0.12	Stone/bedrock	300		10%		9.33		18
21	18/09/2017		0.28		0.01	Bedrock	500	NA			2		33
21	18/09/2017		0.04		0	Bedrock	250		0%		3		42
21	18/09/2017		0		0	Bedrock	340	NA			0		29
22	19/09/2017		0.88		0.08	Bedrock	230		8%		5		-3
22	19/09/2017		0.68		0.16	Rock	310		20%		4.67		9
22	19/09/2017		1		0	Rock	150		18%		6		29
22	19/09/2017		1		0.02	Bedrock	170		28%		5.67		-13

22	19/09/2017		0.24	0.01	Bedrock	350	21%	3.67	-4
22	19/09/2017		1	0.02	Stone	290	19%	6.67	0
22	19/09/2017		0.28	0	Stone	330	24%	2.33	14
22	19/09/2017		0.8	0.02	Stone	320	16%	6.67	-7
22	19/09/2017		0.8	0.02	Bedrock	290	38%	8	29
22	19/09/2017		0.8	0.06	Bedrock	260	30%	5.33	16
22	19/09/2017		0.84	0.08	Bedrock	230	8%	5.67	-13
22	19/09/2017		1	0.02	Rock	310	20%	8.67	-4
22	19/09/2017		0.56	0.08	Rock	150	18%	4	31
22	19/09/2017		0.12	0.01	Stone	170	28%	3	-15
22	19/09/2017		0.64	0.01	Stone	350	21%	6	-13
22	19/09/2017		1	0.02	Stone	290	19%	6	-9
22	19/09/2017		0.36	0.08	Stone	330	24%	3.33	-9
22	19/09/2017		1	0.04	Stone	320	16%	9.33	-11
22	19/09/2017		1	0.04	Bedrock	290	38%	7	-14
22	19/09/2017		1	0.04	Bedrock	260	30%	7.33	4
23	19/09/2017	NA		NA	NA	100	74%	NA	NA
23	19/09/2017		0.44	0.08	Bedrock	140	52%	4.67	24
23	19/09/2017		0.6	0	Bedrock	300	27%	3.67	39
23	19/09/2017		0.84	0	Bedrock	170	41%	5	65
23	19/09/2017		1	0	Bedrock	280	28%	7.67	12
23	19/09/2017		0.88	0	Rock	300	20%	5.67	14
23	19/09/2017		1	0	Rock	290	22%	6.33	12
23	19/09/2017		0.28	0	Rock	290	8%	4.33	-12
23	19/09/2017	NA		NA	NA	50	40%	NA	NA
23	19/09/2017	NA		NA	NA	NA	NA	NA	NA
23	19/09/2017		0.6	0.08	Bedrock	100	74%	3.33	9
23	19/09/2017		0.52	0.03	Bedrock	140	52%	3	-24
23	19/09/2017		0.64	0.04	Bedrock	300	27%	5	33
23	19/09/2017		0.64	0.02	Bedrock	170	41%	4.67	-6
23	19/09/2017		0.92	0	Stone	280	28%	6.67	-12
23	19/09/2017		0.32	0	Rock	300	20%	4.67	-15
23	19/09/2017		0.92	0	Rock	290	22%	5.33	-24
23	19/09/2017		0.96	0	Rock	290	8%	5.67	-2
23	19/09/2017		0.52	0	Stone	50	40%	3	NA
23	19/09/2017	NA		NA	NA	NA	NA	NA	NA
24	20/09/2017		0.48	0.01	Rock	180	31%	4.67	20
24	20/09/2017		0.64	0.01	Rock	180	36%	6	10
24	20/09/2017		1	0.01	Stone/bedrock	290	26%	9	15
24	20/09/2017		0.64	0	Rock	190	52%	6	29
24	20/09/2017		0.6	0.16	Stone/bedrock	300	29%	4.33	4
24	20/09/2017		1	0.16	Bedrock	150	20%	3.67	10
24	20/09/2017		1	0.12	Bedrock	260	27%	5	11
24	20/09/2017		1	0.12	Rock	350	23%	5.67	22
24	20/09/2017		0.88	0.03	Stone	200	18%	6	15
24	20/09/2017		1	0.08	Bedrock	290	28%	5.33	11
24	20/09/2017		0.88	0.02	Rock	180	31%	3.67	-3
24	20/09/2017		1	0.01	Rock	180	36%	7.67	4

