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**Kelp associated floral epiphytes
- Productivity and community structure
in relation to wave exposure and season**

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Forord

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Etter to år med formalindunst og statistisk hjernebryn er endelig oppgaven ferdig. På veien er det mange som har hjulpet meg. Først og fremst vil jeg takke veilederen min, professor Stein Fredriksen¹, for all tålmodighet, gode råd og praktisk hjelp gjennom disse to årene. Dernest vil jeg takke alle som har bidratt til at feltarbeid ga mersmak både faglig og sosialt: Kjell Magnus Norderhaug², Hartvig Christie², Kari Nygaard², Morten Foldager Pedersen³, Lars Riis Nejrup³ og Ulrike Lüder⁴. Takk til Berit Kaasa¹ for god hjelp med karbonanalyser, til Tom Andersen¹, Rune H. Økland¹, Ragnhild Heimstad og Anette Edvardsen¹ for all rådgivning i forhold til statistiske metoder, til Jan Rueness¹ for lån av litteratur og hjelp med enkelte artsbestemmelser, og til Bergljot Behrens¹ for uvurderlig språklige tips. Takk også til Martin Isæus⁵ og Trine Bekkby² for hjelp med GIS og for datasupplering.

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1. Abstract

This study was conducted as part of a kelp forest project which aim is to acquire knowledge about biodiversity and productivity in kelp forest areas. The epiphytic algae associated with the stipe of *Laminaria hyperborea* (Gunnerus) Foslie are important as habitat and food source for numerous faunal species along the Norwegian coastline. My investigations were performed on samples taken from kelp stipes in the area of Finnøy, mid-Norway, in April, June, September and November 2005. I address questions of how the epiphytic community structure and primary production relates to a gradient of wave exposure, and the seasonal aspects of these relationships were also brought into the analyses. Both univariate and multivariate statistical methods were used in this approach. The amount of biomass found on a stipe was first of all related to the length of the stipe, and stipe lengths increased with increasing levels of wave exposure. A definite peak in total biomass was found in September. The species composition of epiphytes on the kelp stipes showed variation with increasing exposure. However, the variation within sites with the *same index of exposure* was also very high, suggesting that differences on a smaller scale may be of great importance. Differences in the species composition between sampling periods were also found. I conclude that both epiphyte species composition and productivity in kelp forest areas are affected by wave exposure, or some factors related to wave exposure, and that the structures of these epiphytic communities change through the season.

2. Introduction

Background

What is an epiphyte?

The term *epiphyte* derives from the Greek *epi-* (meaning ‘upon’) and *phyton* (meaning ‘plant’). An epiphyte is an organism that grows attached to a living autotrophic organism, but does not derive any nourishment from it. In this case, an alga that grows on other algae. Even though these epiphytes are unlikely to deprive their host of nourishment, they may reduce the amount of light available as source of energy (Cebrián *et al.* 1999). Naturally, this could reduce the hosts’ abilities for production and growth. The volume of epiphytes increase drag forces opposed on kelp by water movement and the cover can reduce the reproductive output of their hosts (D'Antonio 1985). So even though epiphytes are not considered parasitic, they generally do have some negative effects on their host. Most epiphytic species can be found on other large seaweed or rock substrate as well (e.g. Norton and Milburn 1972).

Epiphytic algae associated with the kelp, itself a large brown algae, are most probably important primary producers in our kelp forest systems. These organisms use energy provided by the sun and build organic compounds from CO₂, water and essential nutrients through photosynthesis, much like plants on land. This process is absolutely fundamental in providing energy for the rest of the ecosystem.

The Norwegian kelp forest

Primary production rates and diversity of marine macroalgae systems are often compared to those of the most productive terrestrial ecosystems (e.g. Mann 1982). However, there are important structural differences between these two community forms. While terrestrial forests reach canopy heights of 10-30 m, the Norwegian kelps form forests reaching canopy heights of 1-3 m (Sivertsen 1991). Maximum heights of the canopy layer are found at the coast of mid-Norway (Rinde and Sjøtun 2005). Furthermore, the terrestrial forests reach their canopy heights over decades, while the kelps usually need no more than 4-5 years. The maximum

plant age of kelp spans from 13 years in the south to 21 years in the north of Norway, and mean age ranges from 5.9 to 10.5 years over the same south-north gradient (Rinde and Sjøtun 2005).

The Norwegian kelp forests are dominated by *Laminaria hyperborea* (Gunnerus) Foslie. They form forests at relatively wave-exposed sites, from levels of low tide to depths reaching about 30 m and are estimated to cover a total area of between 5 000 and 10 000 km² (Sakshaug *et al.* 2002 and references therein). Annual production of kelp has been estimated to roughly 1000 g C m⁻² (Fredriksen 2003), although this will depend on growth rates and kelp densities, which are shown to vary with latitude (Rinde and Sjøtun 2005). *L. hyperborea* grows on substrates like solid rock and stable boulders in canopy plant densities of 12 individuals m⁻² in the south to 6 individuals m⁻² in the north of Norway (Rinde and Sjøtun 2005). The species' geographical distribution is limited to the North Atlantic and extends from Portugal in the south (Kain 1971b) to the Russian coast of Murmansk in the north (Schoschina 1997).

The marine forest areas are of great ecological as well as economic importance. As habitat and food source, the kelps and their floral epiphytes are able to support a wide variety of faunal species (Høisæter and Ødegaard 1994, Christie *et al.* 1998, Christie *et al.* 2003, Fredriksen 2003, Norderhaug 2004). A great number of these supported animal species, and their predators, are commercially exploited. Finally, the kelp itself is an important resource for some of our coastal communities. It is harvested for its alginates which is, among other uses, a thickening agent in food and cosmetic products.

The rough surface of the kelp stipe is suitable substrate for a vast number of algal and animal species. There are few previous studies concerning epiphytic growth on *L. hyperborea* in Norway. Mortensen (1992) described the epiphytic community of stipes and hapters in Finnmark, north in Norway, where he found that both species composition and amount of epiphytes were related to wave exposure, depth, and height and age of the kelp. He noted *Ptilota gunneri* P.C. Silva, Maggs & L.M. Irvine, *Polysiphonia stricta* (Dillwyn) Greville, *Phycodrys rubens* (Linnaeus) Batters, *Delesseria sanguinea* (Hudson) J.V. Lamouroux and *Callophyllis cristata* (C. Agardh) Kützing as the five most common species. Sørli (1994) gave a detailed description of the epiphytic algal flora on stipes and hapters from Vega, in mid-Norway. She related her observations to herbivore activity, season and depth. In her samples, the most common species were *Polysiphonia stricta*, *Rhodochorton purpureum* (Lightfoot) Rosenvinge, *Palmaria palmata* (Linnaeus) Kuntze, *Ptilota gunneri* and seedlings

of *Delesseriaceae* spp. Gravendeel (1994) gave an account of the connections between the length and age of kelp stipes, the epiphytic cover and the associated stock of amphipods at wave exposed locations nearby Sotra, at the west coast of Norway. She found that growth of epiphytes increased with increasing kelp age (up to 7 years), which was positively correlated with the length and weight of the kelp stipe. *Palmaria palmata*, *Ptilota gunneri*, *Polysiphonia stricta*, *Membranoptera alata* (Hudson) Stackhouse and *Phycodrys rubens* (Linnaeus) Batters seemed to be among the most common species at these locations. This work and other studies from the same area were included in a report by Høisæter and Ødegaard (1994) at the University of Bergen. They point out that large variations occur in epiphytic organisms along a gradient of exposure and on a smaller scale, within areas of approximately same depth and index of exposure (Høisæter and Ødegaard 1994). They also observed a considerable year to year variation along with the expected seasonal changes.

The structure of Norwegian kelp populations, and consequently their associated flora and fauna, is highly influenced by kelp density (Sjötun et al. 1998, Sjötun et al. 2006), depth and wave exposure (Kain 1971a, Sjötun et al. 1993, Høisæter and Ødegaard 1994, Sjötun et al. 1998) and latitude (Sjötun et al. 1995, Rinde and Sjötun 2005). This study focuses mainly on wave exposure.

Extensive studies of floral epiphytes associated with *L. hyperborea* have been done in other parts of the northern 'temperate' Atlantic as well. Examples are studies from the areas around the British Isles (Norton 1977, Harkin 1981, Whittick 1983) and the island of Helgoland (Schultze *et al.* 1990).

Wave exposure

Waves may be generated by seismic activities, streams or boats, but most waves are induced by wind. Wind waves are gravity waves formed by the transfer of wind energy into water. Most wind waves are less than 3 metres high with lengths from 60 to 150 metres in open ocean (Garrison 2005). Three factors affect the growth of these waves: 1) the strength of the wind; 2) the length of time the wind blows, or the wind duration; and 3) the uninterrupted distance over which the wind blows without significant change in direction, also called fetch. These affect the extent of energy transfer from air to sea and thus the wave morphology.

Exposure is a factor related to currents and particularly waves, which in addition to being a physical stress factor, also may act as a key determinant of macroalgal production and community structure through water motion (Hurd 2000). This “key role” is attained through interactions with a complex of abiotic and biotic factors including photon flux, spectral composition, nutrient availability, temperature, herbivore activity and inter- and intraspecific competition for space and resources. All are influenced by water motion as reviewed by Hurd (2000).

Algal productivity in relation to water motion

Light climate

All photosynthetic organisms depend on light, and water motion affects the light climate in the water column. A considerable part of the light hitting the sea is reflected by the surface. The percentage reflected from a flat surface depends on the angle of the sun to the surface, with reflection increasing as the sun's position over the horizon decreases. Waves will for instance increase light penetration when the sun is low, but whitecaps and bubbles in rough seas will at the same time increase reflection and can reduce the light entering the water by as much as 50% (Lobban and Harrison 1994). Therefore, the water column light climate depends both on the sun's position over the horizon and the state, or roughness, of the surface water.

Utilisation of inorganic carbon and essential nutrients

“Water motion has the effect of a double-edged sword” (Wheeler 1988). On one side, Wheeler states, too much motion causes large drag forces which break and dislocate aquatic algae. The plants respond by routing photosynthetic energy into structural modifications that can withstand these forces. On the other side, limited water motion causes enlarged diffusion shells, which restricts productivity by inhibiting a plant's ability to absorb nutrients. Hence, he hypothesises; tradeoffs must occur between drag and diffusion stresses. Moderate amounts of water motion enhance mass transport without excessive drag and enable the high productivity of many algal communities (Wheeler 1988).

High macroalgal production at high levels of water motion has been found in several laboratory studies. Experiments demonstrate that the rates of photosynthesis and inorganic nutrient uptake increase with increasing mainstream velocities until a saturating velocity is reached (Hurd 2000). These velocities seem to be in the same range as those that saturate growth rates (Hurd 2000).

Hurd (2000) points out that the slow growth rates under slow flows (mainstream velocities $< 10 \text{ cm}\cdot\text{s}^{-1}$) typically are attributed to a reduction in the mass transfer of inorganic carbon and nutrients (N and P) to the macroalgal surface due to the presence of a thick diffusion boundary layer (DBL). Of great importance as well, she emphasises that a thick DBL causes reduced flux of photosynthetic by-products (OH^- and O_2) away from the thallus surface, affecting the pH within the DBL. This would cause a considerable change in the form of inorganic carbon available for macroalgal uptake (Falkowski and Raven 1997), having a negative effect on macroalgal photosynthetic rates.

The DBL of an alga *in situ* is highly dynamic. Most macroalgal surfaces are formed so that even slow water flows will cause oscillation of the thallus. This increases velocities and turbulence at the thallus surface, affecting the DBL (or diffusive shell) of the algae by reducing it. Even though mainstream velocities may be under the saturating limit for production and growth, the actual level of water motion experienced by the algae may not (Gerard 1982, Koch 1993). Even in slow flows the thickness of DBLs will change on a timescale of seconds, mostly due to turbulence. In most cases it is unlikely to be persistent enough to limit production *in situ* (Hurd 2000). Thus, Wheeler (1988, see above) probably overemphasised its limiting role on *in situ* macroalgal productivity in slow water flows.

Although the rates of inorganic carbon and nutrient supplies will generally increase with increasing water flows, the abilities of macroalgae to utilise and retain these resources reach a limit. Macroalgae have different physiological adaptations dealing with uptake and utilisation of carbon (Johnston *et al.* 1992, Larsson and Axelsson 1999) and essential nutrients (Wallentinus 1984). The effect of changes in water flow thus depends on the physiological ‘strategy’ and state of the macroalga, the duration of change and the formation of DBL relative to its carbon and nutrient requirements.

Most Norwegian macroalgal communities will experience turbulent mainstream flows caused by passing surface waves, currents, local streams and to some extent disturbances from boat traffic. Macroalgae within kelp forests, which are all exposed to relatively high levels of wave action, are not likely to experience nutrient or carbon constraints on growth caused by slow water flows.

Algal community structure in relation to water motion

Water motion influences macroalgal community structure. Waves can physically harm or remove macroalgae and their herbivores, and studies show that wave exposure is one of the most important factors determining the algal community structure in space (Jorde and Klavestad 1963, Lewis 1964, Wheeler 1988, Høisæter et al. 1992, Hansen and Ingólfsson 1993, Høisæter and Ødegaard 1994, Munda 1994, Leliaert et al. 2000)

Studies of algal community structure in kelp beds around the Cape Peninsula in South Africa revealed a geographical change in algal composition (Leliaert *et al.* 2000). This change was related to seawater temperature and wave exposure, possibly as a consequence of different associated levels of herbivore activity. More animals were assumed to live in the less exposed areas. Purely quantitative measures of small potential herbivores have, however, also been shown to increase with increasing degree of exposure (Høisæter and Ødegaard 1994, Christie et al. 2003). However, the effectiveness of consumers in high stress environments are assumed to be reduced (Menge and Sutherland 1987). While large organisms are more likely to avoid high stress environments, because of their ability to travel greater distances, smaller organisms may have to endure by seeking a micro refuge within the habitat (Menge and Sutherland 1987). A suitable “micro refuge” for small mobile species in a kelp forest would be amongst and sheltered by the kelp stipe epiphytes, or within the sheltered environment of the kelps’ hapter.

It has been suggested that algae with greater structural complexity of thallus should be better at resisting wave shear than structurally simple functional groups such as filamentous algae (Airoldi 2001 and references therein). However, Airoldi states that algae growing in similar sized turfs might respond similarly to wave forces independently of the structural complexity of their thallus. Because of the generally smaller sizes and greater compactness attained by algae when aggregated than when isolated, turf-forming algae could be relatively unaffected by wave exposure (Lobban and Harrison 1994), and might face greater constraints on their morphology and distribution from competition, variable dispersal potentials (Lobban and Harrison 1994, Airoldi 2001 and references therein) and herbivore activity (Leliaert *et al.* 2000). This could apply to epiphytic growth as well. Although kelp-associated epiphytic flora would not be considered ‘turf forming’ in a strict sense, they are highly aggregated.

Kelp morphology in relation to wave exposure

A change in morphology of organisms is often seen in relation to environmental factors. Morphological plasticity is quite common in macroalgae. This ability to adapt is of both functional (Sjötun *et al.* 1998, Stewart and Carpenter 2003) and ecological significance (Gerard and Mann 1979, Hurd 2000 and references therein, Stewart and Carpenter 2003). The most typical form of *L. hyperborea* is found at sites which are exposed to high levels of wave action: It has a digitated, quite thick, relatively small lamina and a long stipe. The ratio between fresh weight lamina and stipe is about 1:1 in canopy plants (Kain 1971a). In sheltered areas as well as in deep water, the stipe is generally shorter and the lamina is usually quite large and thin, entire or split into few segments. The ratio between fresh weight lamina and stipe, 10:1, is much higher in these areas (Kain 1971a). The results from an *in situ* study by Sjötun *et al.* (1998) indicate that some factor connected with high wave exposure enhances growth in *L. hyperborea*. They suggest that wave exposure at a site impose a general influence on growth of all age groups in *L. hyperborea*, while canopy biomass is the most important factor influencing growth of small plants in a kelp forest. The restraining effect of canopy shading on recruitment of kelp was confirmed as important in a study of kelp forests in mid-Norway (Sjötun *et al.* 2006).

Morphology and structure of kelp populations should affect the community structure and productivity of epiphytic organisms. The length, width and surface texture of the stipe determine the amount of available substrate for epiphytic organisms. Density, size and form of laminas influence the light availability beneath the canopy layer. Height, rigidity and density of plants, as well as their epiphytes, determine the volume of habitat for potential feeders and their predators. Kelp morphology and forest structure may also affect wave shear experienced by all organisms associated with this system (Eckman *et al.* 1989).

Estimation of exposure

Methods for estimating ecologically relevant values of wave exposure are of interest both for basic research and coastal management. In general, these have previously been based on either biologically derived indices, or cartographic methods.

To ensure ecological relevance as well as generality, cartographic and biological index methods have to be combined (Isæus 2004). In the study by Isæus (2004) a Geographical Information System (GIS) based cartographic model was developed and calibrated by a

biological index derived from zonation of epilittoral lichens (for further description of the model, see Isæus 2004). This model has since been used in projects along the coast of Norway (e.g. Rinde et al. 2004) and the coast of Sweden (e.g. Eriksson *et al.* 2004). The output from the model is only a relative measure of exposure which has not yet been attempted, at least not to my knowledge, ‘translated’ into units of energy.

Seasonal variations

Most of the floral species found as epiphytes on the stipe of *L. hyperborea* are annual. However, there are some very important exceptions. *Ptilota gunneri*, *Palmaria palmata*, *Membranoptera alata*, *Delesseria sanguinea*, *Phycodrys rubens*, *Polysiphonia stricta*, *Polysiphonia elongata*, *Rhodomela confervoides*, *Rhodomela lycopodioides* and *Laminaria* sp. are all known to be perennial, meaning that at least parts of their thallus may sustain for more than one season.

Sørli (1994) compared both species numbers and states of development of epiphytes sampled in March and September in the area of Vega, Norway. In March she found most algae to be in the early stages of development and of generally quite small sizes. Most species were considerably more developed in September and the total number of species observed was higher in these samples. However, in samples from 5 m depth (comparable to my sample depths) there were no significant differences in species number between the sampling periods.

The epiphytic flora at the stipe of *L. hyperborea* at St. Abbs Head, Scotland was examined by Whittick (1983) between 1968 and 1969. He found four species, *Palmaria palmata*, *Membranoptera alata*, *Phycodrys rubens* and *Ptilota gunneri*, to make up over 95% of the epiphyte biomass. *P. palmata*, *M. alata* and *P. rubens* showed quite similar patterns of seasonal changes in biomass, with a peak in September and a decline in winter. While *P. gunneri*, which is considered to be a species of northern distribution, showed an earlier peak (between May and June) and an earlier decline (between September and October) (Whittick 1983).

The thesis

This thesis is a contribution to a kelp forest project, which aim is to acquire knowledge about productivity and biodiversity in kelp forest areas, especially in relation to wave exposure. My focus will be on the floral epiphytes associated with the stipe of *Laminaria hyperborea*, in particular, their level of production and species composition in relation to wave exposure and season. I will to some extent investigate our observations of *L. hyperboreas'* morphological characters along these gradients and include some modelled variables, to try shedding some light upon observed epiphyte variation and the importance of wave exposure in structuring these communities. There are few previous records of kelp-associated epiphyte productivity in Norway.

My main goals have been:

- 1) To find out if there is a relation between productivity of epiphytic macroalgae and wave exposure in a Norwegian kelp forest.
- 2) To reveal any change in floral species composition of kelp stipe associated epiphytes along a gradient of exposure in a Norwegian kelp forest.
- 3) To reveal any seasonal change in floral species composition of kelp stipe associated epiphytes in a Norwegian kelp forest.

3. Materials and methods

Location

Nine stations nearby Finnøy in the region of Møre og Romsdal, Norway, were investigated. For our project the values of exposure from Isæus' model were divided into three classes of exposure according to the European system of habitat classification, EUNIS. This ensured that stations did represent a range of exposure relevant to these kelp forest studies. The classes were defined as exposed, moderately exposed and sheltered. Three stations were situated at exposed sites, three at moderately exposed and three at sheltered sites (Figure 3.1, see Appendix I, Table 7.1 for geographical coordinates). Apart from exposure, important criteria were: (1) To minimize spatial autocorrelation by picking sites far enough apart to be assumed independent, but (2) at the same time minimize travelling distance so that the stations could be investigated even in difficult weather conditions (pers. comm., Norderhaug 2007).

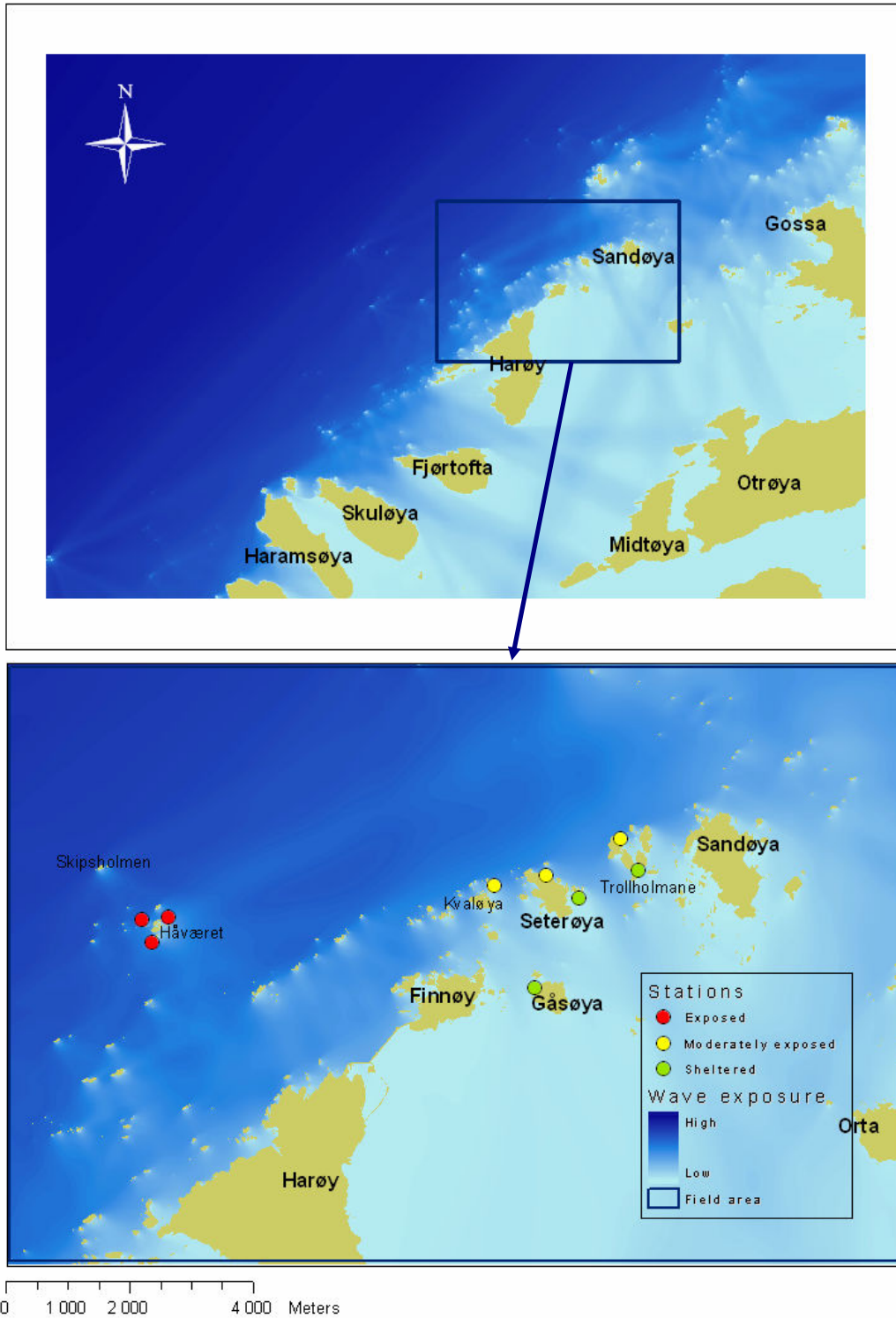


Figure 3.1 Mean value of wave exposure estimated from fetch in 16 directions and five years of wind data in the area of Finnøy (Møre og Romsdal, Norway) according to the Isæus-model (Isæus 2004). (Resolution of 10 x 10 m.)

Sampling and data collection

Sampling from all 9 stations was conducted by SCUBA diving at approximately 5 m depth in April, June, September and November 2005. I was assigned to this project in August, and participated only in September and November.

At each station, three *L. hyperborea* individuals of canopy heights were haphazardly chosen. The laminas were removed, and the stipes were separated from the hapters and wrapped in cloths to ensure that no epiphytes or associated fauna were lost.

