

Turf mats characterization along the Norwegian Skagerrak coastline

*Turf system components and influence from
abiotic factors*

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Skagerrak coastline

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By
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Abstract

Poleward migration of kelp forests worldwide is permitting a shift to the less complex turf algae mats, followed by a cascade effect through trophic levels. Ecosystem characteristics and species vary between ecoregions, making finding a unified understanding of the consequences challenging. Turf mats are short and dense-growing mats with high turnover rates that accumulate considerable amounts of sediment. However, this description is very general and says little about taxa, physiology and abiotic factors, complicating finding a standard definition to use when communicating research on turf. In this study, the hope is to add to the growing knowledge of turf by identifying common trends in turf physiology, sediment content, species and invertebrate groups, as well as effects of abiotic factors along the Norwegian Skagerrak coastline. Herbaceous algae and coralline algae were the most abundant, and they, as well as filamentous algae in autumn, contributed the most to sediment entrapment. Turf biomass had an average of $213 \pm 168 \text{ g m}^{-2}$ in spring and $169 \pm 109 \text{ g m}^{-2}$ in autumn, with the shrubby herbaceous morphological type being the most common. Dominant species constituted of *Chondrus crispus*, *Corallina officinalis* and *Bonnemaisonia hamifera*. Sediment content was primarily influenced by current and had an average weight of $191 \pm 135 \text{ g m}^{-2}$ in autumn and $103 \pm 82 \text{ g m}^{-2}$ in spring. Common invertebrate groups were polychaetes, gastropods and copepods. The results of this study will aid future turf research and monitoring as it represents a snapshot of turf characteristics along the Skagerrak coastline.

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1 Introduction

Increasingly anthropogenically created disturbances are driving global change in ecosystems all over the globe (Malhi et al., 2020). The adverse effects are becoming more and more evident as scientist report unprecedented surges in temperature, pollution emission and other anthropogenically sourced environmental changes (O'Brien, 2012). Furthermore, increase in extreme weather conditions (Rahmstorf & Coumou, 2011) are causing the demise of species and ecosystems that cannot keep up with the rapid evolutionary pressure (Hansen et al., 2001). Specialist species are in particular at risk as their disturbance tolerance tend to be lower, allowing generalist species to gain ground and outcompete them in their own niches (Clavel et al., 2011). Predicting the consequences of these shifts are challenging as they often are a result of multiple factors, yet by studying the new systems, we can glean insight into how to mitigate and prevent further damage. One such shift is rapidly occurring in the marine environment (Doney et al., 2012). Globally complex kelp forests are increasingly replaced by a flattened intertwined algae mat called turf (Wernberg et al., 2019). Turf is an umbrella term that covers a wide variety of systems with similar features worldwide (Connell et al., 2014b). To understand the consequences of the kelp-turf shifts, it critical to study the physiology of the ecosystem and the driving factors behind the change, in the hopes of optimizing conservation efforts.

1.1 Kelp forests function and importance

Kelp forms large marine habitats comprised of vertically growing laminarian and fucalean brown algae (Steneck & Johnson, 2014). They are considered one of the most productive systems on the planet, with an average net primary production of 500 g carbon m⁻² y⁻¹ (Krumhansl & Scheibling, 2012). Kelp forests can be found in on rocky substrate in nutrient-rich, cold water (Mann, 1973) from 0 to > 30 meters depth on both hemispheres (NOAA, 2020). According to Steneck & Johnson (2014), kelp beds can be found along ¼ of the coastlines of the world, making them an important foundation species for a wide variety of coastal regions.

In polar regions, kelps lifecycle allows them to store ATP and sugary compounds produced during the few weeks of light, to later utilize for growth during the polar night when nitrogen and phosphorous is abundant (Johnsen et al., 2020). Towards the equator, warm temperatures and

low nutrient can prevent growth and reproduction of kelp (Reed & Brzezinski, 2009). Extreme warm temperatures can trigger cellular and intercellular damage which slows growth, reduces fecundity, development and survivorship (Davison & Pearson, 1996). An existing Kelp canopy shade the benthic environment below, limiting turf growth by reducing available light (Kim, 2002; Wernberg et al., 2005).

Kelp providing several essential ecosystem services such as shelter, nurseries and habitat (Hartvig Christie et al., 2009). Lower trophic level organisms such as urchins, snails, molluscs, filter feeders and small crustaceans live parts of or their entire lives here. Some fish also use the tall fronds for refuge and nurseries. Lower trophic level algal species associated with kelp forests serve as an important food source for organisms higher up the food chain (Reed & Brzezinski, 2009; Blamey & Bolton, 2018; Vásquez et al., 2014). Most brown seaweeds are generally not grazed upon, as they produce the herbivore deterrent phlorotannin (Graham & Wilcox, 2000). They do on the other hand contribute to marine particulate and dissolved organic matter (Newell & Lucas 1981) which often are essential for other food webs (Bustamante & Branch, 1996; Krumhansl & Scheibling, 2012).

Different kelp taxa lifespans range from 3 to 25 years (Steneck & Johnson, 2014). This perennial life strategy ensures positive feedback that helps maintain the population. The canopy reduces water flow enough so that juvenile kelp find holdfast within the established ecosystem (Layton et al., 2019) while the tall canopy limits light availability for competing algae such as turf forming species below them (Wernberg et al., 2005).