24	20/09/2017		1	0.005	Rock	290	26%	8.67	-13
24	20/09/2017		1	0.08	Rock	190	52%	4.67	4
24	20/09/2017		0.68	0	Rock	300	29%	3	-20
24	20/09/2017		0.88	0.12	Rock	150	20%	4	-2
24	20/09/2017		1	0.01	Rock	260	27%	7.67	12
24	20/09/2017		0.96	0.06	Rock	350	23%	4	-2
24	20/09/2017		0.96	0.01	Rock	200	18%	5.67	11
24	20/09/2017		1	0	Rock	290	28%	5.33	20
25	20/09/2017		1	0	Bedrock	120	48%	6.33	25
25	20/09/2017		1	0.01	Bedrock	200	26%	6.67	18
25	20/09/2017		0.92	0.04	Bedrock	230	28%	5	17
25	20/09/2017	NA			NA	60	58%	NA	NA
25	20/09/2017	NA			NA	90	30%	NA	NA
25	20/09/2017		0.84	0.02	Bedrock	140	31%	3	32
25	20/09/2017		1	0	Bedrock	190	31%	7.33	34
25	20/09/2017		1	0.03	Stone	160	31%	5.33	14
25	20/09/2017		1	0.005	Stone	180	36%	4	35
25	20/09/2017	NA			NA	80	34%	NA	NA
25	20/09/2017		0.96	0.08	Bedrock	120	48%	5.67	0
25	20/09/2017		1	0	Bedrock	200	26%	7	8
25	20/09/2017		0.64	0.005	Bedrock	230	28%	2.33	-13
25	20/09/2017		0.88	0.08	Bedrock	60	58%	7.33	20
25	20/09/2017		0.76	0.4	Bedrock	90	30%	5.33	16
25	20/09/2017		0.48	0.08	Bedrock	140	31%	3	7
25	20/09/2017		1	0.04	Bedrock	190	31%	5.33	-3
25	20/09/2017		0.88	0.16	Stone	160	31%	6	-5
25	20/09/2017		1	0	Stone	180	36%	6.67	9
25	20/09/2017		0.88	0.01	Bedrock	80	34%	7.67	14
26	21/09/2017		0.92	0	Stone	140	19%	2.33	3.5
26	21/09/2017	NA			NA	100	21%	NA	NA
26	21/09/2017		0.52	0	Stone	180	28%	5.33	14.5
26	21/09/2017		0.8	0	Stone	200	23%	4.33	-1.5
26	21/09/2017		0.8	0	Stone	170	28%	4.67	12.5
26	21/09/2017		0.92	0	Stone	160	28%	5.67	-10.5
26	21/09/2017		0.52	0	Bedrock	140	10%	3.33	4.5
26	21/09/2017		0.16	0	Stone	260	22%	2	11.5
26	21/09/2017		0.6	0.005	Stone/bedrock	250	22%	3.67	19.5
26	21/09/2017		0.92	0	Stone	260	17%	6.33	-1.5
26	21/09/2017		0.88	0	Stone	140	19%	3.33	-11.5
26	21/09/2017		0.68	0	Bedrock	100	21%	4.67	20.5
26	21/09/2017		0.84	0	Stone	180	28%	6	14.5
26	21/09/2017		0.72	0	Stone	200	23%	2.33	-20.5
26	21/09/2017		0.68	0	Stone	170	28%	3	-13.5
26	21/09/2017		1	0	Stone	160	28%	3.33	-15.5
26	21/09/2017		0.4	0	Bedrock	140	10%	5	9.5
26	21/09/2017		0.88	0.04	Stone	260	22%	2.67	-11.5
26	21/09/2017		0.68	0.005	Stone/bedrock	250	22%	4	-10.5
26	21/09/2017		0.88	0	Stone	260	17%	3.33	-14.5

27	21/09/2017		1	0.04	Rock	110	44%	5	52.5
27	21/09/2017		0.72	0.03	Rock	210	40%	5	11.5
27	21/09/2017		1	0.08	Rock	180	34%	3.67	8.5
27	21/09/2017		0.96	0.12	Rock	140	26%	4.67	19.5
27	21/09/2017	NA			Rock	70	70%	NA	NA
27	21/09/2017	NA			Rock	50	64%	NA	NA
27	21/09/2017		0.84	0.02	Bedrock	170	41%	6.33	25.5
27	21/09/2017		1	0.04	Bedrock	180	34%	6	6.5
27	21/09/2017		0.84	0.06	Bedrock	290	17%	5.33	7.5
27	21/09/2017		1	0.16	Bedrock	300	10%	8.67	6
27	21/09/2017		0.72	0.24	Rock	110	44%	4.67	11.5
27	21/09/2017		0.96	0.04	Rock	210	40%	5.33	27.5
27	21/09/2017		0.48	0.04	Rock	180	34%	4	5.5
27	21/09/2017		0.92	0.36	Rock	140	26%	4	15.5
27	21/09/2017		0.96	0.04	Bedrock	70	70%	6.33	23.5
27	21/09/2017		0.4	0.04	Bedrock	50	64%	2.33	0.5
27	21/09/2017		0.84	0.04	Bedrock	170	41%	3.67	9.5
27	21/09/2017		0.92	0.02	Stone	180	34%	9	1.5
27	21/09/2017		0.92	0.02	Bedrock	290	17%	5.33	-10.5
27	21/09/2017		0.48	0.03	Bedrock	300	10%	3.67	-5