Each stipe was washed with non-saline water to remove any mobile fauna. These organisms will be investigated by Norderhaug and Christie at the Norwegian Institute for Water Research (NIVA). The length of each stipe was measured. Age was determined by cutting a thin vertical slice of the stipe near basis and counting the growth rings, each ring representing one year according to Kain (1963). The remaining sessile epiphytic flora and fauna was then removed from the stipe for further investigations. Some stipe samples were investigated immediately, but most were fixed with formaldehyde diluted in seawater (to concentrations of 2-4%) and stored in plastic bottles at room temperature away from light.

Each fixed sample was washed and left in saline water under a fume hood for 24 hours or more, allowing the formaldehyde to evaporate. Each sample was roughly sorted by species before gently patted with paper towels to remove excess surface water. The percentage of bryozoan cover was estimated by the eye. Small bags of aluminium foil were made to hold the algae, each bag containing the biomass of *one* species algae (see pg. 28) from *one* stipe. The remaining material, that was not identifiable, was lumped together in its own bag and called "Various". Each bag was labelled and weighed without content, before weighed once again with content. The bags were left in a drying cabinet at 60°C until all biomass was completely dry (2-4 days), before weighed once more and sealed off. To get the weight of biomass, the weight of the bag (without content) was subtracted from the weight of the bag *with content*.

Biomass production in relation to wave exposure and other variables

Stipe length and age of kelp

The length and age distribution of sampled kelp plants were investigated. This was done to reveal possible differences between sampling periods which could influence the models.

Modelling – environment and production

The modelling was done by the help of an integrated suit of software facilities for data manipulation, calculation, statistical analysis and graphical display called R. This immensely useful toolbox is available at <http://cran.r-project.org/>. R can be regarded as an implementation of the S-language which was developed at Bell laboratories by Rick Becker, John Chambers and Allan Wilks (Becker *et al.* 1988).

Trine Bekkby at NIVA provided me with a number of modelled variables (see list of variables below), among these the values from Isæus model of exposure (Isæus 2004).

Variables available for modelling:

Response:

- *Total* - Total epiphyte biomass (g) per stipe
- *“Name of category”*- Biomass of species category per stipe

Predictors:

Measured:

- *Stipe length* - Length of kelp stipe (cm)
- *Stipe age* - Stipe age (growth rings)
- *Month* – Sampling period (April, June, September, November)

Modelled (by NIVA):

- *Slope* - Slope based on a digital model of depth with 10 m spatial resolution. The values (in degrees) spans from 0-90 and is taken as the largest value within a 3x3 window of calculation.
- *RadIndex* - a spatial model of solar irradiation (with a resolution of 10 x 10 m) based on slope and direction relative to optimal slope and directional conditions for

receiving maximal solar irradiation. (Slope and directions are also estimated by a digital model of topography with the same resolution.) Optimal conditions for solar irradiation are set to a value of 1. The further away from this value in negative direction, the less optimal conditions.

- *Light* - a spatial model predicting the percentage of light hitting the surface which reaches the bottom based on estimated secchi depth of 8.25 m and depth. (This is also based on the values from the digital model of topography.)
- *SWM5y* - the values from Isæus model of exposure at the surface. The model is based on the mean strength of wind over five years in 16 directions. The spatial resolution is 10 x 10 m.
- *SWM5yDepth* - the values from Isæus model (*SWM5y*) with corrections for depth (estimated from the digital model of topography).

To avoid any unnecessary numerical problems (apparently, when the scales of two independent variables are very different this may occur (Andersen 2007)), and to make the graphical displays look more appealing, I rescaled both *SWM5y* and *SWM5yDepth*:

- *Exp.value* - $SWM5y / 1.000.000$
- *Exp.depth* - $SWM5yDepth / 1.000.000$

A principal component analysis (PCA) ordination on zero-skewness transformed (Økland *et al.* 2001) environmental data (each variable scaled from 0 to 1) (Appendix I, Figure 7.2) was performed. The PCA investigates the relationships between the stipe data according to recorded and modelled environmental variables. Vectors, showing the direction of maximum change in environmental variables, were fitted by the "envfit" function in the vegan package of R to ease the interpretation of the models.

I wanted to model the epiphytic biomass response to the set of explanatory variables, in order to find out which were likely to be most important in determining the amount of biomass at a stipe. The skewness of the untransformed dataset (Appendix I, Figure 7.1), along with the notion that negative fitted values should not be allowed (negative values for biomass would be absolutely nonsense) led me first to think that a generalized linear model (GLM) of the Poisson-family would be appropriate. This model revealed that the data were overdispersed in relation to the model. To correct for overdispersion I proceeded with a GLM of the

Quasipoisson family. A more thorough description of the theory behind these models is given in Appendix I.

Epiphyte carbon fixation in relation to wave exposure

Analysis of carbon and nitrogen content for each of the eight dominating species categories were done. Because this is a rather expensive procedure we could only analyse one sample of each dominating species from each station. The samples were selected on basis of bryozoan cover noted during sorting. A minute piece of the dried sample was cut trying to avoid bryozoans and other second order epiphytes (defined in Mortensen 1992). A tin capsule was placed on the balance, and the balance tared. The piece of algae was put in the tin capsule which was then wrapped tightly around it, and weighed. This “mini package” was placed in an automatic elemental analyzer (Flash EATM 1112, CE Instruments), for determination of nitrogen and carbon content with the support of a complementary software package (Eager 300). I made some rough estimates of epiphyte production in terms of carbon by combining these results with the results from the biomass study. These estimations were made on basis of the September samples.

The effect of fixation with formaldehyde on biomass and carbon values

Fixation with 4% formaldehyde affected the carbon content of *Megacyclops gigas*, a copepod, to such an extent that the carbon content of preserved animals were reduced by 35% within days in a study by Salonen and Sarvala (1980). A rudimentary study was conducted, to give an idea of what effect fixation has on algal weight and carbon content. *Palmaria palmata*, *Delesseria sanguinea*, *Phycodryis rubens*, *Membranoptera alata*, *Ptilota gunneri*, *Ceramium* sp. and *Rhodomela confervoides*, which are some of the most common algae observed as epiphytes on *L. hyperborea*, were investigated. Samples with little bryozoans were chosen. These were gathered in the area around Finnøy in June 2006. The material was very limited, which put serious constraints on the reliability of the analyses. I chose very simple methods, to avoid overanalyzing data that should not be put too much confidence in.

The material was divided into two approximately equal groups. Wet weight was measured by the same procedure as described above. The sample was measured three times (soaked in water between each time), before averaged. One group was dried immediately, while the other

was fixed in formaldehyde (2-4 %) and stored for a week. Wet weight of the latter was measured and averaged once again after fixation, before the samples were placed in the drying cabinet.

Wet weights were compared before and after fixation and differences were tested in accordance with the Wilcoxon rank sum test. I chose this statistical method because it is much more appropriate than the *t*-test when errors are not ‘normally’ distributed or strongly skewed, and about 95% as powerful with Normal errors (Crawley 2002).

The mean dry to wet weight ratios were calculated in the two ‘treatment’ groups and compared by a Wilcoxon rank sum test to give an idea of the effect of fixation on algal dry weights. Thus, each species was considered a replica. Testing if ratios differed between fresh and fixated samples for each species was not possible.

All samples were investigated by elemental analysis as described above. These results were also analysed by the Wilcoxon rank sum test.

Species composition in relation to wave exposure and other variables

The analysis of species composition was performed on a presence-absence matrix where species with dry weight biomass < 0.005 g was set as absent at stipe. A Detrended Correspondence Analysis (DCA) of species composition on stipes was performed in order to find the main gradients in algal epiphyte species composition. The ordination axes are considered latent variables, or hypothetical environmental variables, in such a way as to optimize the fit of the species data to the unimodal statistical model of how species vary along gradients (ter Braak and Prentice 1988). Environmental vectors were fitted by the ”envfit” function, performed on zero skewness transformed and scaled (from 0 to 1) environmental variables (Appendix I, Figure 7.2). Ordination plots of stipe scores from the DCA were combined with the vectors of maximum change in environmental variables in diplot ordination diagrams. Models of stipe positions along ordination axes (compositional gradients) explained by the environmental variables were made, to show which variables were likely to influence the observed main gradients in species composition. The split-plot GLM method allowed me to investigate the relationship between the plot positions in the ordination diagrams and the environmental variables at different levels of the sampling design (between

sampling periods, between stations and within stations). Change in species number over time and with exposure was analysed by GLM-models of the Poisson family, which is appropriate for count data. The actual change in species composition relative to sampling period and the environmental variable shown to explain most variation was identified by inspection of summary matrixes. All analyses and graphical displays were executed in R.

4. Results:

Epiphyte production in relation to wave exposure and other variables

The principal component analysis (PCA) ordination of the stipes performed on basis of the environmental variables and stipe characteristics (length and age) gave the following eigenvalues (lambda):

Output from R:

	PCA1	PCA2	PCA3	PCA4	PCA5	PCA6	PCA7
lambda	2.6958	1.6636	1.1747	0.8128	0.4627	0.1811	0.00929
accounted	0.3851	0.6228	0.7906	0.9067	0.9728	0.9987	1.00000

About 90 % of the environmental variation was accounted for by the first four axes. I chose to focus on PCA1 and PCA2 (Figure 4.1) since these had the highest eigenvalues and accounted for the most variation.

Table 4.1 Kendall's correlation tests between four PCA ordination axes and the environmental variables. This reveals which environmental variables explain most of the environmental variation between stipes. Significant correlations are marked by italic (significant $p = [0.01, 0.05]$) and bold italic numbers (very significant $p < 0.001$). The larger value of τ , in negative or positive direction, the stronger the correlation. Minimum τ -value obtainable is -1 , and maximum is 1 .

Variable	PCA1		PCA2		PCA3		PCA4	
	τ	p-value	τ	p-value	τ	p-value	τ	p-value
Slope	-0.157	0.022	0.644	<0.001	-0.101	0.139	-0.119	0.082
Stipe age	0.223	0.002	0.308	<0.001	0.436	<0.001	0.512	<0.001
Exp value	0.810	<0.001	0.090	0.190	-0.046	0.504	-0.096	0.160
Stipe length	0.685	<0.001	0.139	0.033	-0.074	0.259	0.019	0.772
Exp depth	0.814	<0.001	-0.016	0.818	0.052	0.445	-0.118	0.084
Light	-0.048	0.480	-0.764	<0.001	-0.214	0.002	0.102	0.136
RadIndex	-0.042	0.542	0.008	0.911	0.628	<0.001	-0.365	<0.001

Stipes and Environment

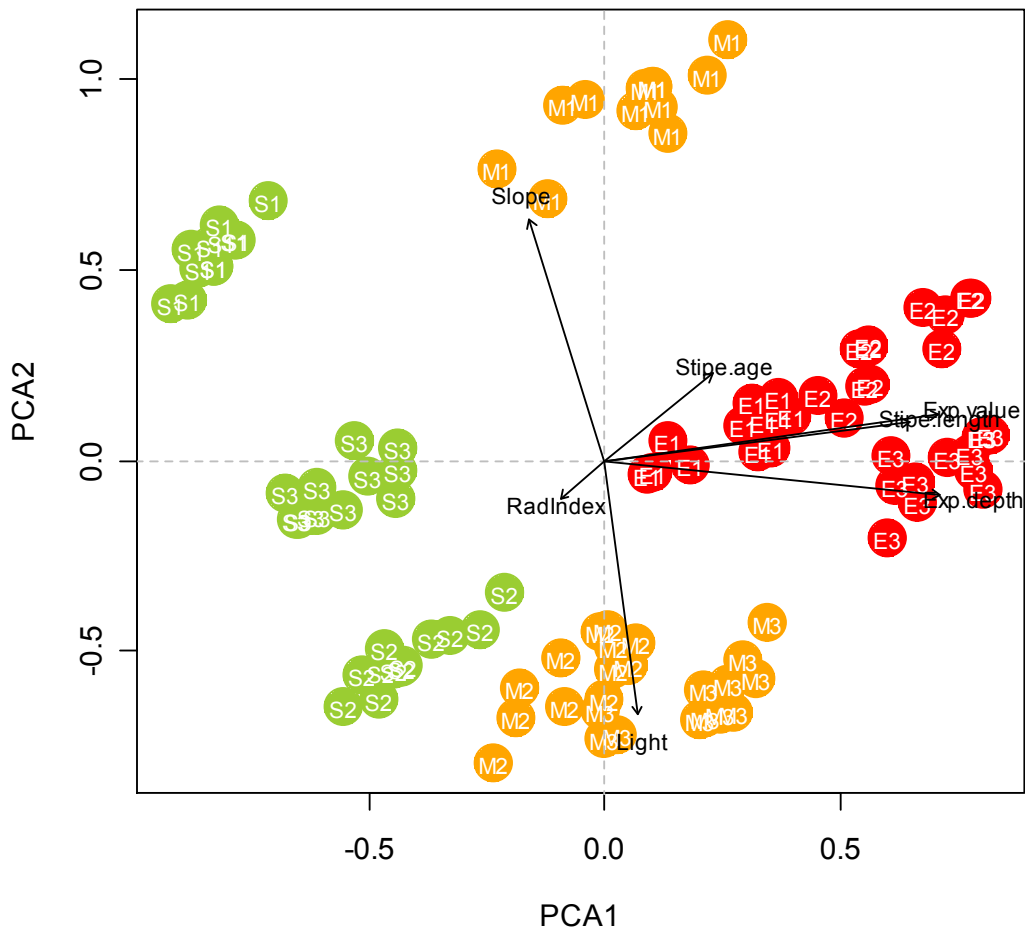


Figure 4.1 Ordination diagram of the PCA on stipes in relation to environmental variables. Vector arrows point in the direction of maximal change, the length of each vector indicating the relative importance of that variable to the positions of the stipes along the two main environmental gradients (PCA1 and PCA2). Each dot represents one stipe (Green – Sheltered, Orange – Moderately exposed, Red – Exposed), and each dot is labelled with the name of the station from which the sample was taken.

There were two quite evident main gradients in the environmental conditions of the stipes that separated the stations from each other (Figure 4.1). The first gradient (PCA1) could best be explained by exposure (“Exp.value” and “Exp.depth”) and the length of the stipe (“Stipe length”) (Table 4.1), which seemed to be highly positively correlated (Figure 4.1). The second PCA axis was best explained by the slope of the seafloor (“Slope”) and part of surface light hitting it (“Light”), which were negatively correlated variables (Figure 4.1). The fact that

exposure was among the variables explaining the most variability between stations is good news, since response to this variable is my main focus.

Biomass production

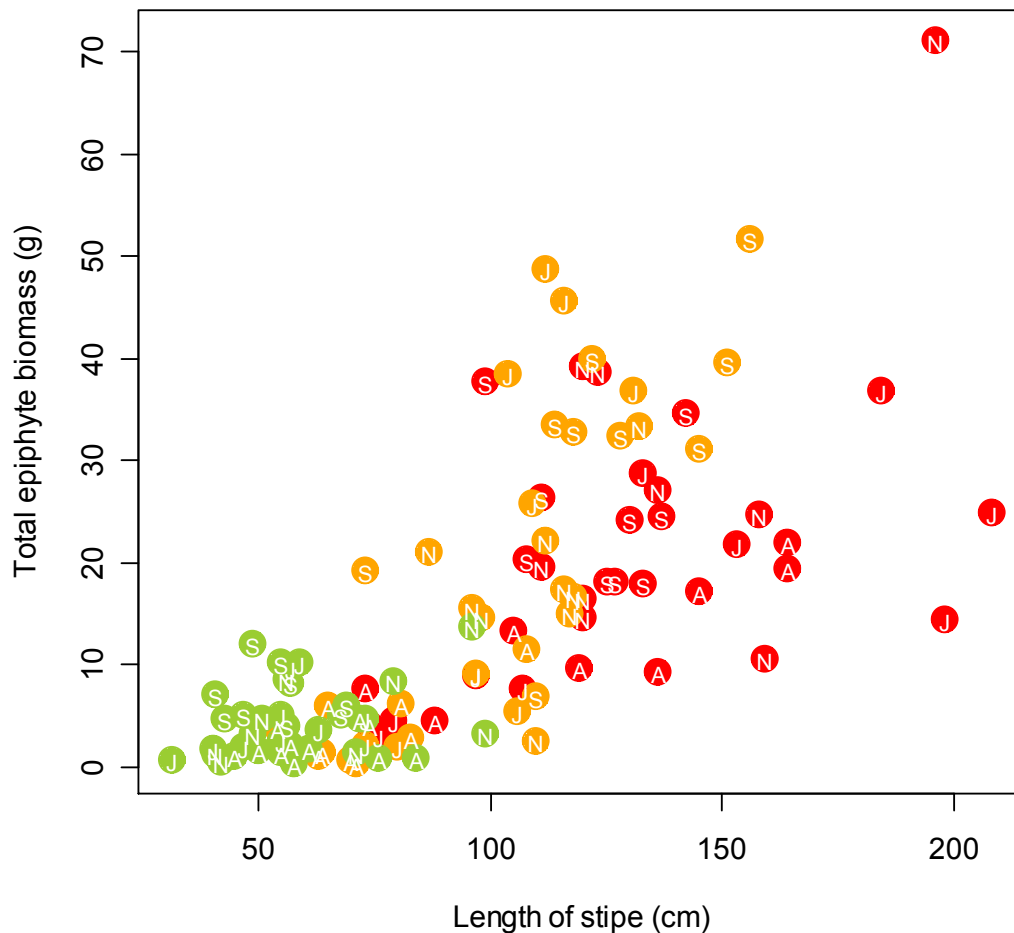


Figure 4.2 Lengths of stipes plotted against total dry weights of epiphyte biomass on the stipes.

(Green – Sheltered, Orange – Moderately exposed, Red – Exposed, A – April, J – June, S – September, N – November).

The lengths of the kelp stipes were generally longer in exposed than in sheltered areas (Appendix II, Figure 7.3). The ranges of lengths were approximately the same in all sampling periods, and plant age ranged from 5 to 10 years for all stations in all sampling periods (Appendix II, Figure 7.4). The dry weight of total epiphyte biomass per stipe was generally

larger in exposed and moderately exposed areas (Appendix II, Figure 7.5). Biomass clearly increased with increasing stipe length, but a large amount of variation occurred (Figure 4.2).

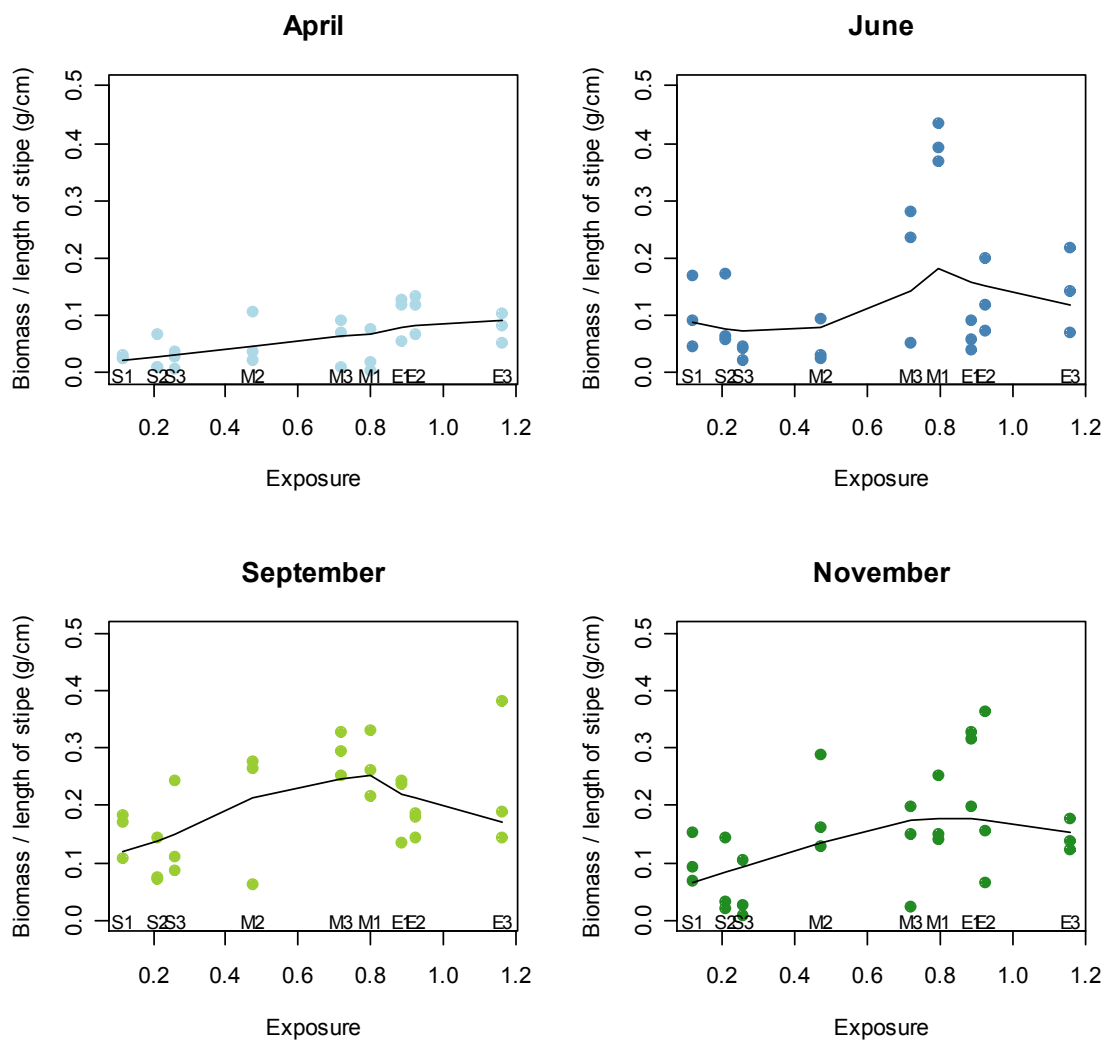


Figure 4.3 Plots describing epiphytic biomass in dry weight per cm kelp stipe with increasing levels of exposure in the four sampling periods. The scale of the “Exposure”-axis is a rescaling of the relative values estimated from Isæus model (2004) of exposure ($SWM5y / 1.000.000$). Station names are plotted along the first axis. The black line is the result of a non-parametric smoother function in R, “lowess”, which carries out a locally weighted polynomial regression of the y-variable on the x-variable. (The ‘smooth’ at each value is influenced by 2/3 of the points.)

When the lengths of stipes were taken into consideration, the following trends in epiphytic biomass were depicted (Figure 4.3): An approximately linear increase in epiphyte biomass per cm stipe with increasing levels of exposure was suggested for April. In June, September and

November however, the biomass seemed to reach a peak around M1 (exposure of 0.8) before it decreased again towards the most exposed stations. The overall peak in epiphytic biomass dry weight per cm stipe was reached in September.

Table 4.2 This table shows the analysis of deviance for the GLM-model of dry weight biomass epiphytes per stipe. The model was fitted as a GLM-model (family=quasipoisson) in R by “bottom-up” selection of parameters (building). (“Df” – degrees of freedom, “Deviance” – deviance explained by incorporation of parameter in model, “Resid.Df” – Residual degrees of freedom, “Resid.Dev” – remaining deviance (residuals) after incorporation of parameter). The residual deviance of “NULL” is the total deviance in the data. “Explained” is the amount of deviance explained by the model and “Part deviance exp” is this amount divided by the total deviance.

Analysis of deviance				
	Df	Deviance	Resid.Df	Resid.Dev
NULL			107	1353.86
Stipe length	1	650.04	106	703.82
Month	3	173.45	103	530.37
RadIndex	1	25.23	102	505.14
Month:RadIndex	3	95.74	99	409.40
Explained		944.46		
Part deviance exp		0.698		

Table 4.3 This table shows parameters from the model of total dry weight biomass epiphytes per stipe. The model was fitted as a GLM-model (family=quasipoisson) in R by “bottom-up” selection of parameters (building). Significant parameters are marked by red p-values.