Kelp has been a part of different human cultures for thousands of years, along with being an important food source (Balasse et al., 2005; Jerardino & Navarro, 2002). Modern-day ecosystem services that profit humans include social, economic and ecological benefits. Furthermore, kelp reefs are utilized for education and science, recreational activities, and they hold cultural importance to ethnic groups such as the Inuit, Sami and Aborigines (Bennett et al., 2016). They also contribute to our economy through tourism, harvesting, and commercial fishing. Last but not least, kelp forests provide the crucial ecosystem services photosynthesis, nutrient cycling, carbon sequestration and erosion protection along coastlines (Smale et al., 2013). Despite the strong evidence for kelps importance, the economic value is challenging to determine. Filbee-Dexter &

Wernberg (2018) estimated kelp forest to be worth 3 million US dollars per km of coastline per year, granted even this is likely an underestimation.

The last decades diminishing kelp forests have been reported by various researchers as a global phenomenon (Connell et al., 2008; Filbee-Dexter et al., 2016; Moy & Christie, 2012; Wernberg et al., 2016). Connell et al. (2008) reported widespread disappearance between the 1990s and 2000s in South Australia, Filbee-Dexter et al. (2016) reported a reduction in the kelp population at the Atlantic coast of Canada. Kelp loss has also been reported in Japan (Tanaka et al., 2012), south Italy (Benedetti-Cecchi et al., 2001), and the Norwegian coastline (Eriksson et al., 2002; Middelboe & Sand-Jensen, 2000). Moy & Christie (2012) have reported an 80% kelp forest loss in the Skagerrak region between the early 2000s and 2012.

1.2 The definition of turf

In recent years, a shrub-like, entangled algae-matt named ‘turf’ has been replacing kelp in the areas experiencing kelp loss (Filbee-Dexter & Wernberg, 2018), yet no official definition of turf exists. The word ‘Turf’ was first used in the 12th century to describe the terrestrial upper layer of soil that is bound by roots and grass (Miriam Webster dictionary, 2020). Later, the term was used for other grasslands types and moss-covered strata (Braun-Blanquet, 1932). “Algal turf” was first applied by Lawson and John in 1977 to describe low growing mats of algae. The term was reinforced further by Stewart (1982) stating its function as to "*Anchor species and epiphytes in intertidal algal turf*". Throughout the years when studying coastlines, marine scientists have used a range of words to describe turf, making literary research challenging.

As of yet, there is no definition of what marine turfs are (Connell et al., 2014). Species composition, physical characteristics and properties are largely generalized. What researchers do agree on is that turf is a short mat of rapidly growing, entangled algae, comprised of a variety of mainly rhodophyte species, but also chlorophytes, some phaeophytes, cyanobacteria and diatoms (e.g. Airoldi & Virgilio, 1998; Connell et al., 2014; Filbee-Dexter & Wernberg, 2018).

Connell et al. (2014) synthesized from over a hundred reviewed articles that turf is most widely recognized to be between 1 and 10 cm tall, and collect large amounts of sediment for its size. Turf species composition varies geographically, but generally contain opportunistic taxa with

high turnover rates (Connell et al., 2014b) that flourish in warm, nutrient-rich waters (Airoldi, 1998; Bartsch et al., 2008; Moy & Christie, 2012). Turf establishes itself on hard rocky surfaces in the intertidal and subtidal zone, where its short, interwoven structure slows water movement and allows sediment to settle (Virgilio et al., 2006; Airoldi & Virgilio, 1998). This makes species identification challenging, further complicated by phenotypic plasticity influenced by wave action, seasonality, and stress factors (Connell et al., 2014b; Hay, 1981).

Turf is a significant component of rocky intertidal and subtidal niches in temperate, tropical and polar latitudes where they usually form small mosaic patches of algae (Connell & Irving, n.d.; Virgilio et al., 2006). Turf communities are generally species-rich and play essential roles in their communities, such as through succession, nutrient cycling and as a food source (Airoldi et al., 1995; Edwards, 1998; Irving & Connell, 2006). They can become dominant as a consequence of nutrient enrichment, high temperatures and anthropogenic disturbance, and are therefore used as an indicator for the health of marine ecosystems (Airoldi et al., 2008; Connell & Irving, n.d.).

1.3 Turf on the rise

Global warming is a widely recognized explanation for the kelp-turf shift (Jueterbock et al., 2013; Moy & Christie, 2012). As the ocean temperatures increase, the less tolerant stages of the kelp life cycle are at risk, causing high mortality and low recruitment and ultimately loss of kelp forests (Moy & Christie, 2012). A cascade through affiliated food webs occurs following the kelp loss, affecting organisms and other ecosystems that depend on it (Filbee-Dexter & Wernberg, 2018).

Kelps are cold-water species that suffer tissue damage when exposed to temperatures over a certain threshold, weakening them to other stressors (Simonson et al., 2015; Wernberg et al., 2010). For example, *Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl & Saunders (formerly known as *Laminaria saccharina*) suffer growth inhibition when exposed to temperatures outside their tolerance range of 0 to 20°C (Lüning, 1990). With the average oceanic temperatures increasing, and an increasing frequency of heatwaves, kelp are forced to migrate poleward, opening up its niche for turf (Filbee-Dexter et al., 2020; Nepper-Davidsen et al., 2019). Where temperature is concerned, turf species tend to have a higher temperature tolerance,

allowing them to survive during ocean warming and heatwave events and gain ground in the freed up space (Lüning, 1993).

Kelp such as *Saccharina latissima* needs a hard rocky substrate to attach and grow securely (Airoldi, 2003) while turf species often have vegetative reproduction. This allows them to grow in sedimented rocky surfaces already occupied by turf, maintaining its dominance (Harris et al., 2015).