Appendix 4

Collinearity between environmental factors tested with a Pearson's Product-Moment correlation test. Collinearity between *A. nodosum* and physical factors is below the dotted line. *r* is the Pearson's correlation coefficient. Association strength indicates the strength of the correlation: 0.1-0.3 = small effect, 0.3-0.5 = medium effect, 0.5-1 = large effect. The effect can be either positive or negative (-).

Factor 1	Factor 2	<i>r</i>	Association strength
Orientation	Exposure	-0.1886685	Small
Inclination	Exposure	0.1442431	Small
Inclination	Zone width	-0.6244549	Large
Inclination	Orientation	-0.1341872	Small
Exposure	Temperature	-0.2401693	Small
Exposure	Salinity	-0.1638122	Small
Temperature	Salinity	0.5200664	Large
<i>A. nodosum</i> volume	Exposure	-0.1008938	Small
<i>A. nodosum</i> volume	Zone width	0.2228721	Small
<i>A. nodosum</i> volume	Inclination	-0.0865261	Small
<i>A. nodosum</i> volume	Salinity	0.0852499	Small
<i>A. nodosum</i> volume	Temperature	0.0983285	Small

Appendix 5

The *V. lanosa* regrowth experiment: Area measurements at different dates. Samples from station 1 in red, samples from station 4 in green. The lighter colours indicate the first samples which were introduced in the pilot study 09.08.2017, while the darker colours indicate the samples which were introduced to the experiment 22.09.2017.

Station	Treatment	Sample	09/08/2017	22/09/2017	02/11/2017	16/03/2018	18/04/2018
1	Control	1.1	20.99	17.20	NA	NA	NA
1	Control	1.2	15.83	15.81	22.63	38.77	39.445
1	Control	1.3	13.24	NA	NA	NA	NA
1	Control	1.4	13.90	11.96	5.66	7.11	5.803
1	Control	2.1	NA	NA	21.07	35.63	NA
1	Control	2.2	NA	NA	30.44	47.56	64.0405
1	Control	2.3	NA	NA	19.25	NA	NA
1	Control	2.4	NA	NA	32.62	28.58	21.695
1	Control	2.5	NA	NA	17.49	NA	17.3825
1	Picked	1.1	8.91	NA	NA	NA	4.2645
1	Picked	1.2	12.66	19.77	5.71	NA	20.713
1	Picked	1.3	17.41	9.18	8.41	31.46	12.0945
1	Picked	1.4	4.66	4.21	2.78	2.12	2.122
1	Picked	2.6	NA	NA	6.64	NA	NA
1	Picked	2.7	NA	NA	10.52	1.99	11.8195
1	Picked	2.8	NA	NA	19.88	29.54	20.533
1	Picked	2.9	NA	NA	11.45	NA	8.98
1	Picked	2.10	NA	NA	8.90	14.86	17.314
4	Control	1.1	13.27	23.33	NA	22.18	26.789
4	Control	1.2	7.18	11.33	10.70	13.64	20.19
4	Control	1.3	51.70	50.82	7.28	NA	NA
4	Control	1.4	26.71	21.61	19.86	NA	NA
4	Control	2.1	NA	NA	32.43	40.10	43.0065
4	Control	2.2	NA	NA	6.34	10.31	15.791
4	Control	2.3	NA	NA	31.14	NA	NA
4	Control	2.4	NA	NA	22.49	NA	25.895
4	Control	2.5	NA	NA	6.11	8.64	10.4945
4	Picked	1.1	15.74	25.40	NA	21.26	24.237
4	Picked	1.2	16.94	14.46	12.16	NA	15.018
4	Picked	1.3	13.93	NA	7.40	NA	4.336
4	Picked	1.4	14.08	17.07	15.62	NA	NA
4	Picked	2.6	NA	NA	26.81	22.06	14.364
4	Picked	2.7	NA	NA	10.26	21.08	27.004
4	Picked	2.8	NA	NA	21.78	11.75	11.5875
4	Picked	2.9	NA	NA	10.12	10.72	6.817
4	Picked	2.10	NA	NA	9.98	NA	NA