Parameters:	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.366845	0.216082	1.698	0.092
Stipe length	0.015027	0.001318	11.405	<< 0.001
June	0.320906	0.209709	1.53	0.129
November	0.7606	0.19305	3.94	< 0.001
September	1.029386	0.188594	5.458	< 0.001
RadIndex	1.640108	1.751578	0.936	0.351
June:RadIndex	-5.231111	1.855774	-2.819	0.005
November:RadIndex	-1.585897	1.897154	-0.836	0.405
September:RadIndex	-1.687785	1.838778	-0.918	0.360

Close to 70% of the deviance from the overall mean was explained by the model (Table 4.2) Stipe length was highly significant ($\alpha=0.05$), accounting for about half of the variation in the dataset (Table 4.2). The parameter estimate (“Stipe length”) was positive indicating a log-

linear positive effect of stipe length on total biomass epiphytes per stipe (see formula (0.1) in Appendix I). The effect was statistically similar in samples from all sampling periods, since no interaction terms between “Month” and “Stipe length” were evident. Sampling period, “Month”, explained a significant part of the remaining deviance (33%). The “Intercept” in Table 4.3 was estimated from April samples. The intercept of the June samples was not statistically different from April, though it was larger (0.37+0.32). In September, when the total biomass reached a seasonal peak, the intercept was considerably larger than in April (0.37+1.02). In November the intercept was lower than in September, but still significantly larger than in April (0.37+0.76). The intercept values in itself gives little meaning ($\eta = 0$, see formula (0.1) in Appendix I), but if the effects of the other parameters are the same in all sampling periods, they do say something about the relative difference between the sample means.

However, as Table 4.3 suggests, RadIndex only affected the June samples. An effect-plot showing the influence of parameters on the model (Appendix III, Figure 7.7), gave me a good reason to investigate this interaction further. The M1 station has a very low value for RadIndex relative to the other stations and at the same time the highest observed ratios of epiphyte biomass to stipe lengths in June (Appendix III, Figure 7.8). A Cooks’ distances plot (Appendix III, Figure 7.9) did not reveal any points of alarming consequence to the model. I chose to go with this model, but will be very careful in interpreting the significance of it. A model without RadIndex had the same order of sampling periods regarding amounts of biomass found and the differences were even more significant (Appendix III).

Tukey ‘Honest Significant Difference’ (HSD) plots of total biomass epiphytes per cm stipe revealed no significant differences between stations when sampling periods were tested separately ($\alpha=0.05$). When sampling periods were lumped together however, all S-stations were significantly different from M1 ($\alpha=0.05$) (Appendix II, Figure 7.6).

Twenty-eight species were observed in this study. The eight dominating species categories made up 48-83% of total epiphyte biomass (Appendix VI, Table 7.3). The nine main categories were:

- 1) ‘*Laminaria*’, comprising *Laminaria hyperborea* (Gunnerus) Foslie, *Laminaria digitata* (Hudson) J.V. Lamouroux and *Saccharina latissima* (Linnaeus) C.E. Lane, C.

- Mayes, Druehl & G.W. Saunders. These were lumped together, since assigning the juvenile plants to different species would be impossible.
- 2) '*Palmaria*', which is *Palmaria palmata* (Linnaeus) Kuntze.
 - 3) '*Phycodryis*', which is *Phycodryis rubens* (Linnaeus) Batters.
 - 4) '*Delesseria*', which is *Delesseria sanguinea* (Hudson) J.V. Lamouroux.
 - 5) '*Membranoptera*', which is *Membranoptera alata* (Hudson) Stackhouse.
 - 6) '*Ptilota*', which is *Ptilota gunneri* P.C. Silva, Maggs & L.M. Irvine.
 - 7) '*Polysiphonia*', where *Polysiphonia elongata* (Hudson) Sprengel and *Polysiphonia stricta* (Dillwyn) Greville dominates.
 - 8) '*Rhodomela*', including both *Rhodomela confervoides* (Hudson) P.C. Silva and *Rhodomela lycopodioides* (Linnaeus) C. Agardh.
 - 9) 'Various', comprising *Callophyllis laciniata* (Hudson) Kützing, *Ceramium* sp., *Dictyota dichotoma* (Hudson) J.V. Lamouroux, *Nitophyllum punctatum* (Stackhouse) Greville, *Sphacelaria cirrosa* (Roth) C. Agardh, *Ectocarpus* sp., *Cryptopleura ramosa* (Hudson) L. Newton, *Apoglossum ruscifolium* (Turner) J. Agardh, *Bonnemaisonia hamifera* Hariot (Trailliella), *Desmarestia viridis* (O.F. Müller) J.V. Lamouroux, *Lomentaria clavellosa* (Turner) Gaillon, *Alaria esculenta* (Linnaeus) Greville, *Plocamium cartilagineum* (Linnaeus) P.S. Dixon, *Phyllophora crispa* (Hudson) P.S. Dixon, *Fucus serratus* Linnaeus, *Cystoclonium purpureum* (Hudson) Batters, some bryozoans, a few tunicates and sponges, and other undefined biological matter.

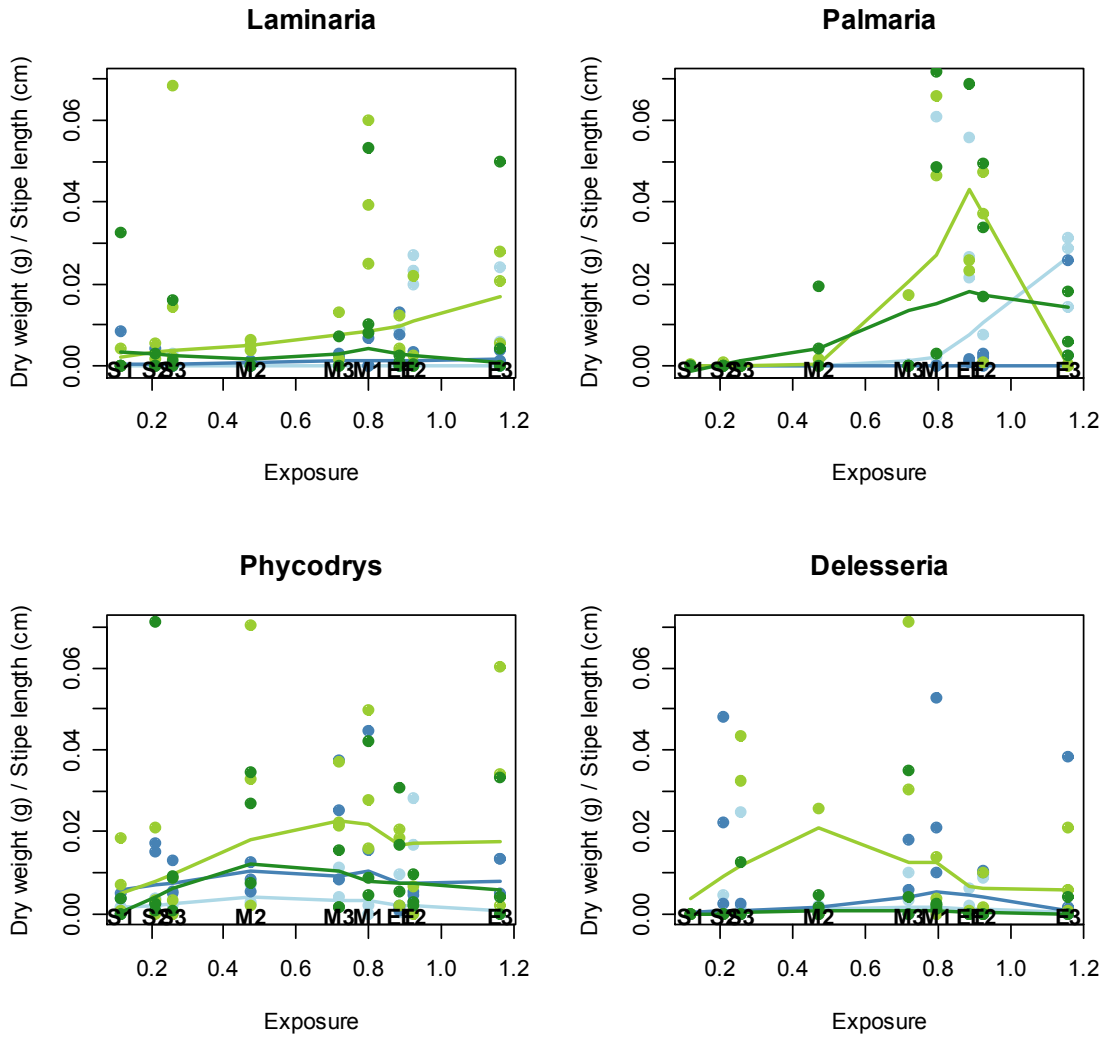


Figure 4.4 Dry weight biomass epiphyte per cm stipe along the gradient of exposure from the four sample periods. The lines are the results of non-parametric smoother functions (in R, “lowess”, which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The ‘smooth’ at each value is influenced by 2/3 of the points.) Light blue – April, dark blue – June, light green – September, dark green – November.

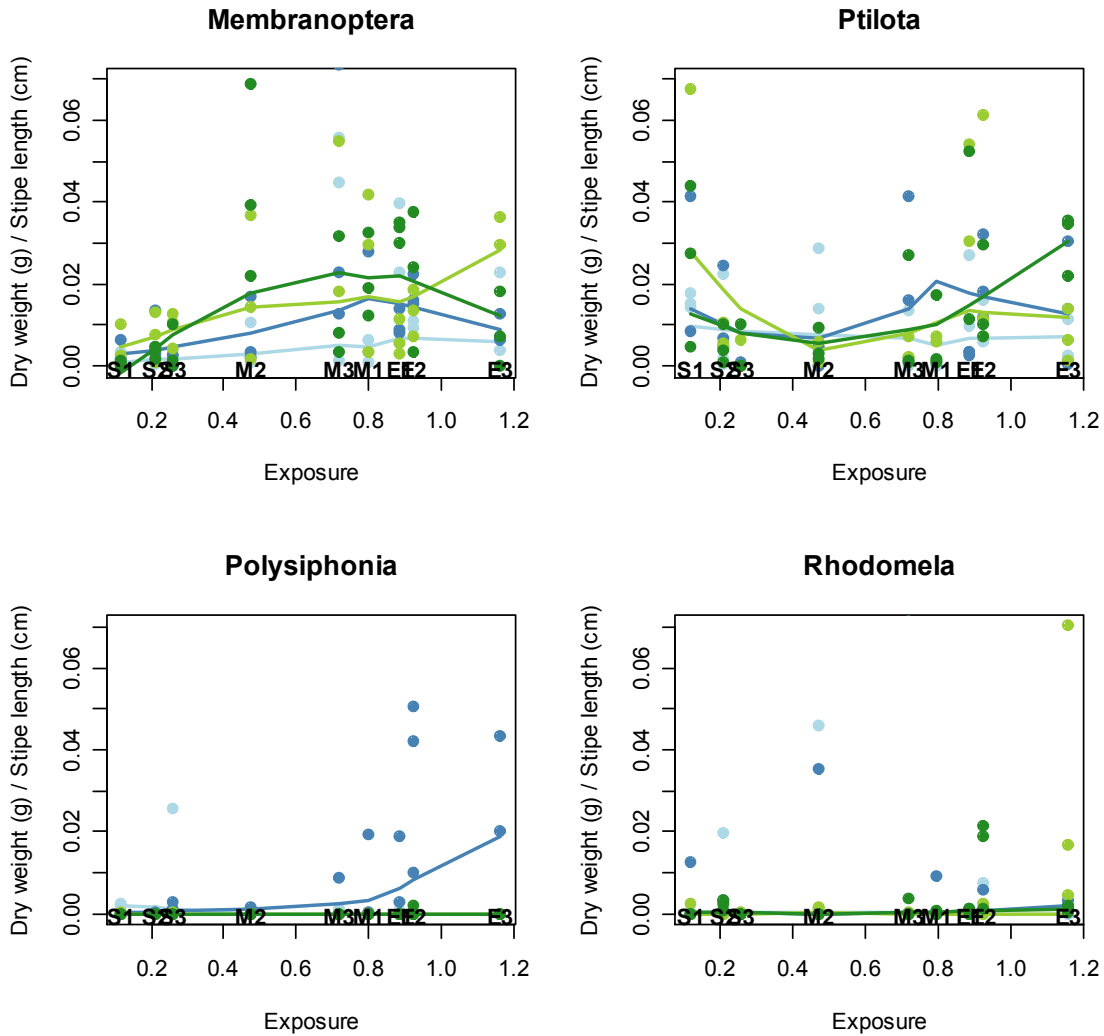


Figure 4.5 Dry weight biomass epiphyte per cm stipe along the gradient of exposure from the four sample periods. The lines are the results of non-parametric smoother functions (in R, “lowess”, which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The ‘smooth’ at each value is influenced by 2/3 of the points.) Light blue – April, dark blue – June, light green – September, dark green – November.

Polysiphonia had its biomass peak in June. *Laminaria*, *Palmaria*, *Phycodryis* and *Delesseria* reached their biomass peaks in September (Figure 4.4) and *Membranoptera* around September-November. Clear seasonal biomass peaks were not evident for *Ptilota* or *Rhodomela* in this study (Figure 4.5).

Laminaria, *Palmaria* and *Polysiphonia* were generally most abundant at the exposed sites, while *Membranoptera*, *Delesseria* and *Phycodryis* seemed more abundant in the moderately exposed areas. *Ptilota* was most abundant in both sheltered and exposed areas. *Rhodomela*

was generally not present in considerable amounts, except at some stipes in sheltered to moderately exposed areas in April and June, and at some exposed sites in September and November, where the values were quite high. A more extensive description is found in Appendix V.

Fixation of carbon

Exposure seems to have little effect on carbon content (%) of algae in this study (Appendix VI, Figure 7.14 and Figure 7.15). Simple linear regressions showed no significant relations ($\alpha = 0.05$), and attempts to estimate epiphyte production in terms of carbon was made on basis of the mean carbon values from September samples for each of the eight dominating species groups. I assumed that most of the identified and sorted material of dominating species was this year's production.

Table 4.4 Mean dry weight biomass of species group (g) per stipe at a station was multiplied by the carbon value (%) for that species group (Appendix VI, Figure 7.14 and Figure 7.15). The results are presented in this table of mean weight carbon (g) contributed by each of the species groups per stipe at the different stations. These data are from samples taken in September. The highest value for each species is in bold formatting.

Station	Laminaria	Palmaria	Phycodrys	Delesseria	Membraopt.	Ptilota	Polysiphonia	Rhodomela	Total
E1	0.30	2.91	0.50	0.02	0.30	3.21	0.00	0.01	7.25
E2	0.38	1.34	0.11	0.16	0.59	1.22	0.01	0.04	3.83
E3	0.68	0.00	0.98	0.33	1.92	0.27	0.00	1.08	5.26
M1	2.05	4.75	1.37	0.27	1.29	0.25	0.00	0.00	9.99
M2	0.17	0.02	0.89	1.46	0.52	0.98	0.00	0.03	4.06
M3	0.21	1.68	0.95	2.32	2.02	0.16	0.00	0.01	7.35
S1	0.03	0.00	0.13	0.00	0.06	1.48	0.00	0.02	1.72
S2	0.05	0.01	0.16	0.63	0.15	0.14	0.00	0.00	1.13
S3	0.49	0.00	0.06	1.07	0.15	0.04	0.00	0.00	1.82

Rough estimates of epiphyte productivity in the study area range from approximately 1 to 10 g C per stipe per year (Table 4.4).

Effects of fixation with formaldehyde

Wet weight

The differences in wet weight before and after fixation were compared (Appendix VI, Table 7.4). The effect of fixation seemed most pronounced in *Palmaria* (30 % reduction), and least in *Ptilota* (1% reduction).

Table 4.5 The differences in wet weight of epiphyte samples before and after fixation were tested by the non-parametric Wilcoxon rank sum (also known as the Mann-Whitney) test ($n=3$). These are the results:

Species	Fresh wet	Fix wet	Wilcox (p-values)
Palmaria	4.01	2.77	0.077
Delesseria	1.89	1.70	0.077
Phycodrys	1.85	1.72	0.100
Membranoptera	1.39	1.28	0.100
Ptilota	1.64	1.62	0.825
Ceramium	12.73	10.73	0.100
Rhodomela	4.59	3.98	0.100

Although raw data suggested a negative effect of fixation on wet weight biomass, especially in *Palmaria*, no significant differences were found when tested with the Wilcoxon rank sum tests (Table 4.5).

Dry weight

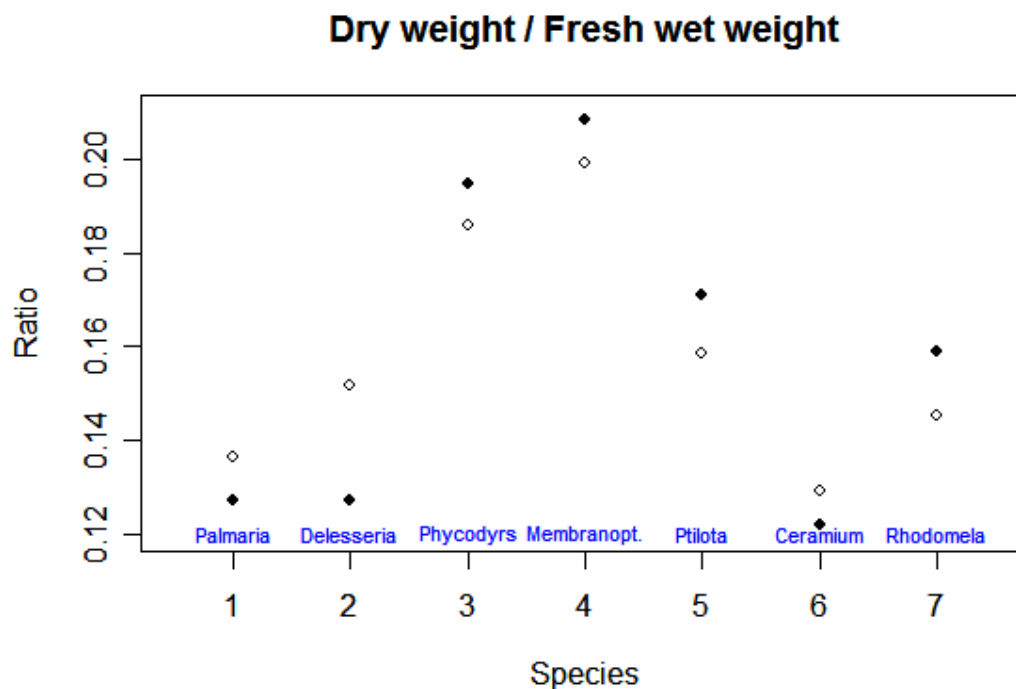


Figure 4.6 Dry to fresh (not fixated) wet weight ratios in the two groups. Open circles represent the samples that were dried fresh. Solid dots represent the samples that were fixed before they were dried.

Looking at the data (Figure 4.6), the differences in weight reduction of fresh and fixated samples, caused by drying, seem minimal. The difference between the mean ratios of the two groups (fresh vs. fixated samples) was not found significant by a Wilcoxon rank sum test (p-value close to 0.9).

Carbon content

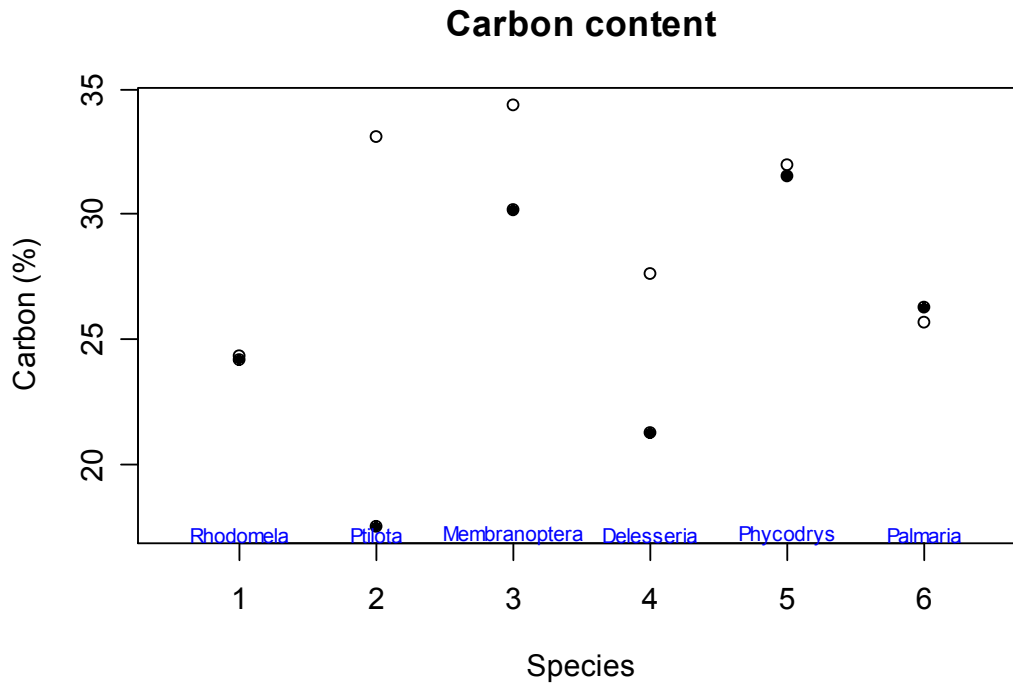


Figure 4.7 Results from carbon analyses. Open circles represent carbon data from samples not fixated. Solid dots represent carbon data from samples fixated with formaldehyde.

The effect of formaldehyde fixation on carbon content of the investigated algae seems to vary, but is mostly negative (Figure 4.7). Comparison between the two ‘treatment’ groups (species lumped together) by a Wilcoxon rank sum test showed no significant difference (p-value = 0.15). No general assumptions should really be made from this, since there were no replications.

Epiphytic species composition in relation to environmental variables

A four dimensional detrended correspondence analysis (DCA) ordination of the species matrix (absence/presence) gave the following eigenvalues:

Output from R:

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.1765	0.1348	0.1399	0.1176
Decorana values	0.2217	0.1586	0.1394	0.1158
Axis lengths	2.6750	1.9388	1.9594	2.2424

DCA1 has the highest eigenvalue of the four ordination axes. Thus, it is the “latent variable” that accounts for most variation of species compositions in the dataset. By dividing the eigenvalue of DCA1 by the sum of eigenvalues for all four axes, I found that DCA1 accounted for about 31% of the variation in the ordination. DCA2 and DCA3 are close in explanatory power (each accounting for about 24% of the ordination), so I chose to plot both against DCA1 in ordination diagrams (Figure 4.8 and Figure 4.9). The position of a stipe along the ordination axes gives information about the species composition relative to that of the other stipes in the diagram. When two stipes are placed close together, their epiphytic species compositions should be very similar. This means that the axes actually present the main gradients in species composition.

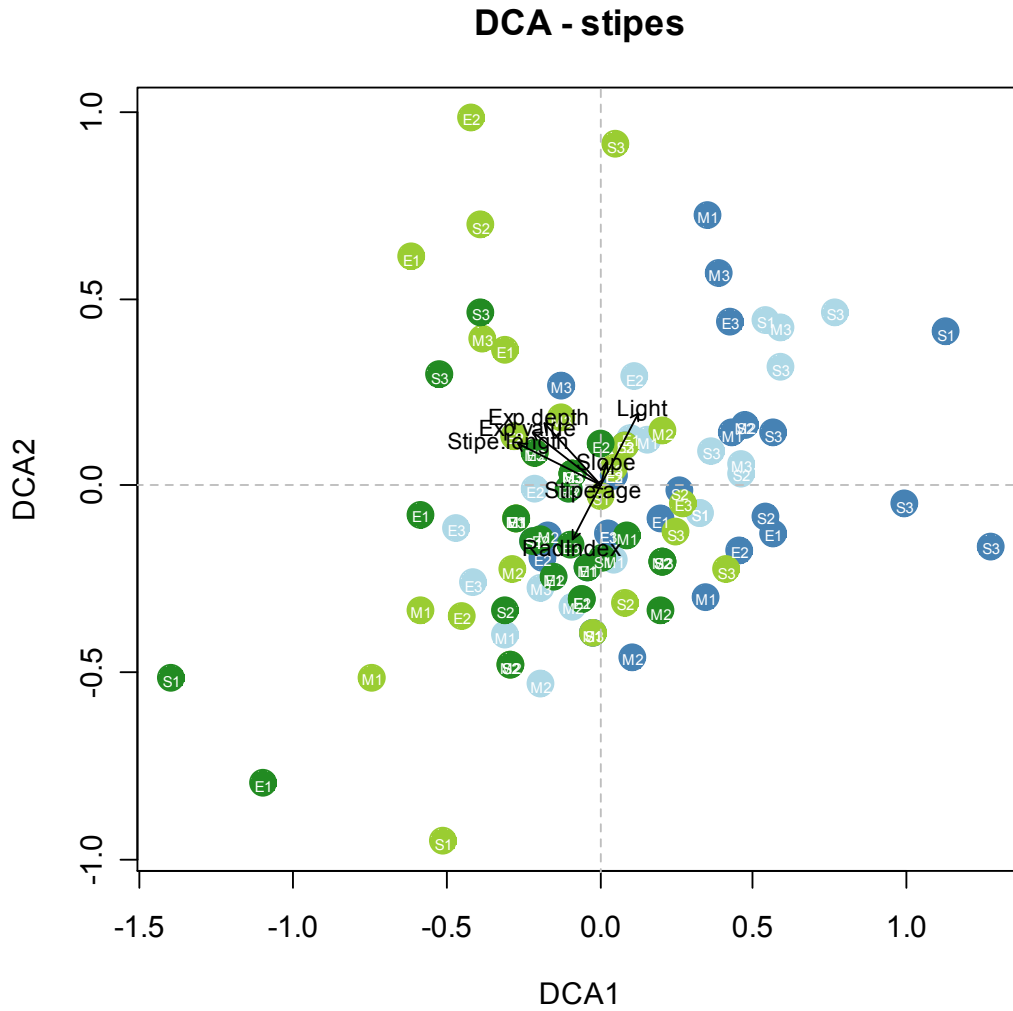


Figure 4.8 DCA-ordination diagram showing two main gradients (DCA1 and DCA2) in species composition (coenoclines). The positions of stipes (samples) are marked by coloured dots with labels, the colour indicating from which month (April – light blue, June – dark blue, September – light green, November – dark green) and the label from which station the sample was taken. The black arrows are environmental vectors pointing in the direction of maximal change of the variable relative to the stipe positions, labelled with variable name (Light, RadIndex, Slope, Exp.value, Exp.depth, Stipe age and Stipe length). Axes units are standard deviation units.