The Skagerrak coastline is more sheltered than the Norwegian west coast, which permits moderate levels of eutrophication (Molvær et al., 2007). Kelp has a preference towards areas with higher water movement velocity and lower nutrient concentrations, which makes this region at higher risk for turf takeover (Chapman & Craigie, 1977; Moy & Christie, 2012). Excessive nutrients have a positive effect on macroalgae diversity, although it reduces productivity (Kraufvelin et al., 2010).

Different adaptations to these abiotic factors are creating intra-ecosystem competition between kelp and turf, affecting distribution and abundance of species (Dayton et al., 1971, 1984). While there is much knowledge of how abiotic factors influence kelp, less is known of how they impact turf. By looking at the variation between local turf systems as a result of abiotic factors, the underlying mechanisms can be revealed and used to understand and compare turf systems worldwide.

1.2 Aims and research questions

Detailed studies are paramount if we are to understand and communicate research of turf systems and find the most effective approach to help forest conservation (Connell et al., 2014). This study aims to describe turf communities along Norwegian Skagerrak coastline and identify how some abiotic factors create variation between turf mats. The parameters used for describing the turf communities were sediment content, species composition, invertebrate community, algal morphological structure and biomass of turf. Abiotic factors were used to explain the variation between turf sites and seasons. The following questions have been asked:

- 1:** Will algal and invertebrate turf community composition vary seasonally and be explainable by current, salinity, temperature and nutrient concentrations?
- 2:** Is there a positive relation between turf, height, biomass and sediment content?
- 3:** Will abundance of algal morphological types influence the sediment content in turf?
- 4:** Will organic sediment correlate positively with turf biomass?
- 5:** Will turf fauna biomass correlate positively with turf biomass?

2 Materials and methods

2.1 Location

Sampling took place in autumn from the 15th till the 19th of October 2018, and in spring from the 20th till the 24th of May 2019, at nine different sheltered to moderately exposed sites along a 37 km stretch of coastline near IMR Flødevigen Research Station, Arendal (Figure 1, 2 and Table 1).

Table 1: Coordinates for each sampling site.

Station	Latitude	Longitude
S7	58.5208	8.9315
S8	58.5116	8.9374
S17	58.4212	8.7716
S5	58.5050	8.8950
S3	58.3972	8.7427
SA4	58.3119	8.5746
SA2	58.2789	8.5325
HB7	58.2546	8.5232
S15	58.4230	8.7563

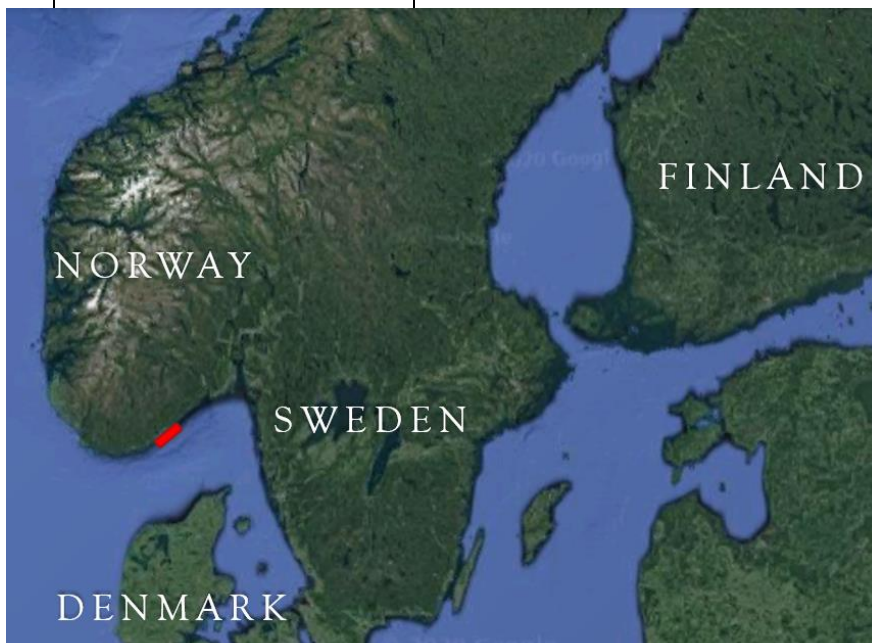


Figure 1: Map of Scandinavia with sampling location marked in red.