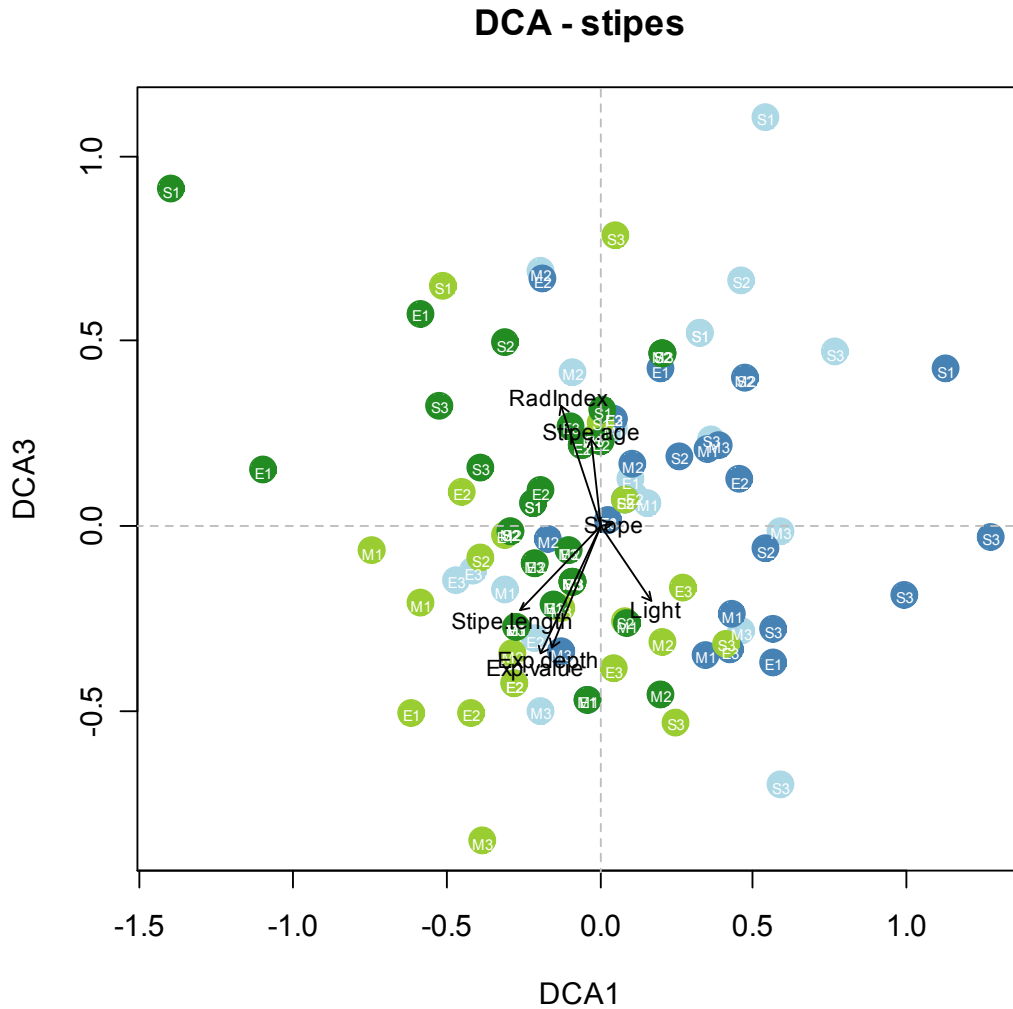


Figure 4.9 DCA-ordination diagram showing two main gradients (DCA1 and DCA3) in species composition (coenoclines). The positions of stipes (samples) are marked by coloured dots with labels, the colour indicating from which month (April – light blue, June – dark blue, September –light green, November – dark green) and the label from which station the sample was taken. The black arrows are environmental vectors pointing in the direction of maximal change of the variable relative to the stipe positions, labelled with variable name (Light, RadIndex, Slope, Exp.value, Exp.depth, Stipe age and Stipe length). Axes units are standard deviation units.

The next step was to relate these gradients to season and environmental variables and find out whether species compositions change through the summer. And furthermore, if any of the main species gradients are related to any of the environmental variables?

Simple analyses of variance on plot positions along the four axes, showed that significant amounts of variation could be related to different sampling periods ($\alpha = 0.05$). Tukeys HSD test for multiple comparisons of sample means gave the following results (Figure 4.10):

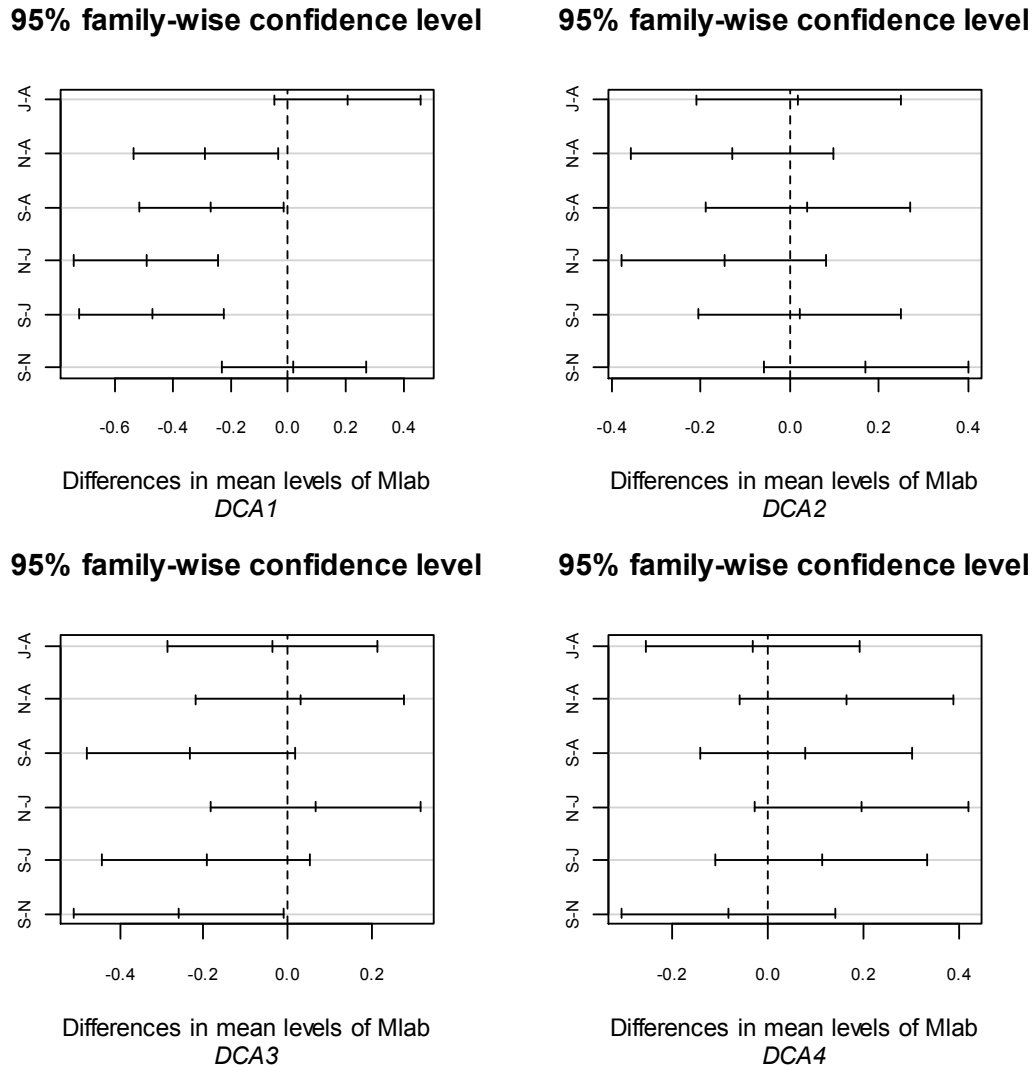


Figure 4.10 TukeyHSD test results of differences in stipe positions along ordination axes between months. Bars showing 95% confidence interval and ticks in the middle marking the mean differences in the positions between the sampling periods. (Mlab – sampling period, A – April, J – June, S – September, N – November). If the bar does not include 0.0, the difference between the mean positions of those two sampling periods are significantly different ($\alpha = 0.05$).

Only DCA1 and DCA3 seemed to have some variation significantly related to sampling period ($p < 0.05$). Along DCA1 there were significant differences between samples from April and September, and from April and November, and between samples from June and September and June and November. No significant differences between April and June or

September and November samples. Hence, the groupings of samples in relation to DCA1 were April-June toward the right and September-November towards the side left of the axis (Figure 4.9). Along DCA3 there was a significant difference only between the September and the November plots. The samples from November were placed slightly above the ones from September. 26 % of variation in positions on DCA1 and 8 % on DCA3 were significantly related to sampling period in this study (Table 4.6).

The short lengths of environmental vectors (Figure 4.8 and Figure 4.9) suggest little influence of the environmental variables on species composition. Few of the vectors point in directions approximately parallel to any of the ordination axes (which would have indicated a strong correlation with them). These observations suggest weak relationships between the environmental variables and the main gradients. This was established by testing each variable against the axes with split-plot GLM.

Of the variables included (Table 4.6) only “Stipe age” and “Stipe length” vary at each level of sampling. The modelled variables have fixed values through all sampling periods. Hence, *they* vary only *between stations*.

Table 4.6 Table of split-plot GLM output from R. Relationships between placement of stipe plots along four the ordination axes (DCA) and each of the environmental variables were evaluated at three levels of sampling. Numbers in green boxes are fraction of total variation along axis explained at that level. Significant variables are marked by red bold italic *p*-values ($\alpha=0.05$).

(*Eff* – effect along axis, *SSexp* – Sum of Squares explained by variable at level, *SSres* – residual Sum of Squares at level, *FVE* – Fraction of variation at level explained by variable, *F* – *F* statistic for test of the hypothesis that *Eff* = 0 against the two-sided alternative, *P* – *p*-value, * - no variation in variable)

Splitplot GLM	Between sampling periods						Between stations within sampling periods						Within stations					
	Eff	SSexp	SSres	FVE	F	P	Eff	SSexp	SSres	FVE	F	P	Eff	SSexp	SSres	FVE	F	P
DCA1	4.48	13.00	0.26				6.59	10.88	0.38				6.41	11.07	0.37			
Slope	* 0.000	4.475	0.000	*	*		+ 0.025	6.565	0.004	0.120	0.732	*	0.000	6.405	0.000	*	*	
Stipe age	- 2.265	2.211	0.506	2.049	0.289		- 0.362	6.228	0.055	1.803	0.189	+	0.409	5.996	0.064	4.846	0.031	
Exp.value	* 0.000	4.475	0.000	*	*		- 0.868	5.723	0.132	4.699	0.038	*	0.000	6.405	0.000	*	*	
Stipe length	- 1.504	2.971	0.336	1.012	0.420		- 1.186	5.405	0.180	6.802	0.014	+	0.117	6.289	0.018	1.318	0.255	
Exp.depth	* 0.000	4.475	0.000	*	*		- 0.575	6.015	0.087	2.965	0.095	*	0.000	6.405	0.000	*	*	
Light	* 0.000	4.475	0.000	*	*		+ 0.520	6.071	0.079	2.654	0.113	*	0.000	6.405	0.000	*	*	
RadIndex	* 0.000	4.475	0.000	*	*		- 0.279	6.311	0.042	1.371	0.251	*	0.000	6.405	0.000	*	*	

DCA2	0.474	10.829	0.04			3.762	7.542	0.33			7.067	4.236	0.63		
Slope	* 0.000	0.474	0.000	*	*	+ 0.040	3.722	0.011	0.332	0.569	* 0.000	7.067	0.000	*	*
Stipe age	- 0.245	0.229	0.517	2.142	0.281	- 0.091	3.670	0.024	0.772	0.386	+ 0.083	6.984	0.012	0.848	0.360
Exp.value	* 0.000	0.474	0.000	*	*	+ 0.045	3.717	0.012	0.372	0.546	* 0.000	7.067	0.000	*	*
Stipe length	- 0.103	0.372	0.217	0.553	0.535	+ 0.008	3.753	0.002	0.069	0.794	+ 0.002	7.065	0.000	0.019	0.891
Exp.depth	* 0.000	0.474	0.000	*	*	+ 0.127	3.634	0.034	1.086	0.306	* 0.000	7.067	0.000	*	*
Light	* 0.000	0.474	0.000	*	*	+ 0.436	3.325	0.116	4.065	0.053	* 0.000	7.067	0.000	*	*
RadIndex	* 0.000	0.474	0.000	*	*	- 0.239	3.523	0.063	2.098	0.158	* 0.000	7.067	0.000	*	*
DCA3	1.117	12.784	0.08			6.390	7.511	0.46			6.394	7.507	0.46		
Slope	* 0.000	1.117	0.000	*	*	+ 0.000	6.390	0.000	0.002	0.969	* 0.000	6.394	0.000	*	*
Stipe age	+ 0.144	0.974	0.129	0.295	0.642	+ 0.551	5.839	0.086	2.928	0.097	+ 0.214	6.179	0.034	2.463	0.121
Exp.value	* 0.000	1.117	0.000	*	*	- 1.597	4.793	0.250	10.327	0.003	* 0.000	6.394	0.000	*	*
Stipe length	- 0.054	1.063	0.049	0.103	0.779	- 0.571	5.819	0.089	3.044	0.091	- 0.066	6.328	0.010	0.738	0.393
Exp.depth	* 0.000	1.117	0.000	*	*	- 1.458	4.933	0.228	9.160	0.005	* 0.000	6.394	0.000	*	*
Light	* 0.000	1.117	0.000	*	*	- 0.499	5.891	0.078	2.628	0.115	* 0.000	6.394	0.000	*	*
RadIndex	* 0.000	1.117	0.000	*	*	+ 1.403	4.988	0.219	8.717	0.006	* 0.000	6.394	0.000	*	*
DCA4	0.615	10.203	0.06			4.004	6.813	0.37			6.198	4.619	0.57		
Slope	* 0.000	0.615	0.000	*	*	- 0.670	3.334	0.167	6.233	0.018	* 0.000	6.198	0.000	*	*
Stipe age	+ 0.327	0.287	0.533	2.280	0.270	- 0.000	4.004	0.000	0.000	0.998	+ 0.047	6.151	0.008	0.544	0.463
Exp.value	* 0.000	0.615	0.000	*	*	+ 0.048	3.957	0.012	0.376	0.544	* 0.000	6.198	0.000	*	*
Stipe length	+ 0.339	0.276	0.551	2.452	0.258	+ 0.197	3.807	0.049	1.608	0.214	+ 0.073	6.125	0.012	0.850	0.360
Exp.depth	* 0.000	0.615	0.000	*	*	+ 0.164	3.840	0.041	1.325	0.259	* 0.000	6.198	0.000	*	*
Light	* 0.000	0.615	0.000	*	*	+ 0.149	3.855	0.037	1.202	0.281	* 0.000	6.198	0.000	*	*
RadIndex	* 0.000	0.615	0.000	*	*	+ 0.319	3.685	0.080	2.685	0.111	* 0.000	6.198	0.000	*	*

26% of total variation along DCA1 could be related to different sampling periods. None of the variables included in this study explained any significant amounts of this variation. 38% of the variation could be related to differences between stations. Of these, 13% was explained by “Exp.value” alone (which means 5% of total variation along DCA1) and 18% by “Stipe length” alone (7% of total). These variables were strongly correlated (Figure 4.1), and thus likely to explain much of the same variation. 37% of total variation was related to differences within stations. 6% of the variation within stations could be explained by “Stipe age” (2% of total along DCA1).

Even though ordination axis DCA2 explains the second most variation in species composition between stipes, the distribution of plots along this gradient showed no significant relation to any of the environmental variables in this study. Only 4% of total variation along this axis was related to different sampling periods, while 33% was related to differences at the station level and 63% to differences at the within stations level.

DCA2 and DCA3 got almost the same eigenvalues, which means that they explain about the same *amount* of variation. 8% of variation in stipe positions along DCA3 was related to sampling period, 46% to differences at the between stations level and 46% to differences at the within stations level. No variation between sampling periods or within stations seemed explained by any of the variables. But, for differences in species compositions *between* stations, “Exp.value”, “Exp.depth” and “RadIndex” seemed to be of significant influence. “Exp.value” explained 25% of this variation (11 % of total along DCA3) and “Exp depth” 23% (10% of total). These two are naturally strongly correlated. “RadIndex” did also explain significant amounts, 22%, of the variation in species composition in samples from different stations along DCA3 (10% of total).

For DCA4, 6% of the total variation was related to differences in stipe positions between sampling periods, 37% to differences in positions between stations and 57% to differences within stations. Slope was the only variable that could significantly explain variation along DCA4, and this was 17% at the between stations level (6% of total along DCA4).

None of the environmental variables in this study could explain the differences in positions of stipes between sampling periods. For DCA1, most of the variation was found between stations (38%). Along DCA2, most of the variation existed within stations (63%). Along DCA3, stipe positions varied just as much within stations as between stations (46%), while positions along DCA4 varied the most within stations (57%).

Variation between sampling periods

Number of species observed was approximately the in same all sampling periods. Fourteen species were found in April, 20 both in both June and September and 16 were found in November. A GLM-model showed no significant influence of sampling period on species number in samples ($\alpha = 0$).

As for the number of observations of each species, the results are summed up in Table 4.7.

Table 4.7 The table shows number of samples that the species were observed in each sampling period. Species names by three- or four-letter abbreviations (see Appendix VII).

	Mem	Div	Pti	Phyc	Del	Pal	Pol	Rho	Lam	Lom	Nit	Cal	Ect	Sph	Des	Cys	Plo	Phyl	Fuc	Ala	Cer	Cry	Apo	Tra	Dic
Apr	27	26	23	21	17	14	11	11	9	4	4	3	1	1	0	0	0	0	0	0	0	0	0	0	0
Jun	26	27	23	26	16	8	15	14	13	7	5	1	2	0	7	2	1	1	1	1	1	0	0	0	0
Sep	27	27	25	24	20	16	3	11	23	0	12	2	1	1	6	0	0	0	0	1	6	2	2	2	3
Nov	25	26	25	24	9	14	1	13	16	0	2	3	0	0	3	0	1	0	0	1	5	0	0	0	2

There were 27 samples from each sampling period. All dominating species were present in most of them. Only *Polysiphonia* showed a clear trend decreasing in observation frequency from April to November. *Lomentaria* was present in observable amounts (registered dry weights) only in April and June, while *Ceramium* had a noteworthy higher frequency of observable amounts in September and November (Table 4.7)

Delesseria was observed in twice as many samples in September compared to November. *Nitophyllum* also showed up in higher frequency in September. A couple of species were present in September but not in November, while only few species present in November were absent in September.

Variation between stations

Numbers of species in samples were investigated by GLM-modelling. Only the parameters for exposure and stipe length were found significant when tested. “Stipe length” ‘knocked out’ ‘Exp.value’ when the two were combined, accounting for about 74 % of the variation.

“Stipe length”, “Exp.value” and “Exp.depth” seemed to be the variables, among the recorded, explaining most variation in species composition between stations. Since stipe length is strongly related to level of exposure, I added the species observations from each station in a sampling period together, and inspected these summarizing matrices with stations ordered from exposed to sheltered. This was done to point out the most pronounced of the actual differences in species compositions behind the results of the DCA-ordination.

Table 4.8 The table shows number of samples the species were observed in April. Stations are ordered by decreasing degree of exposure according to Isæus model (2004). Species names by three- or four-letter abbreviations (see Appendix VII).

April	Cal	Del	Lam	Lom	Mem	Nit	Pal	Phyc	Pol	Pti	Rho	Sph	Ect
E3	0	1	3	0	3	0	3	2	0	3	0	0	0
E2	1	3	3	1	3	2	2	2	0	3	1	0	0
E1	0	3	1	0	3	0	3	3	1	3	2	0	0
M1	0	1	0	0	3	0	3	1	2	2	0	0	0
M3	0	3	0	2	3	1	1	3	1	2	1	0	0
M2	2	2	1	0	3	0	1	3	0	3	3	0	0
S1	0	0	0	0	3	0	0	3	3	3	1	1	0
S2	0	1	0	0	3	0	1	3	2	3	2	0	0
S3	0	3	1	1	3	1	0	1	2	1	1	0	1

In samples from April, *Laminaria* and *Palmaria* were more frequently observed at stipes from exposed than sheltered locations, while *Polysiphonia* on the other hand was more frequently observed in sheltered areas (Table 4.8).

Table 4.9 The table shows number of samples the species were observed in June. Stations are ordered by decreasing degree of exposure according to Isæus model (2004). Species names by three- or four-letter abbreviations (see Appendix VII).

June	Cal	Cer	Del	Lam	Lom	Mem	Nit	Pal	Phyc	Pol	Pti	Rho	Ect	Des	Ala	Plo	Fuc	Cys
E3	0	0	2	2	1	3	1	3	3	2	3	3	0	0	0	0	1	0
E2	1	0	2	2	0	3	0	2	3	3	3	3	1	0	0	1	0	0
E1	0	0	2	2	1	3	0	3	3	2	3	2	0	2	1	0	0	0
M1	0	1	3	1	1	3	2	0	3	2	3	1	0	2	0	0	0	1
M3	0	0	2	2	0	3	2	0	3	1	3	1	0	0	0	0	0	1
M2	0	0	1	1	0	3	0	0	3	1	1	1	0	0	0	0	0	0
S3	0	0	1	1	3	2	0	0	3	3	1	0	1	2	0	0	0	0
S2	0	0	3	1	0	3	0	0	3	1	3	2	0	1	0	0	0	0
S3	0	0	1	1	3	2	0	0	3	3	1	0	1	2	0	0	0	0

In samples from June, *Delesseria*, *Laminaria*, *Palmaria* and *Ptilota* were all more frequently observed in exposed areas (Table 4.9).

Table 4.10 The table shows number of samples the species were observed in September. Stations are ordered by decreasing degree of exposure according to Isæus model (2004). Species names by three- or four-letter abbreviations (see Appendix VII).

Sept	Cal	Cer	Del	Dic	Lam	Mem	Nit	Pal	Phyc	Pol	Pti	Rho	Sph	Ect	Cry	Apo	Tra	Des	Ala
E3	0	0	3	0	3	3	1	1	3	0	3	3	0	0	0	0	0	2	0
E2	0	2	3	1	3	3	3	3	2	1	3	2	0	1	1	1	1	0	0
E1	0	2	3	0	3	3	2	3	3	0	3	1	0	0	1	0	0	0	0
M1	0	0	2	2	3	3	0	3	3	0	3	0	0	0	0	0	0	0	0
M3	0	0	3	0	2	3	2	2	3	0	3	1	0	0	0	1	0	0	0
M2	1	0	2	0	3	3	3	2	3	0	3	2	0	0	0	0	0	2	0
S3	0	1	3	0	3	3	0	0	2	1	1	1	1	0	0	0	0	1	1
S2	0	1	1	0	2	3	1	1	2	0	3	0	0	0	0	0	0	1	0
S1	1	0	0	0	1	3	0	1	3	1	3	1	0	0	0	0	1	0	0

In September samples, *Delesseria* and *Palmaria* both showed a decrease in frequencies of observation towards the more sheltered stations (Table 4.10).

Table 4.11 The table shows number of samples the species were observed in November. Stations are ordered by decreasing degree of exposure according to Isæus model (2004). Species names by three- or four-letter abbreviations (see Appendix VII).

November	Cal	Cer	Del	Dic	Lam	Mem	Nit	Pal	Phyc	Pol	Pti	Rho	Des	Ala	Plo
E3	0	0	1	0	2	2	1	3	2	0	3	3	0	0	0
E2	0	1	0	0	2	3	0	3	3	1	3	3	1	0	0
E1	1	1	0	1	2	3	0	3	3	0	3	2	0	0	1
M1	0	0	3	0	3	3	0	3	3	0	3	1	2	0	0
M3	0	0	2	0	2	3	0	0	3	0	3	1	0	0	0
M2	0	0	2	0	1	3	0	2	3	0	3	0	0	1	0
S3	0	2	1	0	2	3	1	0	3	0	1	0	0	0	0
S2	1	0	0	0	1	3	0	0	3	0	3	3	0	0	0
S1	1	1	0	1	1	2	0	0	1	0	3	0	0	0	0

In November, *Delesseria* was most frequently observed in stipe samples from moderately exposed areas, while *Laminaria*, *Palmaria* and *Rhodomela* were observed at higher frequencies in the moderately exposed to exposed areas (Table 4.11).

5. Discussion

Epiphyte production

General problems

Assessing the significance of water motion on macroalgal production and community structure *in situ* is a difficult task. Direct measures of macroalgal production are difficult to get. One would often choose to use indications like length-measures or weight, which may not be appropriate. Water motion is in many cases measured indirectly as well. In this study we used estimates from a GIS-model based on fetch and five years of wind data. This model does not take into account the effect of seafloor topography, currents or tidal waves. It is possible to measure water motion directly *in situ*, but this would undoubtedly prove much too costly and time consuming for the present project. “A model is only as good as the data put into it”, meaning that both availability of important explanatory variables and the reliability of these data matter. All modelled data in this study were estimated on the basis of a digital topography model with a resolution of 10 m². Smaller topographic features that could be of importance are likely to be omitted. The values for “Light”, “Exp.value” and “Exp.depth” are estimated as fixed values (averages), even though they most certainly change through the season. The use of a secchi depth of 8.25 m for the whole area of Finnøy in estimating “Light”, is based on unpublished data (pers. comm., Bekkby 2007). However, the secchi depths are likely to vary between stations and definitely throughout the season. Uncertainties at all these levels contribute to unreliability of the models in this study.

Even though the total biomass epiphytes comprised mainly floral matter, some bryozoans, sponges and tunicates were present. Bryozoans covering the algae probably made some contributions to the weight, but reliable estimates were impossible to make. In the following, “total epiphyte biomass” will be discussed as though only floral species were present.

Biomass production

Most of the algal species found to dominate in the present study have been frequently observed in previous studies of epiphytic communities associated with Norwegian *L. hyperborea*. (Mortensen 1992, Gravendeel 1994, Høisæter and Ødegaard 1994, Sørli 1994). The total weight of epiphytes on the kelp stipes clearly changed through the season. From

April to September there was a clear increase in biomass as the growth season progressed, while a decline in biomass was found from September to November. This decline is most probably related to a decrease in temperature, which would slow down the growth rates in most of the epiphytes, and to an increase in wind and wave activity, that usually occur along the Norwegian coast as the winter sets in, which would increase tear and dislodgement of the algae. Most dominating species in the area of Finnøy had their biomass peak in September, as in the study by Sørli (1994) from Vega and the study by Whittick (1983) from the coast of Scotland, though some variation did occur.

Total biomass of epiphytes in gram dry weight per stipe was found to increase with increasing levels of exposure. This increase proceeded until the 'moderately exposed' to 'exposed' levels of wave exposure were reached, from where on total biomass decreased somewhat towards the most exposed stations. The lengths of kelp stipes were also shown to increase with increasing levels of exposure. The model revealed that the amount of epiphytic biomass found on a stipe first of all was related to the length of the stipe. Hence, the observed increase in biomass with increasing levels of exposure was convincingly more related to an increase in substrate size than anything else.

Of the modelled environmental variables, only "RadIndex" was proven significant and thus included in the biomass model. However, I am critical to the correctness of this effect. "RadIndex" is a parameter explaining light conditions relative to optimal conditions for solar irradiation (see pg 18). I find it peculiar that production should decrease as the light conditions get closer to optimal, which would mean that production at some point was limited by solar irradiation. On the basis of light measurements at 550 nm wavelength, Norton (1977) suggested that merely 5% of the light entering the sea surface reaches the epiphytes. These results concur with measurements at Finnøy in 2006. Since most of the light does not reach the epiphytes, the relative amount of solar irradiation experienced by the epiphytes have to be quite small even when the topographical conditions for receiving maximal solar irradiation are optimal. I seriously doubt that light will ever reach intensities that may harm algae beneath the canopy in these areas. I do not believe that the negative effect found in June has anything to do with solar irradiation. I believe that this result is an artefact created by peculiarly high amounts of biomass at all three plants from M1 in June. Since this station had the lowest value of "RadIndex", and there was a gap between this station and the others on the scale of "RadIndex", M1 had a particularly strong effect on this parameter estimate

(Appendix II). Furthermore, in September and November, the parameter estimates for “RadIndex” were very close to zero, while in April it was slightly positive (though not significant) (Table 4.1). When many variables are included in building a model, the probability that at least one may come out as significant, even if in fact it is not, does increase. One should not trust models blindly, but inspect data and summary statistics thoroughly and use logic and reason before drawing any conclusions. On the basis of my own logic and reasoning I concluded that the significance of the RadIndex, that was suggested by the model, should not be trusted.

The question remain: Can exposure significantly explain any additional biomass variation in this study? When modelled, the answer was no, statistically it could not. However, when the epiphyte weights (g) were normalized by stipe lengths (cm), there were still biomass peaks (in g cm^{-1}) at the moderately exposed areas. These patterns suggest a somewhat unimodal response to exposure with optimum in the moderately exposed areas. Such responses are impossible to model adequately by the method used here. This means that the lack of parameter significance in the model could be due to lack of model fit just as well as to no actual effect of exposure on epiphytic biomass. However, the Tukey HSD-test of biomass to stipe length ratios showed significant differences only between the sheltered stations and the M1-station (moderately exposed) (Appendix II, Figure 7.6). Furthermore, since the mean ratios were at least twice as high in moderately exposed areas compared to sheltered areas, and this difference seemed to be part of a pattern related to wave exposure (Figure 4.3), I find this topic in need of further discussion.

As pointed out earlier, thick DBLs have often been regarded as explanations for reduced production and growth rates in slow water flows. However, water flows sufficiently slow to cause persistent DBLs able to inflict nutrient and carbon limitations on macroalgal growth are not likely to occur frequently *in situ*. Norwegian kelp forests form at relatively exposed sites, and macroalgae within these forests are in particular not likely to experience these kinds of constraints.

Differences in light climate as a consequence of different degrees of wave activity (Lobban and Harrison 1994, Falkowski and Raven 1997) might be offered as an explanation for different levels of production at the stations (Falkowski and Raven 1997). However, all stations were exposed to a lot of wave activity, and the differences from station to station were probably not large enough to cause differences in light climate that would be significant

to epiphyte productivity. On the other hand, there is another factor related to exposure that could be of greater importance in determining the light climate beneath the canopy in kelp forests. If, as suggested by Sjøtun *et al* (1998), canopy biomass is the most influential factor for the growth of small kelp plants in a kelp forest, the same factor might influence the floral epiphyte growth as well. We do know that there usually is considerable differences in lamina morphology between sheltered and exposed sites, (Kain 1971a) and that laminas are generally larger at sheltered localities. If the densities of kelp plants are the same at all sites, the logical consequence would be more shading, poorer light conditions, and probably lower epiphytic productivity beneath the canopy in sheltered areas. However, Foldager Pedersen (pers. comm., 2007) and his team did some light measures beneath the canopy at exposed and sheltered stations in 2006 (the year after my samples were taken) and found no obvious differences. Still, I find it important to point out these two factors as possible explanations for differences in epiphyte productivity along a gradient of exposure.

It is important to remember that the recorded biomass is a function of at least two things; 1) production of biomass and 2) loss of biomass. Loss of biomass is mostly due to wear and dislodgement caused by water movement and to herbivore activity. Potential epiphyte consumers in the Norwegian kelp forest are amphipods, isopods, limpets, sea slugs, crabs and sea urchins. Different levels of herbivore activity associated with different levels of exposure is a topic that really deserves attention. Although number of small faunal individuals associated with kelp would be expected to increase as the volume and cover of floral epiphytes increase (Høisæter and Ødegaard 1994, Christie *et al.* 2003), to my knowledge, there have not been attempts to quantify these differences over a gradient of exposure. Besides, the total number of animals in samples from only one point in time says little about for instance the herbivore pressure that can be expected on the algae. The number of individuals per volume epiphytes could give an indication, but not convincingly without data on feeding strategies of herbivores and omnivores, their rates of reproduction and loss rates due to predation and other factors. In other words, these systems are very difficult to unwind. I will precede this discussion by applying pure reasoning, since little of relevance was found in the literature.

Relatively calm water columns will probably provide more energetically advantageous foraging conditions for herbivore organisms *and* their predators (Menge and Sutherland 1987). Kelp forests are assumedly quite effective dampers of wave energy (Eckman *et al.*

1989), though Mork (1996) and Andersen *et al* (1996) found them ineffective when it comes to large swells. The level of wave induced water movement beneath the canopy layer is probably relatively similar regardless of surface conditions. Differences in wave exposure, on the scale of the present study, may therefore be insignificant to relatively stationary herbivores (and omnivores), like limpets, amphipods and isopods living there. Subjected to occasional disturbances, these small organisms may exploit the shelter of aggregated algae (turfs and epiphyte assemblages) and kelp hapters, whereas larger animals probably gain little from these micro refuges. For relatively large grazers, and potential predators of grazers, an occasional increase in environmental stress (for instance from swells or storms) and conditions above the canopy could be of greater importance. Both swells and storms are likely to affect the exposed sites more than the sheltered areas. Perhaps these larger animals would be better off in the more sheltered sites, where their ability to move above the dense forest can be exploited at lower energy costs, and where they are less subjected to short-term increases in water movement stresses. If densities of animals preying on small grazers are higher, the total number of small grazers could be higher in sheltered compared to exposed areas over a long period of time, in spite of fewer counts of small herbivores at *one point in time*. Furthermore, pressure opposed by the herbivorous sea urchins may be higher in sheltered areas (Sivertsen 1997). If herbivores (and omnivores) are more abundant over a longer period of time, and grazing by sea urchins is more extensive at sheltered sites, the result would be higher grazing pressure on algae in these areas (Lubchenco and Gaines 1981). Epiphytes at exposed sites, on the other hand, are probably slightly more subjected to the forces of water movement (especially from large swells and storms) which also increase loss rates through wear and dislodgement (Wheeler 1988).

I find it likely that the observed pattern of biomass (Figure 4.1), if real, is more related to differences in loss rates than productivity at the sites. If true, the reasoning in the above paragraph explains the observed variation in biomass per cm kelp stipe (increasing from sheltered to moderately exposed before decreasing towards the most exposed stations) without attributing it to different levels of production, which would contradict the theory supported by Hurd and others. It is important to keep in mind, however, that my observations did vary quite a lot. After all, only the differences between the S-stations and M1 were proven statistically significant, and only when all sampling periods were lumped together. Nevertheless, I find it too much of a coincidence that random variation should produce so similar patterns in June, September and November.

Previous studies have pointed to the age of the kelp stipe as one of the most important factors determining the amount and coverage of floral epiphytes associated with it (Whittick 1983, Mortensen 1992, Gravendeel 1994, Høisæter and Ødegaard 1994, Sørli 1994). In the present study, age had no significant effect on total epiphyte biomass. However, the stipe age range of sampled kelps was quite narrow (5-10 years), and I see no immediate ground for arguing against hypotheses suggesting it as important. I would, however, be careful about stating the count of growth rings as the ultimate method for determining age. The number of growth rings could be more related to different growth conditions and growth strategies in periods of the kelps life than actual years lived (pers. comm. Fredriksen 2007).

Whittick (1983) suggested competitive interactions between *Ptilota* and *Palmaria* in shallow waters, and between *Ptilota*, *Membranoptera* and *Phycodrys* in deeper waters. The results from my studies support this to some extent. *Ptilota* is most abundant in the sheltered and exposed areas, while biomass per stipe length is considerably lower in moderately exposed areas. This distribution could indicate some kind of competitive interaction with the species having their optima in the moderately exposed areas, namely *Membranoptera*, *Delesseria* and *Phycodrys*. *Ptilota* and *Palmaria* 'colonize' much the same parts of the stipe and competitive interactions between the two (as suggested by Whittick 1983) would explain the general absence of *Palmaria* from sheltered localities. *Palmaria* may have been absent simply because *Ptilota* and other species occupied the substrate of these areas first, and left no room for *Palmaria* sporelings to settle. Another possible scenario is that the herbivore pressure was greater on juvenile *Palmaria*, giving more space to *Ptilota*. However, I have not found any literature that supports the latter. *Palmaria* grows in highest abundances on the youngest part of the stipe, close to the lamina, where the surface is smooth (Harkin 1981, Whittick 1983, Høisæter and Ødegaard 1994). Smooth surfaces are considered less suitable as epiphyte substrate (e.g. Whittick 1983). In support of this, few epiphytes other than *Palmaria* were registered at the upper parts of stipes in the study by Sørli (1994) even though the light conditions probably are better there. *Palmaria* have quite high limits for light saturated photosynthesis compared to other red algae (Johnston et al. 1992), which could make it a relatively poor competitor for space in low light conditions, but probably more successful in better light conditions. This statement is supported by Harkins' study (1981), where *Palmaria* increased in distribution along the stipe when laminas of the kelp hosts had been removed. *Palmaria* is probably better adapted to attachment and persistence at smooth surfaces than the other species. The smooth stipe areas are longer at exposed sites, since the rate of stipe growth

is higher under exposed conditions. Furthermore, movement of lamina might cause more physical damage to algae growing close to it. *Palmaria* has a quite thick and robust thallus which could be able to withstand this kind of stress more than others. This suggests very strongly that *Palmaria* is absent from sheltered areas because *Ptilota* and other epiphytes are stronger competitors for stipe substrate typical for these areas. Even though *Palmaria* loses in competition for space in sheltered areas, it may be able to grow more efficiently in exposed areas. After all, it is able to settle and grow on smooth parts of the stipe where the light conditions are quite good and other algae, like *Ptilota*, struggle to attach and persist.

Laminaria and *Polysiphonia* were also present with higher amounts of biomass in the exposed areas. However, the data especially for *Laminaria* did vary a lot. The biomass patterns of *Membranoptera*, *Delesseria* and *Phycodryis* fit well with the overall picture of highest amounts of epiphyte biomass in moderately exposed areas. Lastly, *Rhodomela* seems to appear more or less randomly. Nevertheless, when it does appear, it is found in quite large amounts. Because it seems to be successful when first settled, this *might* suggest recently low abundances of sporelings in the field area

Fixation of carbon

Rough estimates of epiphyte productivity in the study area range from approximately 1 to 10 g C per stipe per year (Table 4.4, pg 32). Assuming kelp densities of 10 plants m⁻², as done in productivity estimates for *Laminaria hyperborea* (Fredriksen 2003), these estimates adds up to 10 g C in wave sheltered areas to 100 g C m⁻² yr⁻¹ in more exposed areas, which depends mainly on substrate availability in the area. The carbon estimates were computed from average biomass in September, since most dominating species had their biomass peaks in this period. Considering the fact that some species were already on the “retreat” by then, this will contribute to an underestimation of annual production. The biomass in September is naturally not a satisfying measure of annual biomass production for a number of reasons. Considerable amounts of biomass will be removed by herbivore activity, dislodgment and breakage of algae caused by water motion through the summer. Furthermore, some biomass could be remnants of production from other seasons, since some of the species are perennial. However, most of the ‘old’ material would probably have been so deteriorated or overgrown by bryozoans that it would be hard to identify. Unidentified floral material was lumped together with sessile animals in the “various” category. Production estimates in terms of carbon were produced on the basis of dominating species categories only. The process of fixation could have influenced

the carbon content in algae negatively (as in the copepod study by Salonen and Sarvala (1980)), but rudimentary investigations suggested it to be of no significance. The analyzed material was not replicated, so the statistical analysis was performed on the whole group of species, each species regarded as a replica. This is not adequate, and I would recommend further investigation before stating that fixation by formaldehyde does not affect the carbon values in elemental analyses of algae. It is also worth noting that homogenization of samples did not take place before the elemental analyzes. Since different parts of the algae could contain different proportional distributions of the elements, it could influence the results. Nevertheless, I am confident that my estimates are satisfactory.

Epiphytic species composition

Precautions

Previous kelp forest ecologists have chosen the method of constrained ordination for similar studies of epiphyte community structure (e.g. Mortensen 1992, e.g. Gravendeel 1994). Constrained ordination efficiently discard variation in species composition that is not represented by the explanatory variables (Økland 1996 and references therein). Thus, the opportunity to discover gradients the ecologist was not previously aware of, and generate new hypotheses, is lost. When we know so little about which factors may contribute in structuring the algal community, and important variables very possibly can be left out, I find the method of constrained ordination inappropriate.

Ordinations (which are different from constrained ordinations) produce three kinds of ordination axes: 1) Structure axes, which reflect true gradients in the data; 2) polynomial distortion axes, which are mathematical artefacts appearing due to lack of fit of data to the model; and 3) noise axes, which depict random residual variation in the data (Økland 1999 and references therein). Because of polynomial distortion axes, the use of total inertia (summation of axes eigenvalues) as a measure of total variation in a dataset is disputed. In the presence of polynomial distortion axes, the amount of compositional variation extracted on ecologically interpretable ordination axes (structure axes) will be underestimated by the eigenvalue-to-total-inertia ratio (Økland 1999). When I use the terms ‘variation explained’ and ‘variation accounted for’ it is important to keep in mind that I am talking about variation in the ordination. The *amounts* of variation do not necessarily reflect the relations outside ‘the

world' of my dataset, but they do have relevance as relative measures comparable within the dataset.

Use of split plot GLM for the statistical analysis of the ordination was the most appropriate method I could think of. I wanted to take a closer look at the distribution of variation at different levels of the sampling design. I found it valuable to be able to compare variation in species composition between these levels. However, the complexity of the GLM increases the probability of assigning significance to parameters that in fact have no effect and can easily contribute to over-interpretations of the results.

Variation between sampling periods

A DCA ordination of the species matrix revealed significant differences in species composition between sampling periods. Samples from June and April were revealed as significantly different from September and November samples, but the mean difference only explained about 8% of the total variation in the ordination diagram. November and September samples were significantly different from each other, explaining about 2%. Considering the observed frequencies of species each sampling period, some of these differences could be explained in terms of general trends. Of the dominating species only *Polysiphonia* and *Delesseria* seemed to contribute to these trends. I suggest the species composition does change somewhat through the season but that the changes, though statistically significant, are generally small. The number of observed species also changed through the season, but these changes were not considered statistically significant.

Variation between stations

The species composition of floral epiphyte on stipes varied more within than between stations. This means that underlying gradients related to differences between stations, either geographically or ecologically, are less influential than differences on a smaller scale or random events within stations. There probably is one or more gradient structures related to the stations, but they are relatively unimportant for explaining the total variation in species composition. Nevertheless, some of these gradients was significantly explained (in a statistical sense) by the environmental variables included in this study. Exposure, stipe length and RadIndex seemed to be the most important in explaining differences in species composition between stations (2-3% of total variation in the ordination diagram); while stipe age was the only variable that significantly explained any variation within stations (1% of

total variation in the ordination diagram). However significant, the amounts were small compared to both total variation in the ordination and variation along the axes, and perhaps not of ecological importance in determining the species composition on stipes in the age group of five to ten years (growth lines).

Exposure explained more of the variation in species composition between stations than any of the other observed variables (3% of the total variation in the ordination diagram, 11% of the total variation along DCA3 and 25% of the variation between stations along the same axis). In view of this, I found it appropriate to inspect the summary data matrix ordered by decreasing degree of exposure. Some general patterns were revealed. Higher frequencies of some dominating species were evident at the more exposed stations, while other species seemed to appear in observable amounts more or less randomly (Table 4.8 to Table 4.11). *Palmaria* and juvenile *Laminaria* were markedly more often observed at exposed locations in all sampling periods. *Delesseria* showed somewhat the same pattern, but was observed at highest frequencies in moderately exposed areas in November. Other dominating species, namely *Membranoptera*, *Phycodrys* and *Ptilota*, were present at most stipes at all stations in all sampling periods. The number of species observed at a stipe was significantly related to stipe length, probably as a consequence of more available substrate, and perhaps more heterogeneous substrate (as argued in the discussion of competitive interactions between *Ptilota* and *Palmaria*) followed by an ease in competitive pressure.

Quite large amounts of variation at different levels could not be explained by any of the variables included here. The most obvious potentially important variable that has not been considered is temperature. I doubt it would have explained differences between stations, since temperatures probably are quite homogenous in the field area, but it most certainly would have been significant in explaining differences between sampling periods. The spatial structure of the field area, and the positions of the stations, could also have been of some consequence to species composition. Currents and local stream patterns may influence spore dispersal by algae and create geographical species patterns (Norton 1992). This would probably not influence the appearance of the dominating species, which are likely to have generally high spore abundances, and are able to persist for several years when first settled. However, geography could be of significance in explaining the distribution of not so common species.

Contrary to earlier studies (e.g. Sørli 1994), no significant relation between number of species and stipe age was found. As previously discussed, the range of plant age in this study was quite narrow, and this could be the reason. However, from analyses of the ordination, age seemed significant in determining species composition of stipes within the stations. Further investigation of species composition in relation to stipe age is beyond the scope of this thesis.

Summary and concluding remarks

Total biomass of epiphytes associated with the stipe of *Laminaria hyperborea* was first of all related to the stipe length. Since kelp respond to increased wave exposure by growing longer stipes, more biomass was found in exposed areas. Most epiphytic biomass was found in samples taken in the month of September.

The amount of carbon fixated by floral epiphytes in the kelp forest was estimated to lie between 10 and 100 g C m⁻² yr⁻¹ depending mainly on substrate availability. The carbon content (%) in algae did not vary significantly along the gradient of exposure in September.

Number of species counts on a stipe was significantly related to the stipe length.

Most dominating species were found in high relative abundances at most stipes at all stations and in all sampling periods. However, there were some exceptions. Especially *Palmaria palmata* and juvenile *Laminaria* sp were found more frequently and in higher relative abundances in exposed than in sheltered areas.

The hypothesis of competitive interactions between *Palmaria palmata* and *Ptilota gunneri* suggested by Whittick (1983) was supported by this study. In the present study indications of competitive interactions between *Ptilota gunneri* on one side and *Membranoptera alata*, *Delesseria sanguinea* and *Phycodryis rubens* on the other side were also suggested at 5 m of depth.

Species composition of floral epiphytes associated with the kelp stipe showed some seasonal variation, but the species numbers did not vary significantly.

Some differences between stations in species compositions were found. The variation was more related to the degree of wave exposure than any other measured or modelled variable in

this study. However, the amount of variation accounted for was very small, because only few of the recorded species showed a systematic presence/absence-response to exposure.

The species composition seemed to vary just as much within as between stations. I suggest that differences in species composition between different stations are generally small, and that environmental variation on a smaller scale or random events may be just as important in determining species composition at stipes in the age group of five to ten years.

I conclude that both epiphyte abundances (in biomass) and the species composition of floral epiphytes vary with exposure. In the case of biomass this relationship is related to the size of the substrate and possibly also to differences in loss rates between stations. Furthermore, I conclude that seasonal variations occur in both cases.

The kelp forest systems and their structures are determined by a complex of interacting abiotic and biotic factors. The importance of each factor could vary from site to site and between years. To generalize on the basis of just one study, conducted in a rather limited area over a short period of time, would be a seriously blunt simplification and most probably wrong. Nevertheless, it is infinitely important to continue the efforts of trying to unwind the mystery of these complicated interactions. We *need* to understand how the kelp forest system works in order to protect it through environment and resource management. This is imperative for sustaining marine diversity of life along the Norwegian coastline, and in turn, sustaining our coastal communities, their culture, and parts of the national economy.