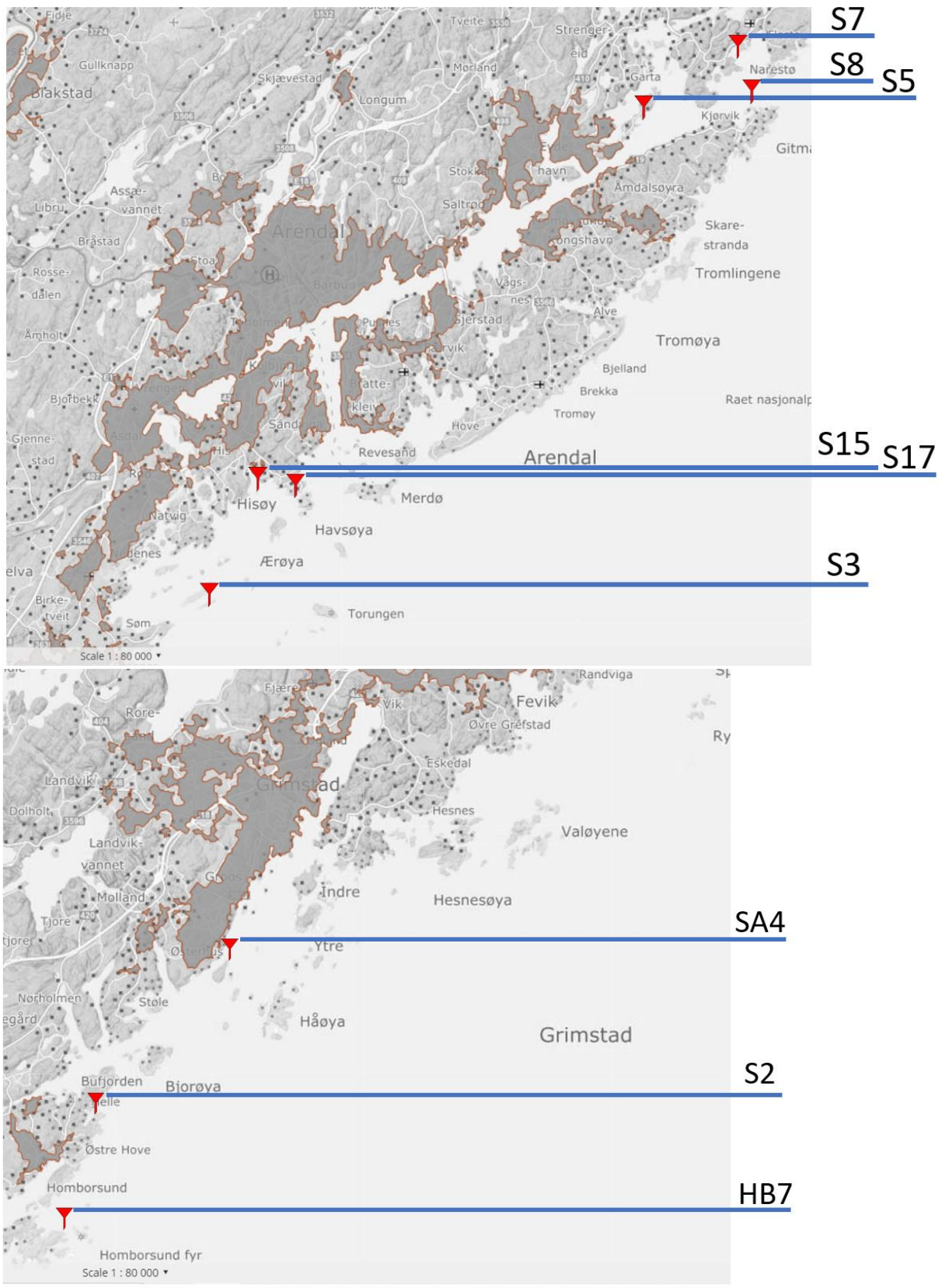
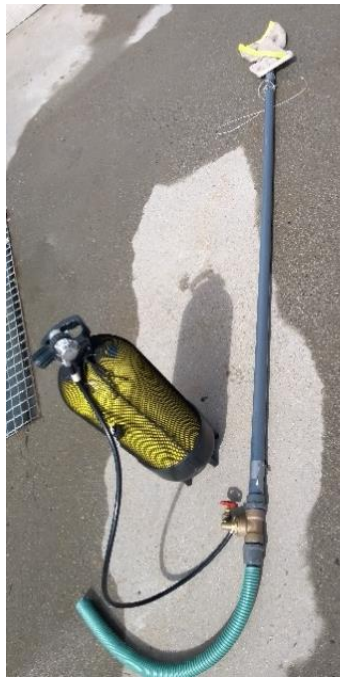
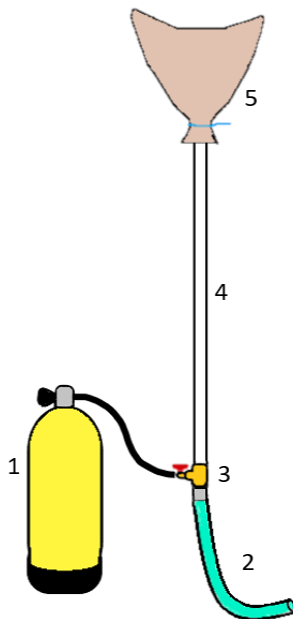


Figure 2: Map displaying sampling site locations. *Shaded areas indicate urban population. Map retrieved from: <https://kart.ssb.no/befolkning>.*

2.2 Field procedure

Two divers collected three random samples at nine different sites between 5- and 7-meters depth using a suction sampler (Figure 3). Turf dominated some of the sampling sites completely (Figure 4 A). In more detail, two divers dove down, one with the suction sampler (Figure 4 B), and placed a 50x50 cm metal frame on a random patch of turf (Figure 4 C). Turf height was measured in each corner and in the middle of the metal frame. The measurements were recorded on a writing plate. One diver would then turn on the airflow in the suction sampler ‘vacuuming’ within the square while the other diver used a paint scraper to detach algae from rock, clean spot (Figure 4 D). Organic and inorganic material within the frame was suctioned up through the pipe by the airflow from the tank. The material was trapped in a meshed bag attached to the top of the pipe with two cable ties. After finishing one sample square, divers cut the cable ties fastening the bag to the pipe with secateurs, securing the sample in the mesh bag using a new cable tie (Figure 5 A). A new mesh bag was then attached to the top of the pipe with cable ties for the next sample. Back on land, each sample was put in separately labelled plastic containers (Figure 5 B) and fixed with 4% formalin and saltwater for preservation until they could be processed in the lab.