6. References

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7. Appendix

Appendix I

Table 7.1 *Table of stations with labels, geographical names and geographical coordinates.*

Level of exposure	Station (Φ , γ)	Station (Φ , γ)	Station (Φ , γ)
Sheltered	S1 (Gåsøya) (62.79977°N, 6.524457°E)	S2 (Seterøya) (62.81345°N, 6.559947°E)	S3 (Trollholmane) (62.81771°N, 6.557763°E)
	M1 (Kvaløya) (62.81612°N, 6.513389°E)	M2 (Seterøya) (62.81755°N, 6.529221°E)	M3 (Håværet) (62.82361°N, 6.551579°E)
Moderately exposed	E1 (Grønværet Sør) (62.80545°N, 6.406455°E)	E2 (Grønværet Nord) (62.80896°N, 6.410684°E)	E3 (Bollene) (62.8071°N, 6.400087°E)
Exposed			

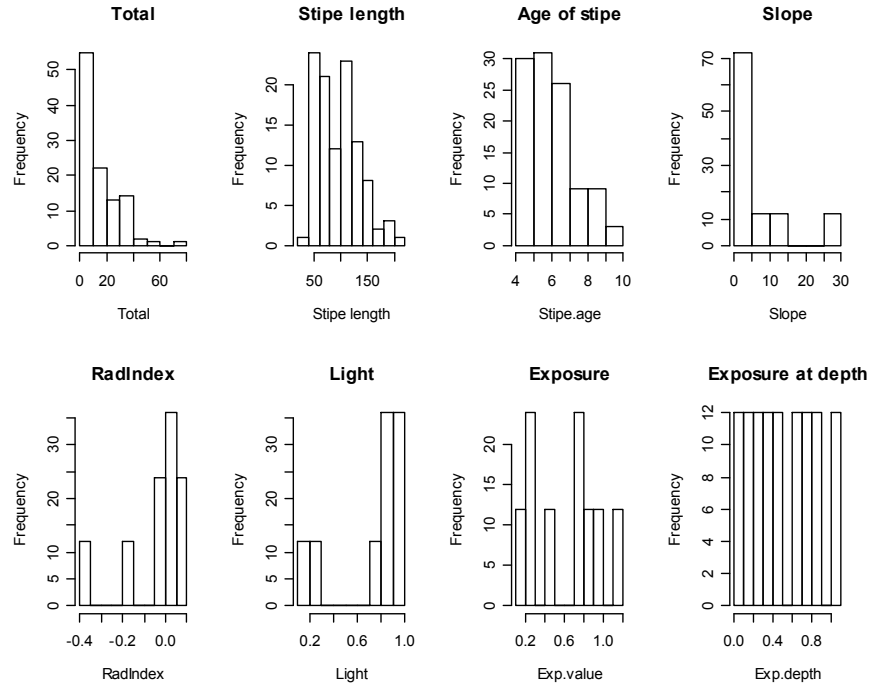


Figure 7.1 This figure displays histograms of all untransformed variables available for modelling. “Total” shows dry weight epiphytes (g) per stipe, the remaining are histograms of environmental variables. The measured variables (“Total”, “Stipe length”, “Age of stipe” and “Slope”) are strongly skewed to the left.

These data (Figure 7.1) were used in GLM-modelling. Transformations of the data are a part of the GLM-method, but occur within the software. The models of dry weight epiphyte biomass were built using the glm function available in R. The Poisson family uses the log link function, which means that the y-variable is log transformed before the linear predictor of the model is estimated. The linear predictor is a linear sum of the effects of the explanatory variables (0.1).

$$\eta_j = \sum_{j=1}^p x_{ij} \beta_j \quad (0.1)$$

Where η is the linear predictor, x are the values of p different explanatory variables, and β are the parameters to be estimated from the data.

To get the fitted value, the linear predictor is computed by applying the reciprocal of the link function (back-transformed). In this case, the fitted value (μ) is the antilog of the linear predictor (0.2).

$$\mu_i = e^{\eta_i} \quad (0.2)$$

As I came to discover, the assumptions made by the Poisson family were not fully met by my data. After model fitting, the data clearly showed overdispersion, which tells us that the error structure is not *really* Poisson. The variance in a Poisson distribution is identical to the mean. In this case, summary statistics of the model showed that the variance was in fact larger than the mean.

I went on building a new GLM model, this time of the Quasipoisson family. The Quasipoisson family differs from the Poisson family in that the dispersion parameter is not fixed at one. This is a quasi-likelihood approach, which permits extra variation by multiplying the variance term by a factor. The fitted values will be identical to those from the Poisson model, but the standard errors will be larger, and as a consequence, the p-values as well. So, terms that might seem significant in the Poisson model, will not in the more appropriate Quasipoisson version.

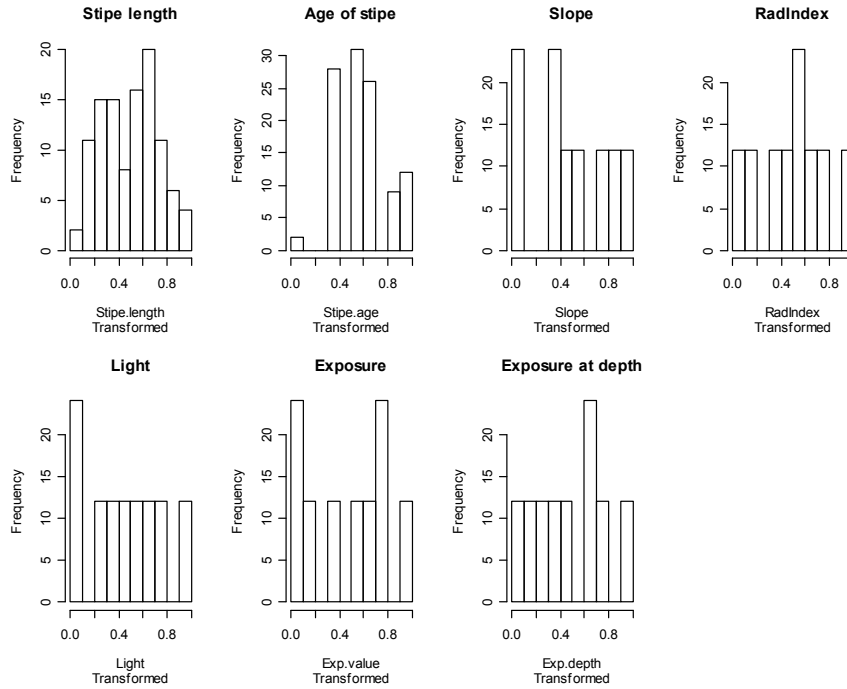


Figure 7.2 Histograms of zero-skewness transformed and scaled environmental variables. “Total” shows dry weight epiphytes (g) per stipe, the remaining are histograms of environmental variables.

Transformed data (Figure 7.2) were used for PCA-ordination and fitting of environmental vectors in the DCA-ordination. The data has to be transformed to meet the requirements of these methods. Transformations were done with the help of Microsoft Excel according to Økland (2001).

Appendix II

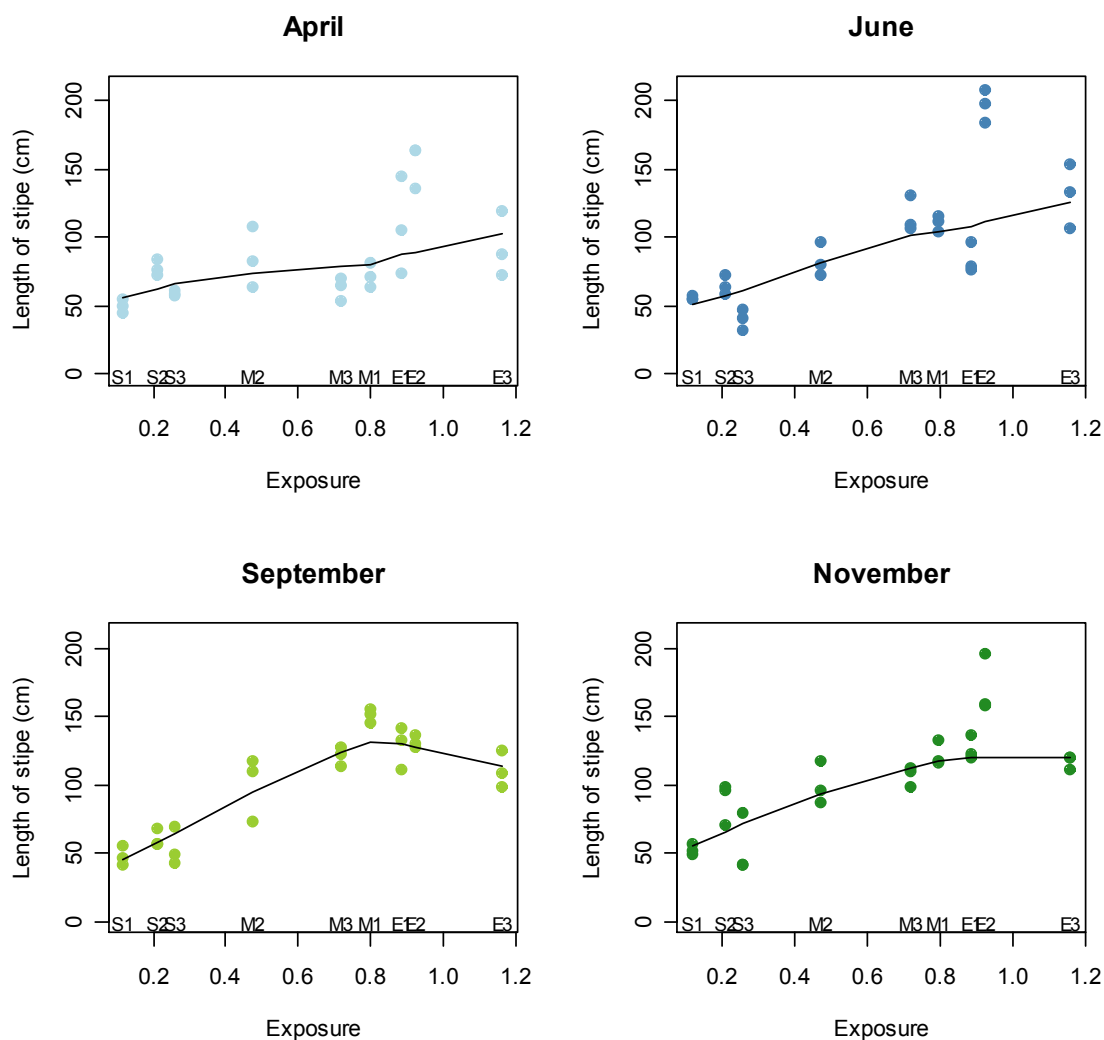


Figure 7.3 These plots show the distribution of kelp stipe lengths with increasing levels of exposure in April, June, September and November. The scale of the “Exposure”-axis is a re-scalation of the relative values estimated from Isæus model of exposure ($SWM5y / 1.000.000$). Station names are plotted along the first axis. The black line is the result of a non-parametric smoother function, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variable on the x-variable. (The ‘smooth’ at each value is influenced by 2/3 of the points.)

In April and June the relationship was rather linear. A peak in stipe length around M1 (exposure of 0.8) was suggested in September. In November, the increase in stipe length reached a limit at M1. E2 had very long stipes all sampling periods.

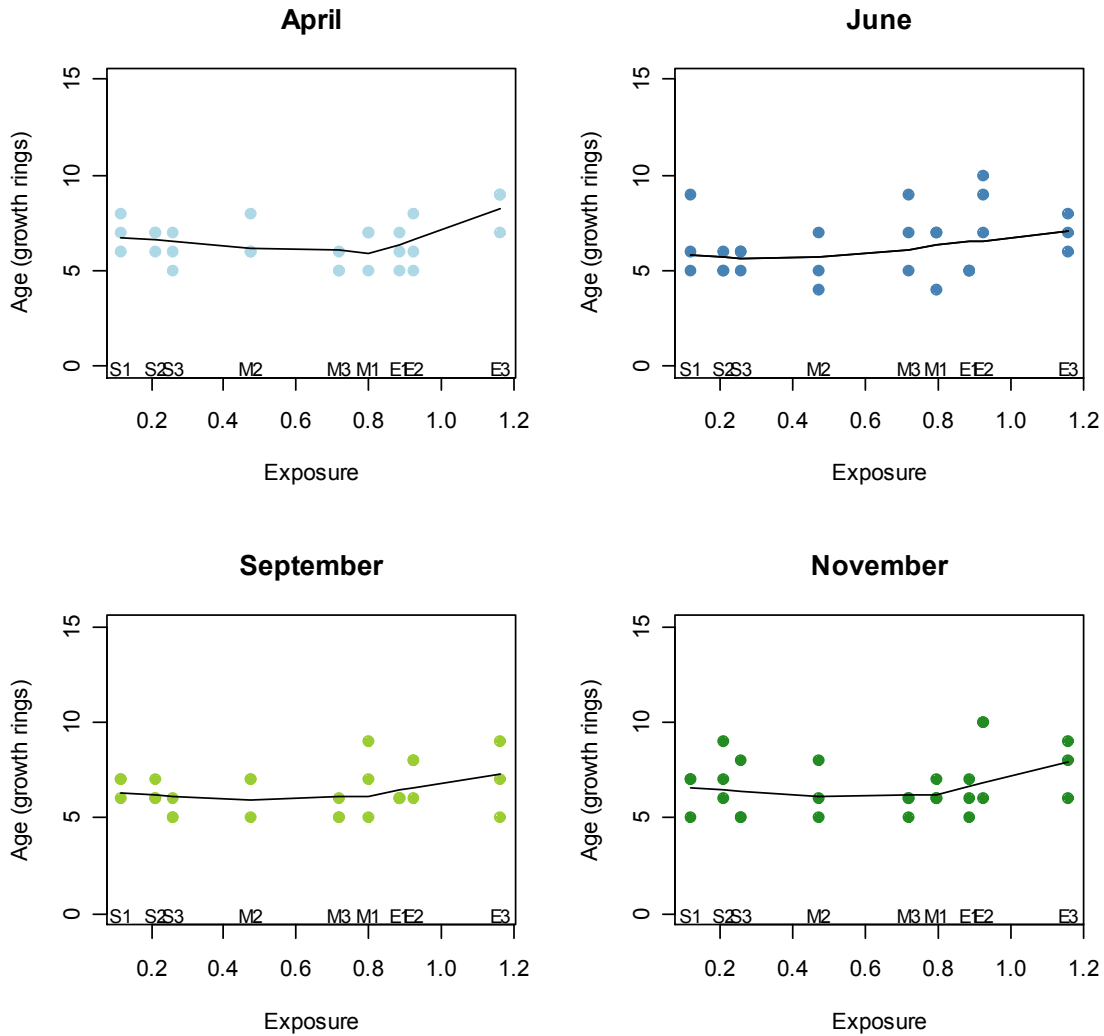


Figure 7.4 These plots show the distribution of kelp age with increasing levels of exposure in April, June, September and November. The scale of the “Exposure”-axis is a re-scalation of the relative values estimated from Isæus model of exposure ($SWM5y / 1.000.000$). Station names are plotted along the first axis. The black line is the result of a non-parametric smoother function, “lowess”, which carries out a locally weighted polynomial regression of the y-variable on the x-variable. (The smooth at each value is influenced by 2/3 of the points.)

A slight increase in kelp age was suggested towards the most exposed stations. However, no significant increases were found by linear regression analyses.

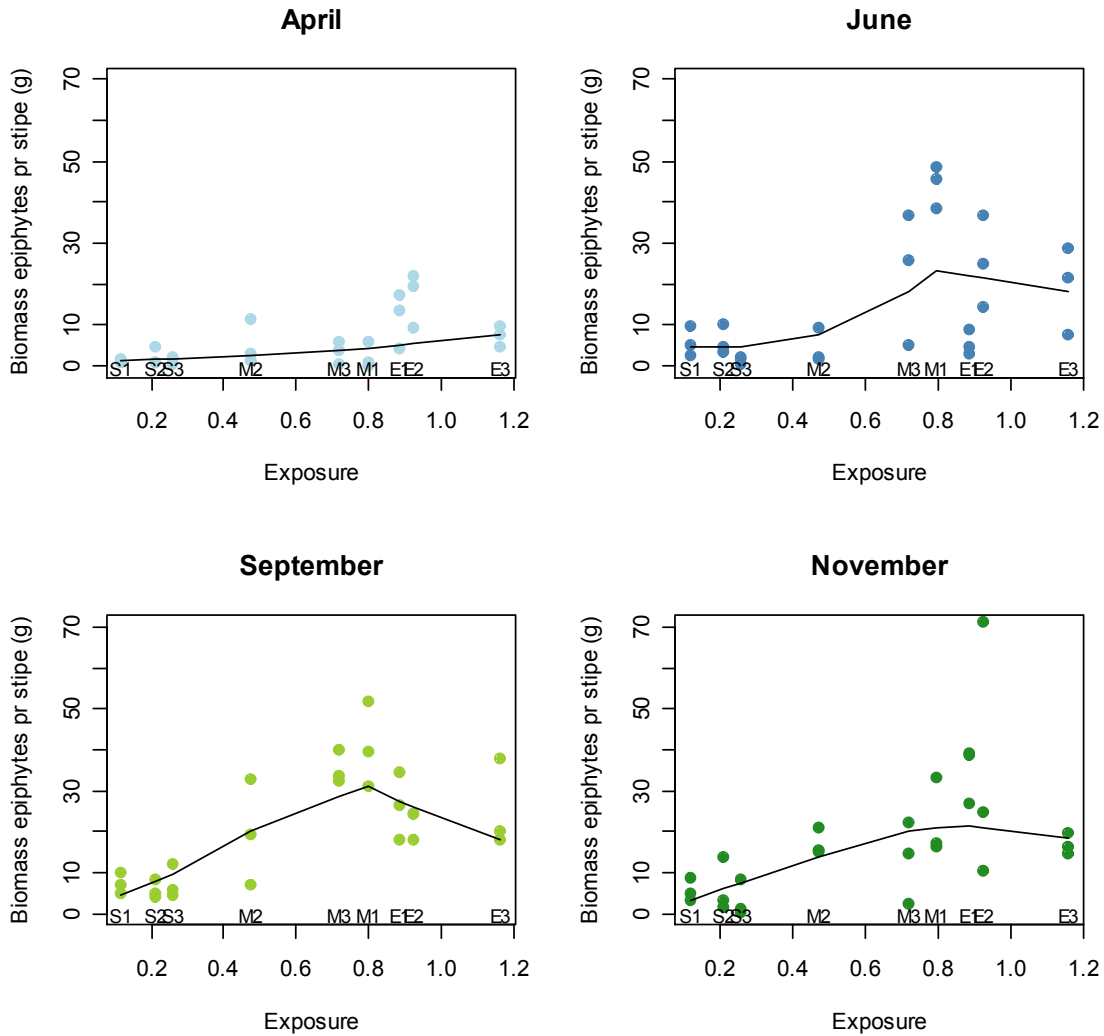


Figure 7.5 Plots of total epiphyte biomass in dry weight per stipe with increasing levels of exposure for April, June, September and November. The scale of the “Exposure”-axis is a re-scalation of the relative values estimated from *Isæus* model of exposure ($SWM5y / 1.000.000$). Station names are plotted along the first axis. The black line is the result of a non-parametric smoother function, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variable on the x-variable. (The smooth at each value is influenced by 2/3 of the points.)

In April the relationship seems somewhat linear. In June, September and November a peak in biomass around M1 (exposure of 0.8) is suggested, before it decreases again towards the most exposed stations.

Appendix III

95% family-wise confidence level

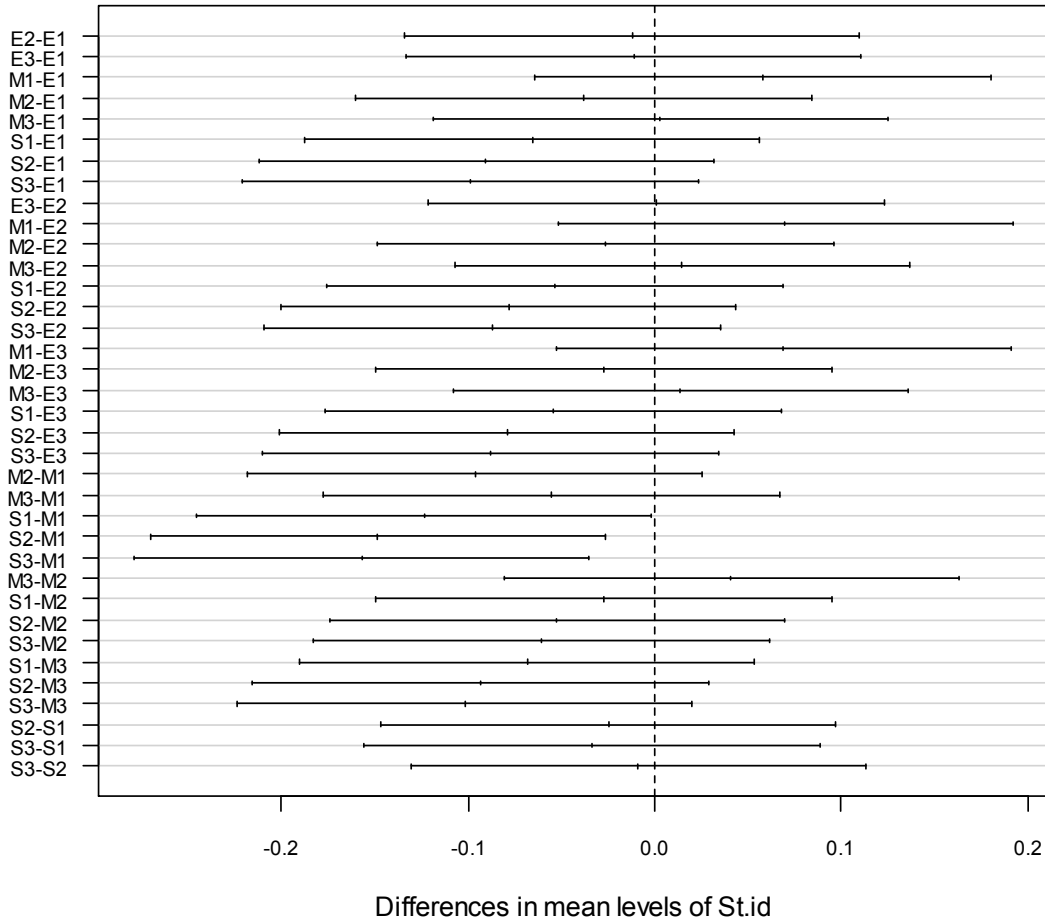


Figure 7.6 This figure depicts the results from the TukeyHSD-test of the difference between mean dry weight epiphyte biomass to stipe length ratios at stations when all sampling periods were lumped together.

Måned*RadIndex effect plot

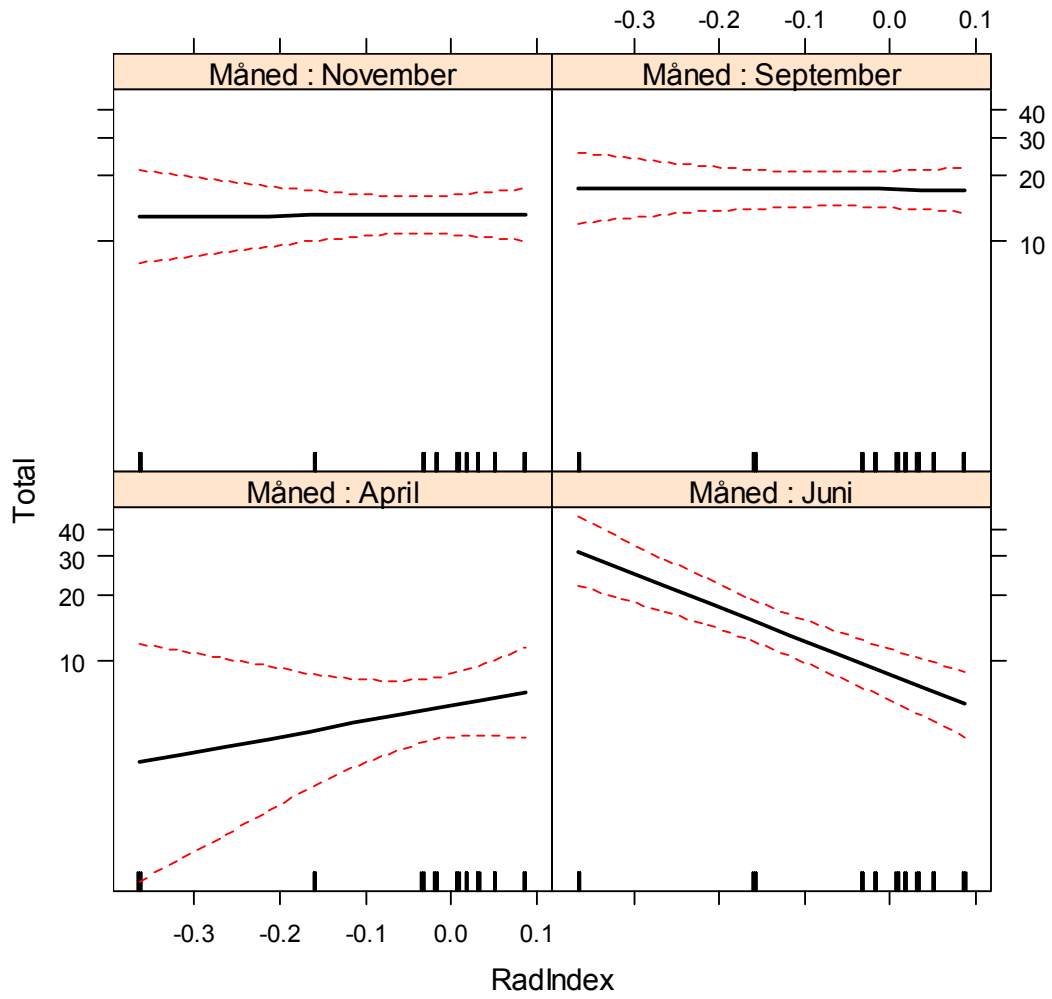


Figure 7.7 These are effect plots, visualising the effect of RadIndex in the GLM-model predicting biomass epiphytes per stipe.

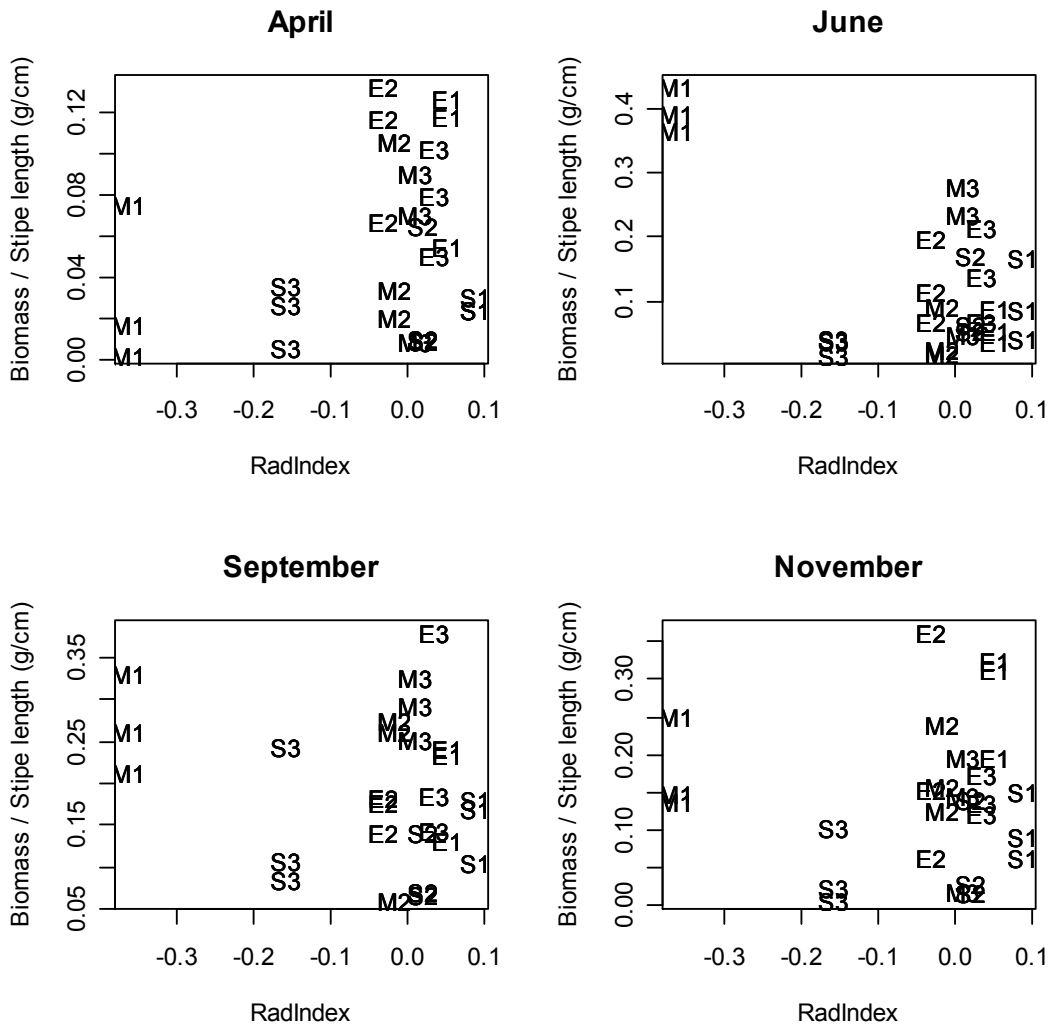


Figure 7.8 These plots show RadIndex plotted against biomass to stipe length ratios for each sampling period.

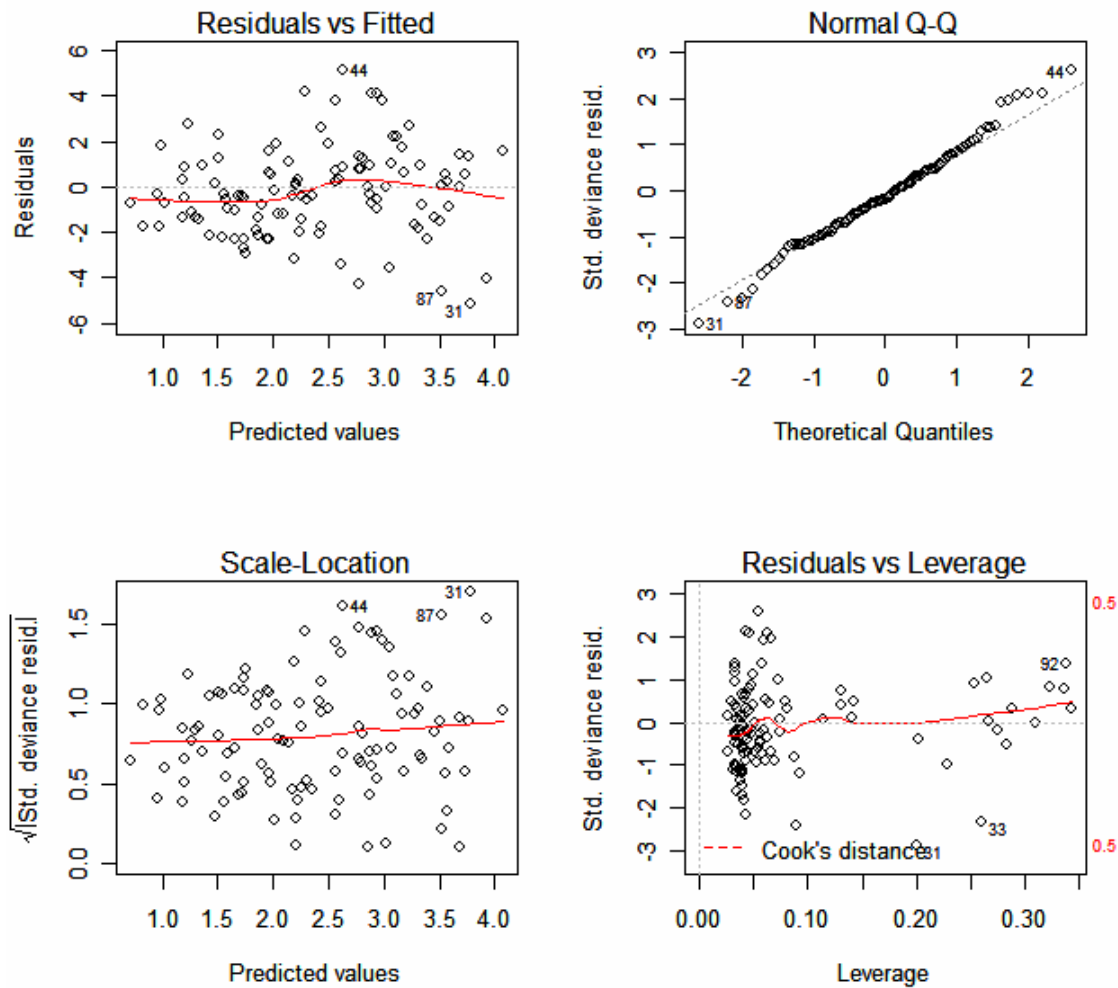


Figure 7.9 These are summary plots describing the fit of the GLM-model predicting biomass per stipe.

Quasipoisson model without RadIndex:

Output from **R**:

```

> summary(eps.modell.test)

Call:
glm(formula = Total ~ Stilklengde + Måned, family = quasipoisson)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-5.8691  -1.6821  -0.5987   0.9918   7.1468

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.387520   0.240132   1.614 0.109634

```

```

Stilklength 0.014474 0.001432 10.106 < 2e-16 ***
MånedJuni 0.644856 0.224756 2.869 0.004994 **
MånedNovember 0.806443 0.218226 3.695 0.000354 ***
MånedSeptember 1.077511 0.212133 5.079 1.69e-06 ***
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasipoisson family taken to be 5.451968)

Null deviance: 1353.86 on 107 degrees of freedom
Residual deviance: 530.37 on 103 degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 5

```

Appendix IV

Table 7.2 *This is the reduced matrix of epiphyte biomass in dry weight (g) per stipe. (Only biomass of dominating species, the "various" category and total epiphyte biomass at the stipes are shown.)*

Month	Exp.level	St.id	P.nr	Stipe length	Stipe age	Laminaria	Palmaria	Phycodrys	Delesseria	Membranopt	Ptilota	Polysiphonia	Rhodomela	Various	Total
April	E	E1	1	145	5	0	3.13	1.38	0.9	3.33	3.91	0	0.1	4.5	17.25
April	E	E1	2	105	7	0.94	5.84	0.01	0.08	4.19	1.04	0.07	0.11	1.13	13.41
April	E	E1	3	74	6	0	1.96	0.11	0.15	0.44	0.26	0	0	1.21	4.13
April	E	E2	1	164	6	3.8	0.18	2.73	1.54	2.53	1.66	0	0	9.42	21.86
April	E	E2	2	136	8	3.71	0	0	1.16	1.27	0.83	0	1.02	1.24	9.23
April	E	E2	3	164	5	3.29	1.28	4.63	0.2	1.84	2.64	0	0	5.48	19.36
April	E	E3	1	119	9	0.73	1.72	0.47	0	2.71	0.3	0	0	3.65	9.58
April	E	E3	2	88	7	0.01	2.55	0.02	0.06	0.02	1.01	0	0	0.85	4.52
April	E	E3	3	73	9	1.77	2.28	0	0	0.29	0.16	0	0	3.05	7.55
April	M	M1	1	63	5	0	0.14	0	0.01	0.41	0.01	0.01	0	0.51	1.09
April	M	M1	2	81	7	0	4.92	0.15	0	0.28	0.06	0.04	0	0.69	6.14
April	M	M1	3	71	7	0	0.05	0	0	0.07	0	0	0	0.12	0.24
April	M	M2	1	83	8	0.02	0.02	0.59	0.05	0.08	1.17	0	0.04	0.96	2.93
April	M	M2	2	64	6	0	0	0.14	0	0.16	0.24	0	0.06	0.77	1.37
April	M	M2	3	108	6	0	0	0.32	0.2	1.15	3.12	0	4.95	1.82	11.56
April	M	M3	1	65	5	0	0	0.55	0.64	3.64	0.88	0	0	0.21	5.92
April	M	M3	2	54	6	0	0	0.6	0.22	2.41	0.04	0.05	0.01	0.51	3.84
April	M	M3	3	70	5	0	0.02	0.3	0.23	0.08	0	0	0	0	0.63
April	S	S1	1	55	7	0	0	0.09	0	0.05	0.83	0.11	0	0.28	1.36

April	S	S1	2	50	6	0	0	0.08	0	0.17	0.88	0.02	0	0.43	1.58
April	S	S1	3	45	8	0	0	0.06	0	0.02	0.65	0.1	0.02	0.25	1.1
April	S	S2	1	84	7	0	0	0.14	0	0.08	0.05	0.03	0.12	0.49	0.91
April	S	S2	2	76	7	0	0.02	0.29	0	0.04	0.14	0	0	0.32	0.81
April	S	S2	3	72	6	0	0	0.26	0.31	0.18	1.62	0.06	1.42	0.89	4.74
April	S	S3	1	61	7	0	0	0	1.5	0.03	0	0.02	0.01	0.13	1.69
April	S	S3	2	58	5	0.18	0	0	0.04	0.01	0	0	0	0.13	0.36
April	S	S3	3	57	6	0	0	0.11	0.1	0.21	0.02	1.47	0	0.2	2.11
June	E	E1	1	97	5	0.73	0.18	0.1	0.03	1.36	0.33	1.82	0.13	4.19	8.87
June	E	E1	2	76	5	0	0.07	0.04	0	0.67	0.25	0.2	0.01	1.82	3.06
June	E	E1	3	79	5	1.05	0.09	0.14	0.03	0.63	0.19	0	0	2.46	4.59
June	E	E2	1	198	10	0	0.58	1.04	2.01	3.06	2.33	1.94	0.1	3.31	14.37
June	E	E2	2	184	9	0.63	0	0.86	1.91	4.1	3.35	9.32	0.13	16.45	36.75
June	E	E2	3	208	7	0.03	0.49	0.55	0	3.34	6.72	8.79	1.24	3.65	24.81
June	E	E3	1	133	7	0.49	11.94	1.76	0	0.92	4.04	5.75	0.42	3.5	28.82
June	E	E3	2	107	8	0	0.3	0.55	0.15	1.37	1.52	0	0.05	3.69	7.63
June	E	E3	3	153	6	0.22	3.92	2.06	5.83	0.98	0.1	3.09	0.3	5.28	21.78
June	M	M1	1	104	4	0	0	8.88	2.18	2.89	10.71	0	0	13.75	38.41
June	M	M1	2	116	7	0.77	0	5.19	1.16	12.03	8.85	2.26	1.08	14.25	45.59
June	M	M1	3	112	7	0	0	1.75	5.89	9.02	10.64	0.03	0	21.39	48.72
June	M	M2	1	97	7	0	0	1.23	0.15	1.66	0.45	0.16	3.42	2.11	9.18
June	M	M2	2	73	5	0	0	0.62	0	0.24	0	0	0	1.27	2.13
June	M	M2	3	80	4	0.12	0	0.43	0	0.18	0	0	0	1.13	1.86
June	M	M3	1	106	9	0	0	0.9	0	1.37	1.73	0	0	1.35	5.35
June	M	M3	2	131	5	0.39	0	4.93	0.77	3	10.9	1.15	9.73	5.95	36.82
June	M	M3	3	109	7	0.25	0	2.76	1.95	8	4.53	0	0	8.26	25.75
June	S	S1	1	55	6	0	0	0.26	0	0.03	0.46	0	0	1.7	2.45
June	S	S1	2	57	9	0	0	0	0	0.11	5.6	0	0.72	3.28	9.71
June	S	S1	3	55	5	0.47	0	0.19	0	0.36	2.28	0	0	1.68	4.98
June	S	S2	1	63	6	0	0	0.96	0.16	0.3	0.42	0	0.04	1.71	3.59
June	S	S2	2	59	5	0	0	1.02	2.82	0.8	1.44	0.02	0	4.12	10.22
June	S	S2	3	73	5	0.32	0	0.17	1.63	0.22	0.35	0	0.23	1.8	4.72
June	S	S3	1	40.5	6	0	0	0.53	0	0.11	0	0.12	0	1.06	1.82
June	S	S3	2	47	5	0.02	0	0.26	0.11	0.12	0.05	0.03	0	1.39	1.98
June	S	S3	3	31.5	6	0	0	0.16	0	0	0	0.04	0	0.45	0.65
September	E	E1	1	133	6	0.581	3.448	0.257	0.122	0.429	7.195	0	0	5.966	18
September	E	E1	2	142	6	1.75	3.32	2.63	0.05	1.62	17.63	0	0.12	7.47	34.59
September	E	E1	3	111	6	0.38	17.14	2.27	0.04	0.6	3.4	0	0	2.47	26.3
September	E	E2	1	127	6	0.03	4.74	0.26	1.28	2.36	1.45	0	0	8.04	18.16
September	E	E2	2	137	8	3.02	0.1	0.88	0.2	1.86	8.4	0	0.3	9.77	24.53
September	E	E2	3	130	8	0.35	6.15	0	0.04	0.97	0.92	0.05	0.02	15.71	24.21
September	E	E3	1	125	9	2.59	0	0.26	2.6	3.7	0.17	0	0.57	8.19	18.08
September	E	E3	2	99	7	0.55	0.03	3.36	0.57	9.34	0.65	0	6.98	16.21	37.69
September	E	E3	3	108	5	3.04	0	6.52	0.06	3.94	1.53	0	1.81	3.4	20.3
September	M	M1	1	151	7	5.934	9.969	4.176	2.111	6.332	1.1	0	0	10.02	39.64
September	M	M1	2	145	9	8.726	6.718	2.296	0	0.472	0.179	0	0	12.77	31.16
September	M	M1	3	156	5	3.891	22.36	7.72	0.549	4.649	0.944	0	0	11.62	51.73
September	M	M2	1	118	5	0.77	0	3.87	11.32	1.72	0.7	0	0.16	14.18	32.72

September	M	M2	2	73	7	0.36	0.13	5.15	0	2.68	7.77	0	0.09	3.02	19.2
September	M	M2	3	110	7	0.43	0.02	0.23	2.8	0.21	0.11	0	0	3.09	6.89
September	M	M3	1	122	5	0.21	0	2.59	10.6	9.25	0.28	0	0	17.02	39.95
September	M	M3	2	114	5	0	1.98	2.55	8.1	6.28	0.85	0	0	13.78	33.54
September	M	M3	3	128	6	1.66	11.85	4.72	3.86	2.35	0.3	0	0.06	7.69	32.49
September	S	S1	1	47	7	0	0	0.033	0	0.004	3.185	0	0	1.81	5.032
September	S	S1	2	41	7	0	0.02	0.29	0	0.42	4.94	0.01	0	1.37	7.05
September	S	S1	3	55	6	0.23	0	1.02	0	0.14	4.91	0	0.13	3.7	10.13
September	S	S2	1	68	6	0	0.05	1.43	0	0.53	0.33	0	0	2.76	5.1
September	S	S2	2	57	7	0.09	0	0	6.12	0.06	0.31	0	0	1.6	8.18
September	S	S2	3	56	6	0.32	0	0.18	0	0.74	0.6	0	0	2.08	3.92
September	S	S3	1	69	6	0.99	0	0.22	2.22	0.29	0	0	0.03	2.23	5.98
September	S	S3	2	49	5	3.36	0	0	6.31	0.62	0.32	0.01	0	1.37	11.99
September	S	S3	3	43	5	0.1	0	0.38	1.86	0.46	0	0	0	1.9	4.7
November	E	E1	1	120	7	0	8.26	2.02	0	3.63	17.39	0	0.12	7.73	39.15
November	E	E1	2	123	6	0.31	17.09	3.78	0	4.17	6.46	0	0.12	6.77	38.7
November	E	E1	3	136	5	0.14	19.49	0.74	0	4.77	1.55	0	0	0.36	27.05
November	E	E2	1	196	10	30.05	3.33	1.89	0	4.74	1.99	0.36	3.69	25.15	71.2
November	E	E2	2	158	10	0	7.83	0.3	0	5.93	4.68	0	3.39	2.49	24.62
November	E	E2	3	159	6	0.05	5.39	0.43	0	0.57	1.18	0	0.2	2.79	10.61
November	E	E3	1	111	6	5.56	0.68	3.7	0.46	2.03	2.46	0	0.21	4.53	19.63
November	E	E3	2	120	9	0	0.3	0	0	0	4.24	0	0.13	11.8	16.47
November	E	E3	3	120	8	0.5	2.2	0.48	0	0.89	4.16	0	0.03	6.42	14.68
November	M	M1	1	118	6	1.19	5.75	0.51	0.28	1.47	0.1	0	0	7.24	16.54
November	M	M1	2	132	6	7.05	9.49	1.15	0.24	4.29	2.27	0	0.09	8.7	33.28
November	M	M1	3	116	7	0.92	0.35	4.9	0.12	2.19	0.19	0	0	8.71	17.38
November	M	M2	1	96	5	0	1.89	0.73	0	6.63	0.89	0	0	5.39	15.53
November	M	M2	2	117	6	0	0.49	3.13	0.16	4.59	0.2	0	0	6.32	14.89
November	M	M2	3	87	8	8.81	0	3.01	0.38	1.92	0.28	0	0	6.67	21.07
November	M	M3	1	110	5	0.81	0	0.17	0.44	0.38	0.14	0	0	0.5	2.44
November	M	M3	2	98	6	0	0	1.51	0	3.13	2.64	0	0.34	7	14.62
November	M	M3	3	112	6	14.25	0	0.17	3.92	0.89	0.1	0	0	2.81	22.14
November	S	S1	1	49	5	0	0	0	0	0	0.24	0	0	3.05	3.29
November	S	S1	2	56	7	1.83	0	0.2	0	0.06	2.47	0	0	4.04	8.6
November	S	S1	3	51	7	0	0	0	0	0.06	1.4	0	0	3.32	4.78
November	S	S2	1	96	9	0.29	0	6.84	0	0.44	0.97	0	0.33	4.88	13.75
November	S	S2	2	71	6	0	0	0.17	0	0.13	0.29	0	0.05	0.72	1.36
November	S	S2	3	99	7	0	0	0.05	0	0.38	0.08	0	0.23	2.49	3.23
November	S	S3	1	79	5	1.29	0	0.68	0.98	0.81	0.8	0	0	3.82	8.38
November	S	S3	2	41	8	0	0	0.37	0	0.06	0	0	0	0.7	1.13
November	S	S3	3	42	5	0.05	0	0.03	0	0.01	0	0	0	0.29	0.38

Table 7.3 This is a table of dominating species and their contribution to total epiphyte biomass at the stations in the four sampling periods.

Exposure	April			June			September			November		
	E	M	S	E	M	S	E	M	S	E	M	S
<i>Laminaria</i>	13 %	0 %	1 %	2 %	1 %	2 %	6 %	8 %	8 %	14 %	21 %	8 %
<i>Palmaria</i>	18 %	15 %	0 %	12 %	0 %	0 %	16 %	18 %	0 %	25 %	11 %	0 %
<i>Phycodrys</i>	9 %	8 %	7 %	5 %	12 %	9 %	7 %	12 %	6 %	5 %	10 %	19 %
<i>Delesseria</i>	4 %	4 %	13 %	7 %	6 %	12 %	2 %	14 %	27 %	0 %	4 %	2 %
<i>Membranopt.</i>	16 %	25 %	5 %	11 %	18 %	5 %	11 %	12 %	5 %	10 %	16 %	4 %
<i>Ptilota</i>	11 %	16 %	29 %	12 %	22 %	26 %	19 %	4 %	24 %	17 %	4 %	14 %
<i>Polysiphonia</i>	0 %	0 %	12 %	21 %	2 %	1 %	0 %	0 %	0 %	0 %	0 %	0 %
<i>Rhodomela</i>	1 %	15 %	11 %	2 %	7 %	2 %	4 %	0 %	0 %	3 %	0 %	1 %
Various	29 %	17 %	21 %	29 %	32 %	43 %	35 %	32 %	30 %	26 %	34 %	52 %
Total	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
Total-Various	71 %	83 %	79 %	71 %	68 %	57 %	65 %	68 %	70 %	74 %	66 %	48 %

Appendix V

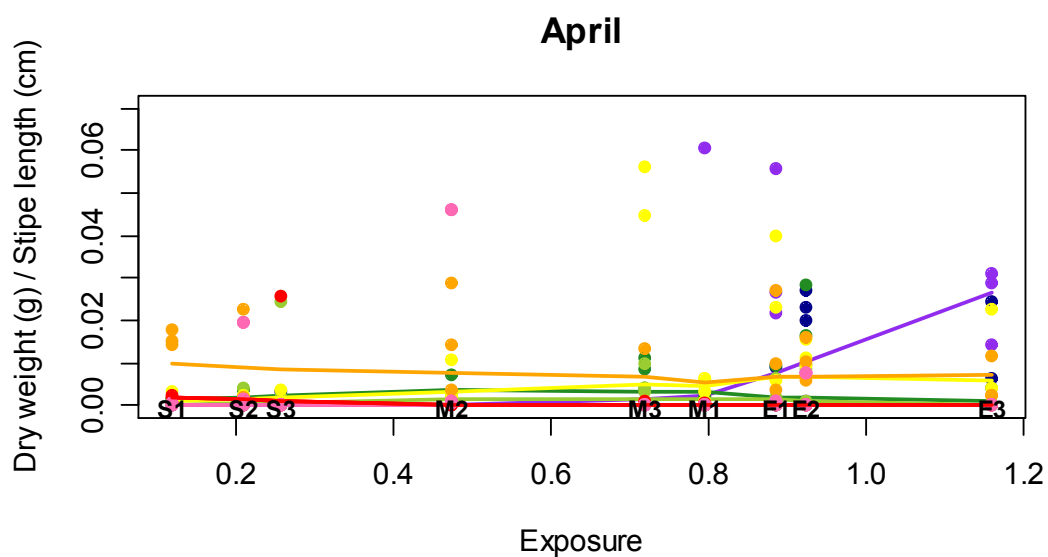


Figure 7.10 This figure displays biomass to stipe length ratio data from April for the eight most common species groups of algae found in this study. *Laminaria* – dark blue, *Palmaria* –

purple, Phycodryas – dark green, Delesseria – light green, Membranoptera – yellow, Ptilota – orange, Polysiphonia – red, Rhodomela – pink. The lines are the results of non-parametric smoother functions, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The smooth at each value is influenced by 2/3 of the points.) Each dot is data for one species group from one (three in total) stipe at that station.