*Figure 3: Suction sampler.
1) Oxygen tank with valve, connected to the brass pipe by a low-pressure hose.
2) Flexible suction tube.
3) Brass pipe with a red valve.
4) Rigid plastic pipe.
5) A fine mesh bag zip-tied to the top of a rigid pipe. Air flows through pipe when both valves are opened, moving water up, pulling sediment, algae and organisms into the meshed bag.*

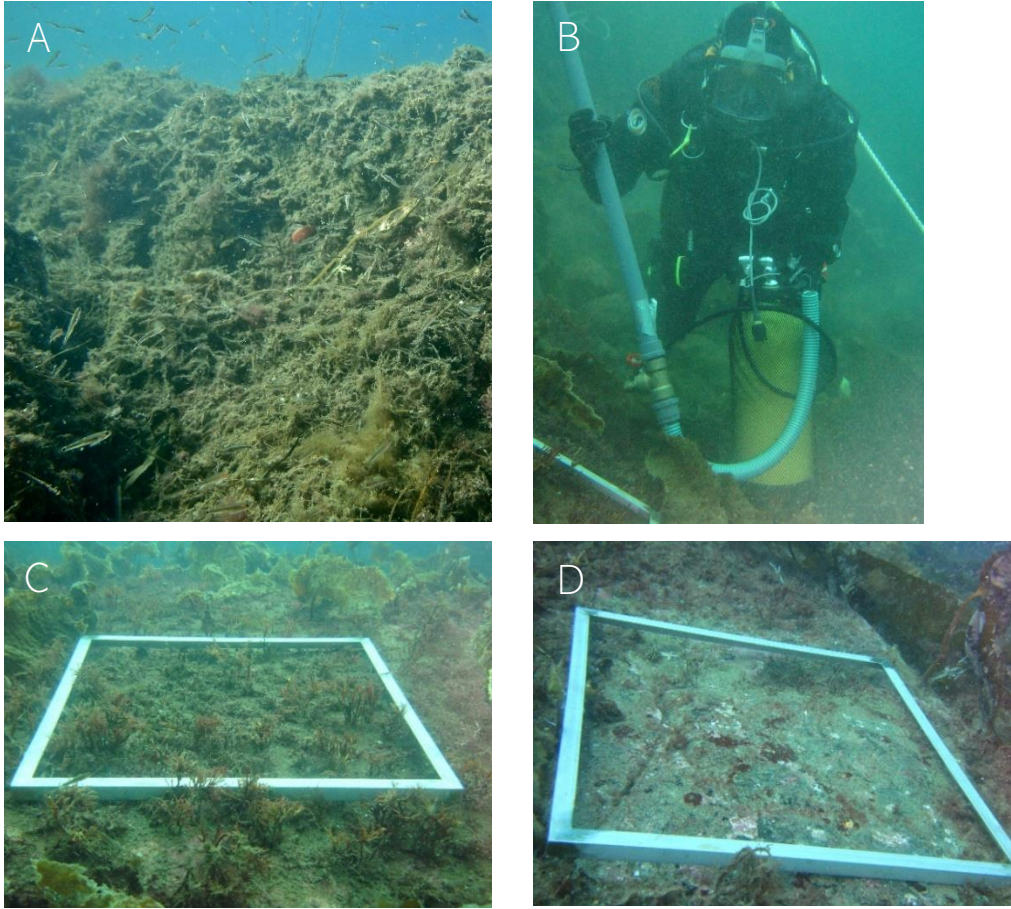


Figure 4: A) Typical turf habitat. Small fish were observed in this one (site SA4). B) Diver with suction-sampler. C) Site SA2 with metal frame placed on turf patch. D) Site HB7 after scraping and sampling.



Figure 5: A) Meshed bags containing collected samples. B) Marked Sample containers ready for samples.

2.3 Processing samples in the lab

Under a fume hood (while utilizing safety gear), samples were removed gently from the container and placed in a tub of water to loosen sediment and invertebrates. Algae were then moved to another tub with clean water and rinsed again. This process was repeated until the water became clean as it ensured less damage to organisms. The sedimented water was poured through a stack of sieves, starting with the coarsest sieve on top. A hose in the fume hood was utilized to wash the material through the sieves, sorting them into three different grain sizes (>0.5 mm, > 0.18 mm and > 0.063 mm). Material from the 0.5 mm sieve consisted of algae and invertebrates. The rinsed algae were placed in the uppermost sieve and washed with higher pressure to dissolve any remaining sediment or organisms.

The invertebrates from the 0.5 mm sieve were sorted into general groups (and dried at 60 °C before being weighed to acquire dry biomass weight. The following is a list of the invertebrate groups that were expected to be found.

Polychaetes	Echinoderms	Molluscs	Decapods	Amphipods
Tunicates	Oligocheates	Polylachophora	Nematodes	Bryozoa
Sponge	Anemone	Cumacea	Copepode	

Next, the algae were sorted into four functional groups (Figure 6). The term herbaceous algae was chosen for algae with an erect, rigid morphology, as it described the algae it represents better than for example cartilaginous.

<u>Herbaceous</u>	<u>Calcareous</u>	<u>Filamentous</u>	<u>Foliaceous</u>
Retains some shape when pulled out of water. Erect	Calcareous caseing. Erect.	Collapses into “slimy” blob when removed from water. Resembles cotton in water.	Thin leaflike structure
			
E.g. <i>Chondrus crispus</i>	E.g. <i>Corallina officinalis</i>	E.g. <i>Cladophora sp.</i>	<i>Ulva sp.</i>
Sources: www.dreamstime.com	www.miljolare.no	www.limnolife.de	http://www.fao.org/

Figure 6: Four functional groups the samples were sorted in to and examples from each.

After the algae were sorted, they were dried at 60 °C and weighed to gain dry biomass weight.

Sediment from the medium-sized sieve (0.18 mm) was collected in a plastic tray and dried at 60 °C. Before this, one of three sediment samples (not yet dried) from each site was selected to estimate biomass of smaller invertebrates. 15 ml of sediment was extracted from the original sediment sample. From the 15 ml tray, a smaller sample (20%) was extracted and diluted. This subsample was used to identify small invertebrates under a microscope.

These small invertebrates were sorted into the same invertebrate groups as above, dried at 60°C and weighed on a lab weighing scale. This weight was then calculated to represent the original sediment sample in the following way:

If x equals the weight of the invertebrate sample, then:

$$x / 20 * 100 = \text{invertebrate biomass in a 15 ml tray.}$$

This was then multiplied by the number of trays the original sediment sample contained.

Sediment from the 0.063mm sieve was placed directly in a pre-weighed and labelled aluminium tray (Figure 7 C) and dried at 60°C.

The dried sediment from the 0.18mm sieve (Figure 7 B) was, after weighing, ground in a mortar into a semi homogenous mix. A portion of this was placed in a pre-weighed and labelled aluminium tray, reweighed, and burned at 400°C along with the 0.063mm sediment. These trays were then weighed again, the weight subtracted from the pre burning weight and 2x aluminium tray weight to find organic content. For the sediment from the 0.18mm sieve, the weight was recalculated to represent the original sediment sample.



Figure 7: A) Herbaceous algae. B) Coarse sediment from 0.18mm sieve. C) Fine sediment from 0.063mm sieve

2.4 Additional environmental data

Salinity, temperature, and current data was provided by Jon Albertsen at IMR. Nutrient data were supplied by Lars-Johan Naustvoll also at IMR.

A time series from the turf mat stations were retrieved from a three-year (April 2017-March 2020) long simulation using the three-dimensional hydrodynamical model ROMS (Regional Ocean Modelling System, <http://myroms.org>) with 160 m \times 160 m horizontal resolution covering the inner Skagerrak. A similar model system, NorKyst800, covering the entire Norwegian coast and providing data along the open boundaries of the Skagerrak model is described in detail in

Asplin et al. (2020). Temperature, salinity and current data were modelled for 5 m depth for each of the sampling stations (Figure 2 and Table 1).

Nutritional values were acquired through daily CTD sampling at one location outside of nye Flødevigen IMR.

These abiotic factors were taken into consideration to examine what influence they had on the turf ecosystem, to examine what effect they had on the variations found in the turf samples. For all environmental measures except nutrients, a period of 5 months prior to sampling dates was selected to determine effects on species composition, biomass and sediment content. For nutrient data values from 3-10 meters depth was selected, as there was only one sampling location.

2.4.1 Temperature

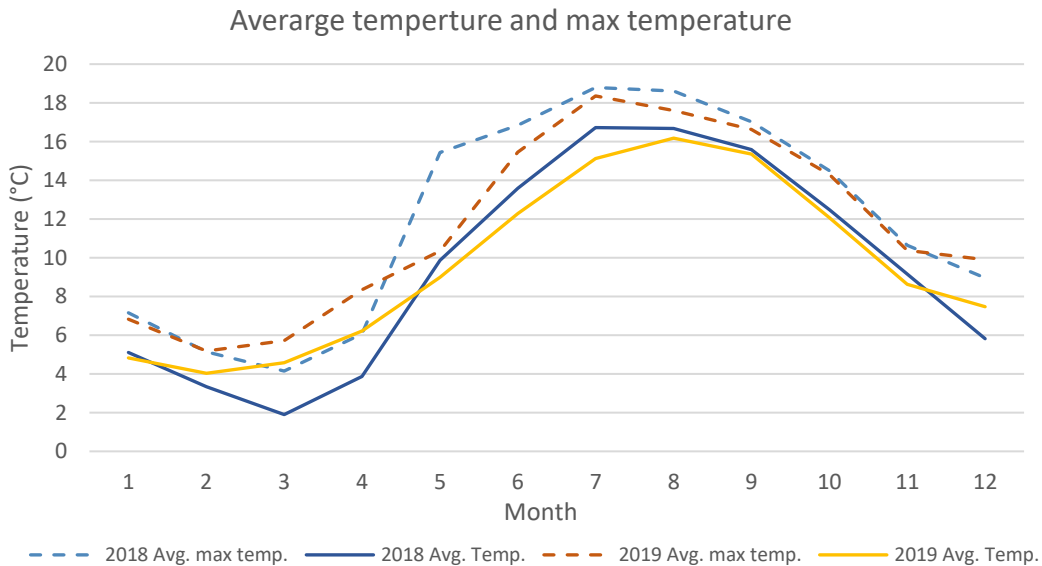


Figure 8: Average monthly **temperature**, as well as monthly max temperature for 2018 and 2019. Data supplied by Jon Albertsen at the Institute for marine research (IMR)

Figure 8 shows the average and the maximum temperature for the five months prior to sampling dates in autumn (month 6 to 10 in 2018) and spring (month 1 to 5 2019). Maximum temperature before sampling was 18.9°C in 2018 and 10.3°C in 2019. In the winter months of 2019 temperatures stayed above 3°C before spring sampling, while it went as low as 0.6°C in March 2018.

Modelled temperatures variation was negligible between sampling stations. S5, S7 and S8 had more significant seasonal variation in temperature both in 2018 and 2019, having lower average temperatures in winter and higher in summer by approximately 0.4°C than the other stations. 2018 had a colder ocean temperature in winter and early spring while exceeding 2019's late spring and summer temperatures. Max temperature never exceeded 19°C.