Laminaria made up 1% of total biomass at the sheltered stations (S1, S2 and S3), 0% at the moderately exposed stations (M1, M2 and M3), and 13% at the exposed stations (E1, E2 and E3) in April (Table 7.3). Looking at Figure 7.10 and the raw data (Appendix IV) there seems to be a quite evident increase towards the most exposed stations, with high biomass to stipe length ratios especially at E2 and E3, though not revealed by the regression line.

Palmaria made up 0% of total biomass at the sheltered stations, 15 % at the moderately exposed stations, and 18 % at the exposed stations. Looking at the figure and the data from April, *Palmaria* is virtually absent until the exposure reach a value of 0.8 (M1). The values for the exposed stations are generally quite high, especially at E1 and E3.

Phycodryas made up 7% of total biomass at sheltered stations, 8% at moderately exposed stations, and 9% at the exposed stations. The ratios are generally quite low, though two stipes at E2 have markedly higher values than the others.

Delesseria made up 13% of total biomass at the sheltered stations, 4% at moderately exposed stations, and 4% at the exposed stations. The ratios are generally quite low, with the exception of the value for one stipe at S3.

Membranoptera made up 5% of total biomass at sheltered stations, 25% at moderately exposed stations, and 16% at the exposed stations. The ratio values are low at the sheltered stations, but vary more approaching the more exposed stations with especially high values for two stipes at M3 and two stipes at E1 and one at E3.

Ptilota made up 29% of total biomass at sheltered stations, 16% at moderately exposed stations, and 11% at the exposed stations. The ratio values are quite high and stable throughout the gradient of exposure.

Polysiphonia made up 12% of total biomass from the sheltered stations, but was virtually absent from exposed and moderately exposed stations. Ratios were generally close to zero, except from one stipe at S3.

Rhodomela made up 11% of total biomass at sheltered stations, 15% at moderately exposed stations, and 1% at the exposed stations. The ratio values were generally close to zero with some exceptions. S2, M2 and E2 had one stipe each with considerable amounts (dry weight) *Rhodomela* per cm stipe.

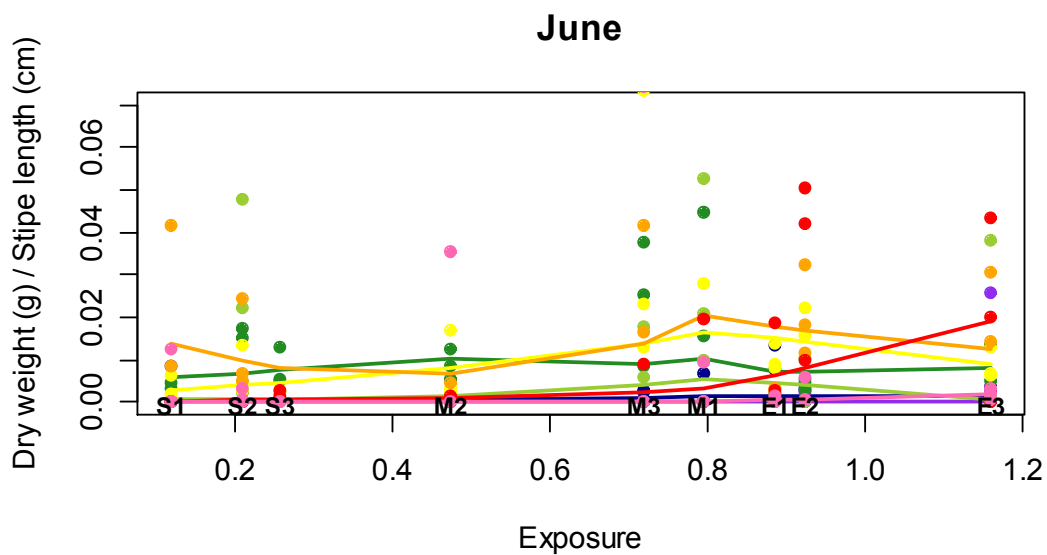


Figure 7.11 This figure displays biomass to stipe length ratio data from June for the eight most common species groups of algae found in this study. *Laminaria* – dark blue, *Palmaria* – purple, *Phycodrys* – dark green, *Delesseria* – light green, *Membranoptera* – yellow, *Ptilota* – orange, *Polysiphonia* – red, *Rhodomela* – pink. The lines are the results of non-parametric smoother functions, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The smooth at each value is influenced by 2/3 of the points.) Each dot is data for one species group from one (three in total) stipe at that station.

Laminaria made up 1% of total biomass at sheltered stations, 1% at moderately exposed and 2% at exposed stations in June. The ratios dry weight biomass to stipe lengths were generally low at all stations.

Palmaria made up 12% of total biomass at exposed stations, but was virtually absent from stations both in the moderately exposed and the sheltered categories. The dry weight biomass per cm stipe was generally close to zero with the exception of one stipe at E3.

Phycodrys made up 9 % of total biomass at sheltered stations, 12% at moderately exposed stations and 5 % at exposed stations. The ratio values were quite stable in the middle of the overall ratio range, with some higher values at M1 and M3.

Delesseria made up 12% of total biomass at sheltered stations, 6% at moderately exposed stations and 7% at exposed stations. The values of dry weight per cm seemed to vary a lot all along the gradient of exposure.

Membranoptera made up 5% of total biomass at sheltered stations, 18% at moderately exposed stations and 11% at the exposed stations. The ratio values showed a general increase towards M1 before declining again towards the more exposed stations.

Ptilota made up 26% of total biomass at sheltered stations, 22% at moderately exposed stations and 12% at the exposed stations. The ratios showed quite a lot of variation all along the gradient of exposure.

Polysiphonia made up 1% of total biomass at sheltered stations, 2% at moderately exposed stations and 21% at exposed stations. The ratios were close to zero at sheltered stations, but increased markedly towards the most exposed stations.

Rhodomela made up 2% of total biomass at sheltered stations, 7% at moderately exposed stations and 2% at exposed stations. The ratios were again close to zero with some exceptions of really high values S1, M2, M1 and E2.

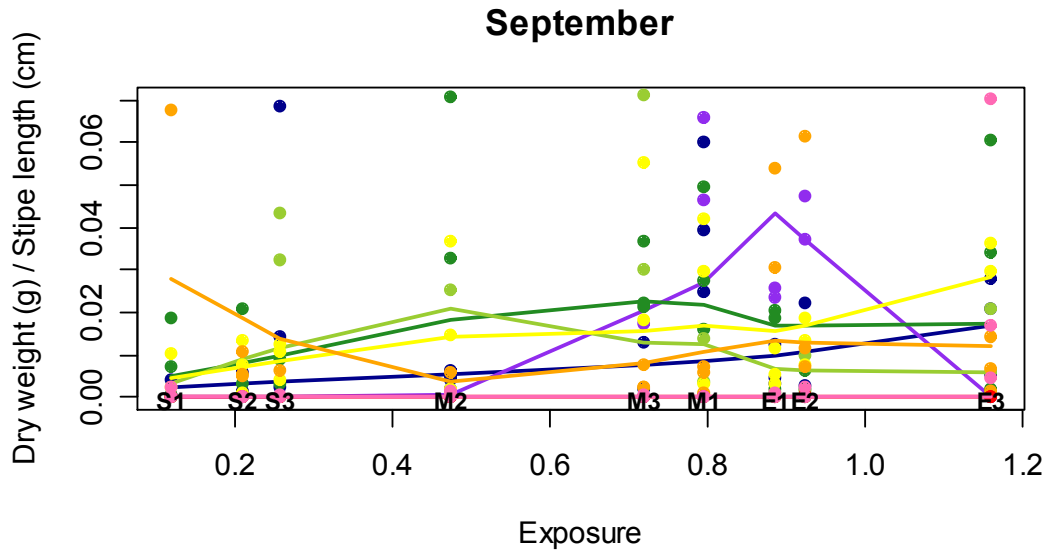


Figure 7.12 This figure displays biomass to stipe length ratio data from September for the eight most common species groups of algae found in this study. *Laminaria* – dark blue, *Palmaria* – purple, *Phycodrys* – dark green, *Delesseria* – light green, *Membranoptera* – yellow, *Ptilota* – orange, *Polysiphonia* – red, *Rhodomela* – pink. The lines are the results of non-parametric smoother functions, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The smooth at each value is influenced by 2/3 of the points.) Each dot is data for one species group from one (three in total) stipe at that station.

Laminaria made up 8% of total epiphyte biomass at both sheltered and moderately exposed stations and 6% at exposed stations in September. A general increase in biomass per cm stipe was observed towards the more exposed stations, but there was one stipe with extremely high value at S3. All three stipes at M1 had very high values.

Palmaria was observed, but in very small amounts, at the sheltered stations, made up 18% of total biomass at moderately exposed stations and 16% at exposed stations. There is a clear peak in biomass per cm stipe between the upper part of the moderately exposed stations (M3 and M1) and the lower part of the exposed stations (E1 and E2). At the most exposed station (E3) only small amounts of *Palmaria* were found.

Phycodrys made up 6% of total biomass at the sheltered stations, 12% at the moderately exposed stations, and 7% at the exposed stations. The ratio values were quite variable, but generally higher at moderately exposed and exposed stations than at sheltered.

Delesseria made up 27% of total biomass at the sheltered stations, 14% at the moderately exposed and 2% at the exposed stations. The ratios were quite variable, with perhaps a peak around the upper of the sheltered and the moderately exposed stations.

Membranoptera made up 5% of total biomass at the sheltered stations, 12% at the moderately exposed and 11% at the exposed stations. Also for *Membranoptera*, ratio values were quite variable, especially at the moderately exposed stations, but showed a general increase towards the exposed areas.

Ptilota made up 24% of total biomass at the sheltered stations, 4% at the moderately exposed and 19% at the exposed stations. The ratios were actually generally quite low with some extreme exceptions from all the stipes at S1, two stipes at E1 and one at E2.

Polysiphonia was virtually absent from all stations in September.

Rhodomela contributed close to nothing to total biomass at sheltered and moderately exposed sites, but made up 4% at exposed stations. The ratios were generally very low except at E3 where there were some quite high values.

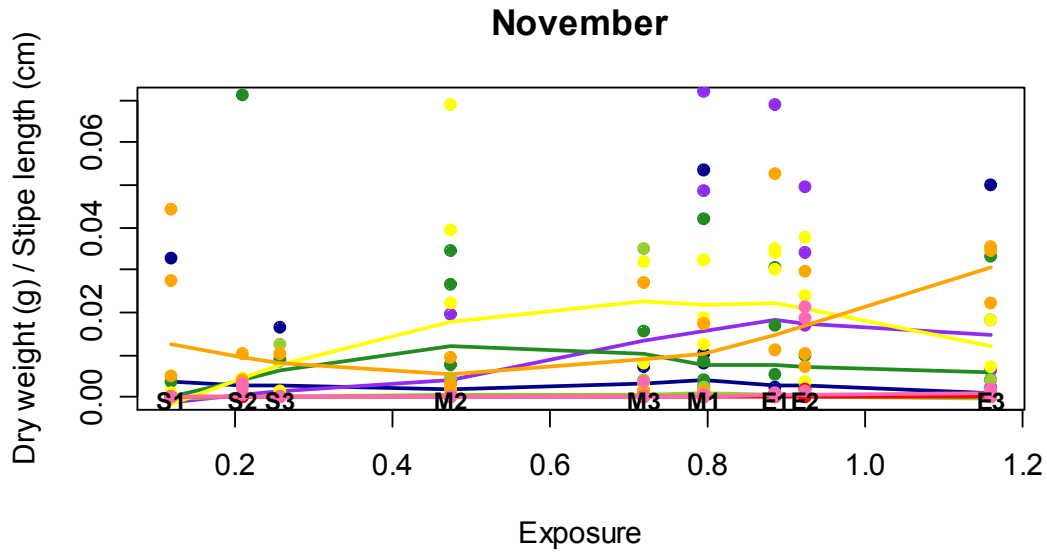


Figure 7.13 This figure displays biomass to stipe length ratio data from November for the eight most common species groups of algae found in this study. *Laminaria* – dark blue, *Palmaria* – purple, *Phycodrys* – dark green, *Delesseria* – light green, *Membranoptera* – yellow, *Ptilota* – orange, *Polysiphonia* – red, *Rhodomela* – pink. The lines are the results of non-parametric smoother functions, “lowess” (in R), which carries out a locally weighted polynomial regression of the y-variables on the x-variables. (The smooth at each value is influenced by 2/3 of the points.) Each dot is data for one species group from one (three in total) stipe at that station.

Laminaria made up 8% of total epiphyte biomass at sheltered stations, 21% at moderately exposed and 14% at exposed stations in November. The biomass per cm stipe values were generally quite low with some exceptions.

Palmaria was absent from sheltered stations, made up 11% of total biomass at moderately exposed and 25% at exposed stations. The ratios increased towards the more exposed stations, and were highest at M1, E1 and E2.

Phycodrys made up 19% of total biomass at sheltered stations, 10% at moderately exposed stations and 5% at exposed stations. The ratios were very variable, but generally higher at the moderately exposed stations, with the exception of one extremely high value at S2.

Delesseria made up 2% of total biomass at sheltered stations, 4% at moderately exposed and only minute amounts at exposed stations. The ratio values were generally very low, with one exception at S3 and one at M3.

Membranoptera made up 4% of total biomass at sheltered stations, 16% at moderately exposed and 10% at exposed stations. The data suggested a peak in biomass per cm stipe between the moderately exposed and exposed stations. Some really high values were found at M2.

Ptilota made up 14% of total biomass at sheltered stations, 4% at moderately exposed and 17% at exposed stations. The ratio values were high from two stipes at S1, quite low at S2, S3 and M2, but increased again towards the more exposed stations.

Polysiphonia was absent from all stations in November.

Rhodomela made up 1% of the total biomass at the sheltered stations, contributed very little (close to zero) at moderately exposed, but contributed about 3% of the total biomass at exposed stations. The ratios were generally very low. The highest values were found at E2.

Appendix VI

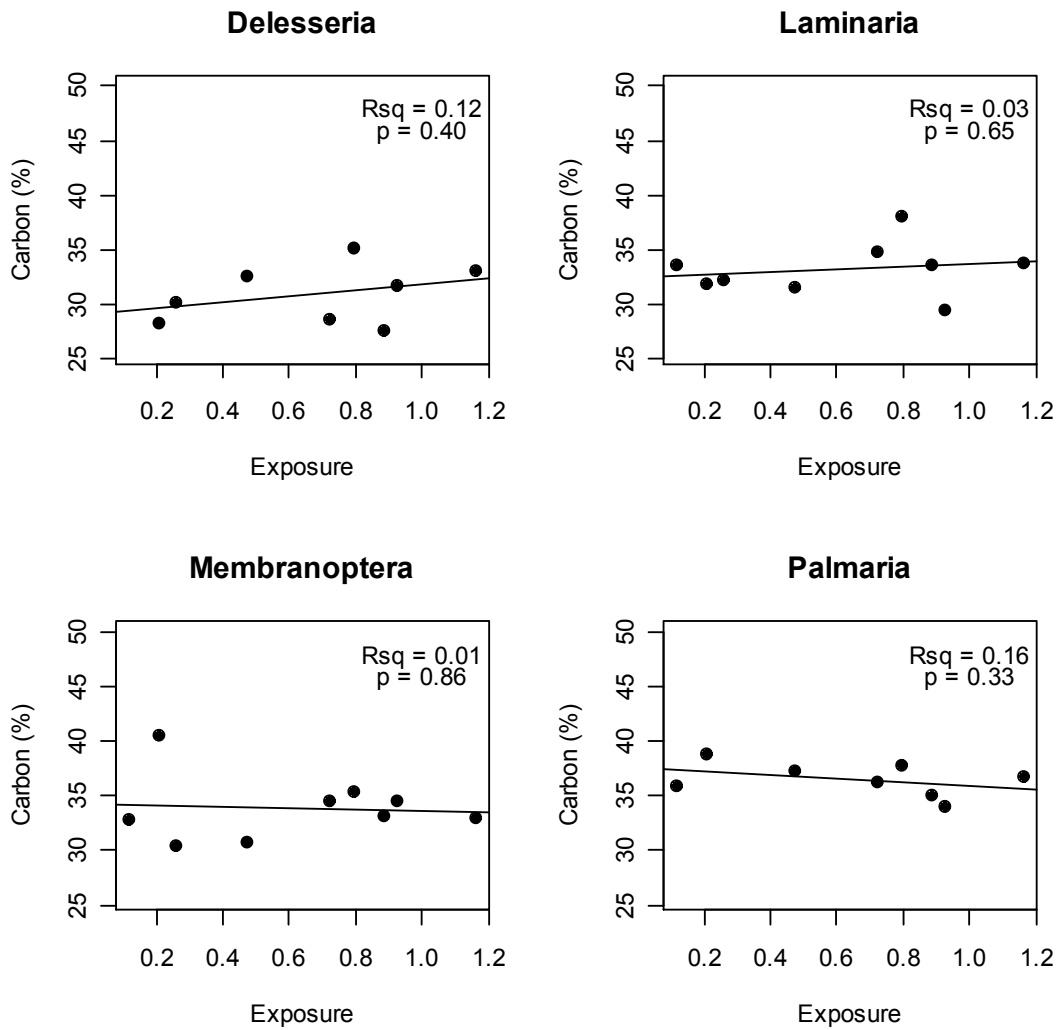


Figure 7.14 Results from the carbon content analyses of September samples. Black lines are regression lines from simple linear regressions. “Rsqu” is part variation explained by the regression and the p-value indicates the significance of the regression model.

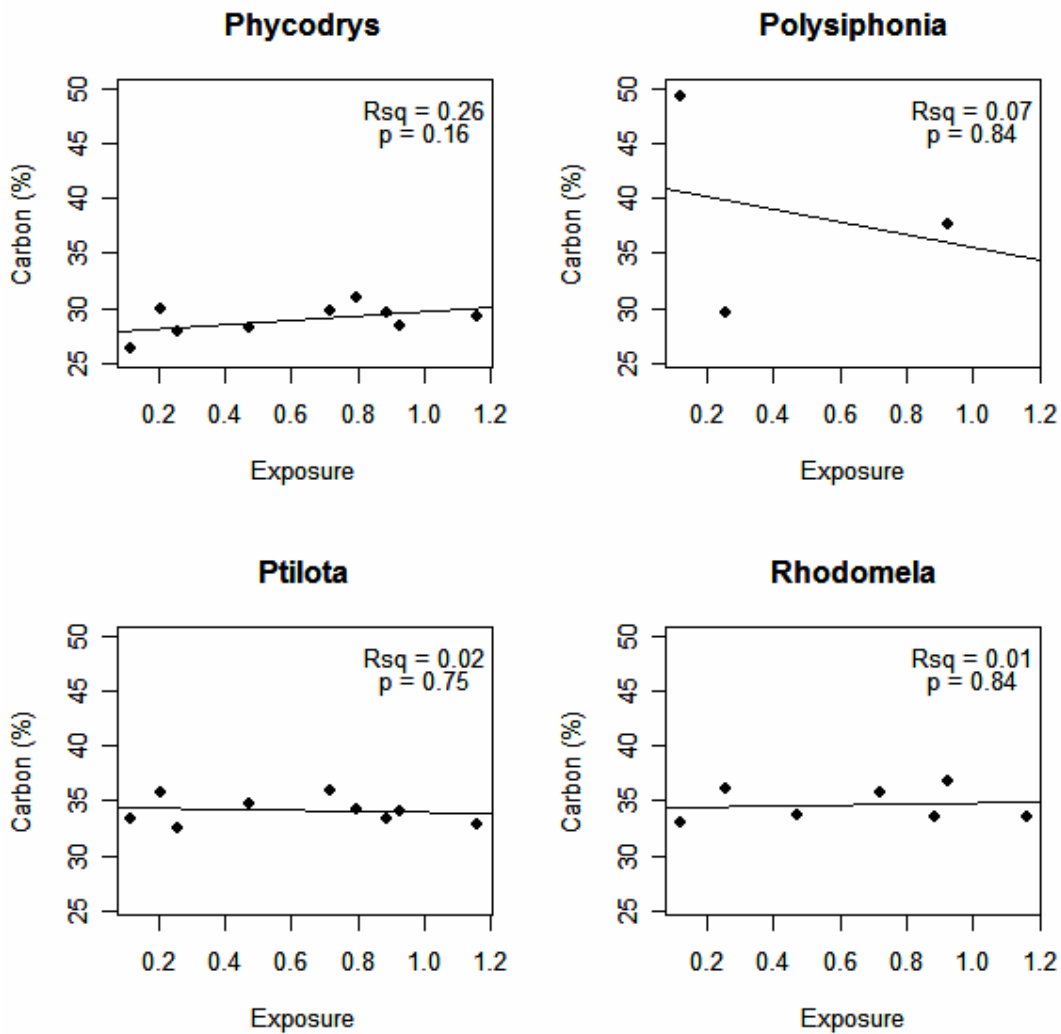


Figure 7.15 Results from the carbon content analyses of September samples. Black lines are regression lines from simple linear regressions. “Rsqr” is part variation explained by the regression and the p-value indicates the significance of the regression model..

Table 7.4 This is a table showing wet weights before and after fixation. “Fresh” – average fresh wet weight. “Fix” – average fixated wet weight. “Diff” – differences between average fresh and fixated wet weights. “Ratio” – Diff divided by Fresh (% reduction in weight after fixation).

Species	Wet 1	Wet 2	Wet 3	Fresh	Wet 4	Wet 5	Wet 6	Fix	Diff	Ratio
Palmaria	4.02	4.02	3.99	4.01	2.81	2.77	2.74	2.77	1.24	0.31
Delesseria	1.88	1.91	1.88	1.89	1.72	1.74	1.65	1.70	0.19	0.10
Phycodrys	1.89	1.86	1.79	1.85	1.77	1.72	1.66	1.72	0.13	0.07
Membranopte	1.37	1.39	1.41	1.39	1.25	1.27	1.32	1.28	0.11	0.08
Ptilota	1.68	1.60	1.63	1.64	1.63	1.67	1.55	1.62	0.02	0.01
Ceramium	12.52	13.07	12.60	12.73	11.03	10.61	10.55	10.73	2.00	0.16
Rhodomela	4.64	4.53	4.59	4.59	3.98	3.96	3.99	3.98	0.61	0.13
Average				4.01				3.40	0.61	0.15

Appendix VII

Three or four letter species abbreviations:

- Mem - *Membranoptera alata*
- Pti - *Ptilota gunneri*
- Phyc - *Phycodrys rubens*
- Pal - *Palmaria palmata*
- Pol - *Polysiphonia elongata, Polysiphonia stricta*
- Rho - *Rhodomela confervoides, Rhodomela lycopodioides*
- Lam - *Laminaria hyperborea, Laminaria digitata, Saccharina latissima*
- Lom - *Lomentaria clavellosa*
- Nit - *Nitophyllum punctatum*
- Cal - *Callophyllis lacinata*
- Ect - *Ectocarpus sp.*
- Sph - *Sphacelaria cirrosa*
- Des - *Desmarestia viridis*
- Cys - *Cystoclonium purpureum*
- Plo - *Plocamium cartilagineum*
- Phyl - *Phyllophora crispa*
- Fuc - *Fucus serratus*
- Ala - *Alaria esculenta*
- Cer - *Ceramium sp*

- Cry - *Cryptopleura ramosa*
Apo - *Apoglossum ruscifolium*
Tra - *Bonnemaisonia hamifera* (Trailliella)
Dic - *Dictyota dichotoma*