2.4.2 Salinity

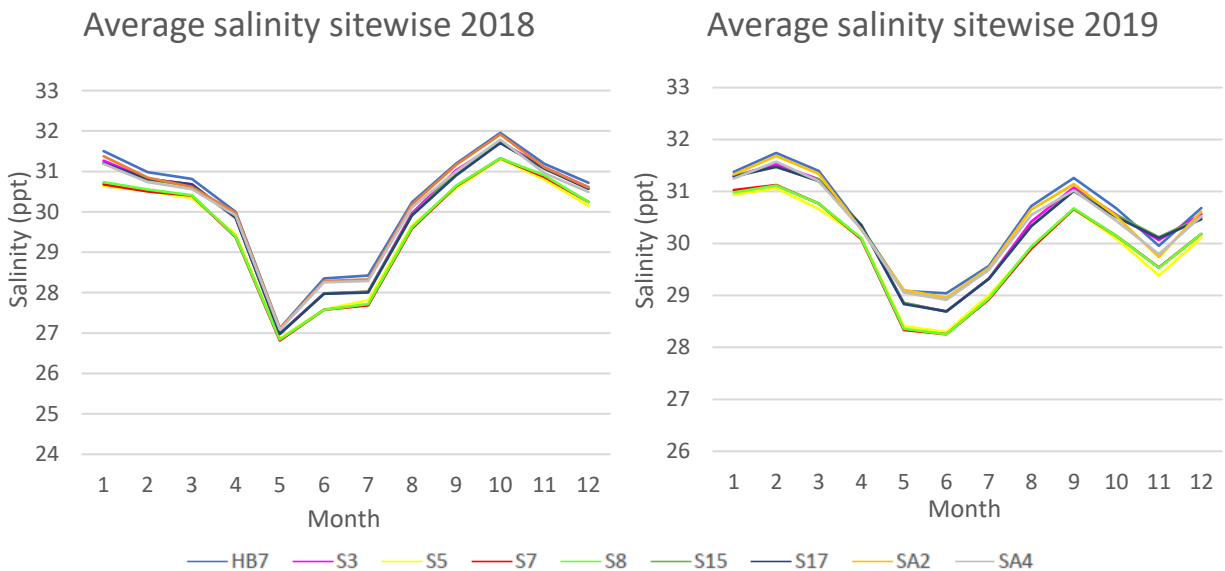


Figure 9: Line graph showing average monthly salinity for each site modelled at 5 m at for each station. Data supplied by Jon Albertsen at the Institute for marine research (IMR)

Salinity was consistently below the ocean's salinity average of 35 ppt (Sutton, 2010) Salinity was on average lower in autumn and higher in spring, possibly due to more rainfall and less evaporation in the colder months. The sites in descending average salinity are HB7, SA2, S15, S3, S17, SA4, S8, S7, S5. This held true for both years (Figure 9).

The lowest salinity was observed in May 2018 at ~27 ppt, while in May 2019 it ranged between 28.3 - 29.5 ppt. Salinity remained low for May through July. Maximum variation between stations in the same month could be up to 1 ppt. The highest modelled salinity was observed October 2018 for station HB7 at 31.8 ppt and was otherwise high January-March both years.

2.4.3 Currents

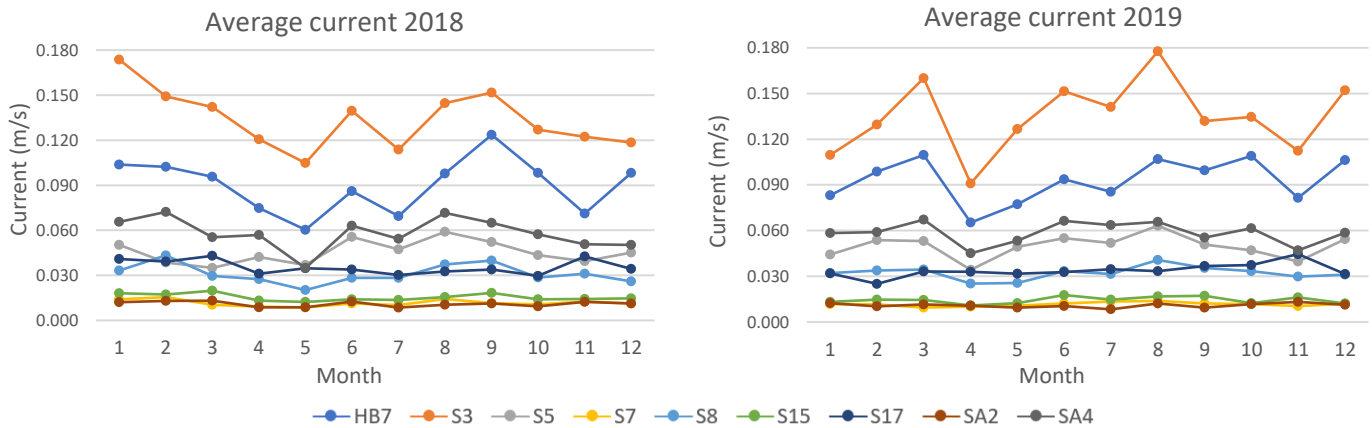


Figure 10: Modeled average monthly current speed for each sampling station from A) 2018 and B) 2019 at 5 meters. Data supplied by Jon Albertsen at the Institute for marine research (IMR).

There was a small but distinct difference in current influence from site to site. Sites ordered from highest to lowest current are S3, HB7, SA4, S5, S17, S8, S15, S7, SA2. Wave exposure (table 3) for each site was also considered as an influencing factor. Wave exposure is calculated by measuring the distance to land in 16 directions and calculating average wave exposure (SWM). This gives an estimate of fetch distance but excludes variations in wind and tide.

How current and wave action compared:

Wave exposure measures (SWM) supports the current models that S3 has the highest levels of water motion, followed by HB7, both categorized as medium exposed stations. SA2 has higher SWM of the protected stations, supported by the current model (Figure 10). According to the current model, S5 and SA4 overlap, while SA4 and S5 as the most protected of the sites. S17 and S8 have similar current measures and are only slightly lower than S5 between June and October with an overlap in the other months (Figure 10). In table 3, S15 is ranked between S8 and S15, while the current model indicates that S15, S7 and SA2 are the most protected sites.

Table 2: Wave exposure (SWM) at each of the nine sampling sites and their exposure level.

SITE	EXPOSURE LEVEL	SWM
S3	Medium exposed	191418
HB7	Medium exposed	126409
SA2	Protected	90775
S8	Protected	62552
S15	Protected	54175
S17	Protected	44037
S7	Protected	41577
SA4	Protected	33487
S5	Very protected	7674

2.4.4 Nutrients

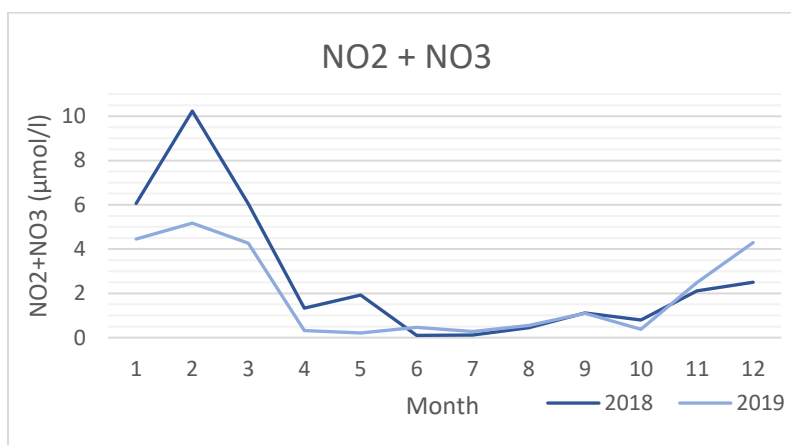


Figure 11: Inorganic nutrient concentration measures collected by CTD from Ærøydypet near IMR nye Flødevigen. Data supplied by Lars-Johan Naustvoll at the Institute for marine research (IMR).

Nutrient levels were higher in the spring season for 2018 than in 2019 (Figure 11). February 2018 CTD samples measured 10.2 $\mu\text{mol NO}_2 \pm \text{NO}_3$ per litre. In 2019 the same month measured 5.7 $\mu\text{mol/l}$. The months leading up to sampling in October 2018 nutrient concentration remained below 1 $\mu\text{mol/l}$, while they remained above 4 $\mu\text{mol/l}$ till march before dropping to 0.3 in April and May in 2019. A first set comprising of chlorophyll, nitrate, nitrogen species, phosphorus, oxygen, nitrite, ammonium and total nitrogen were all of part of this data, yet nitrite and nitrate were chosen as the most biologically relevant variable as they are the limiting factor for primary production. The following is an extrapolation of sampling site proximity to urban populations

(Figure 2), and thereby exposure to nutrient-loaded runoff, from high to low: SA4, S15, SA2, S5 and S17, HB7, S7 and S8, S3

2.5 Statistical analysis

Upon finding a statistically significant effect of site on total algae weight using ANOVA, Tukey's honest significant difference multiple comparison test was performed on algae weight means.

Linear regression was performed on species count by mean current. A prior assessment of normality of distribution was carried out with the Shapiro-Wilk test, and upon finding significant p-value, the dependent variable was transformed to an adequate power determined using Box-Cox transformations. The degree of the model was then selected based on the lowest Aikake Information Criterion (AIC) value. The amount of variation in biotic variables explainable by abiotic variables was quantified as R-squared values and tested for significance with permutation tests (n=99999).

Algae species abundance score was calculated by summing up all abundance numbers within each season separately and dividing by the number of samples (9).

Variation partitioning by redundancy analysis was used to quantify the contributions of current, salinity and temperature on algae species, creating a Venn diagram.

A non-metric multidimensional scaling (nMDS) was performed on algae community composition using the Bray-Curtis distance. Five months of mean 90th percentile current, salinity and temperatures preceding sampling were fitted onto the latter ordination.

Sites were hierarchically clustered (UPGMA) by algae species for both seasons. Node support was computed using approximately unbiased bootstrapping p-values (Suzuki & Shimodaira, 2006).

2.6 Litterateur search

A systematic literature search was conducted using the following search engines:

Google Scholar	https://scholar.google.com
Elsevier	https://www.elsevier.com/search-results?query=algae
Web of Science	https://clarivate.com/webofsciencegroup/solutions/web-of-science-core-collection/
bioRxiv OA	https://www.biorxiv.org
DUO	https://www.duo.uio.no
Researchgate	https://www.researchgate.net

For up to date algae species names and information, the website AlgaeBase.org (Guiry & Guiry, 2020) was utilized.

3 Results

Quantitative data of sediment content, algae biomass, invertebrate biomass and species composition found in the turf samples were analysed. Seasonal variation naturally altered species composition, sediment content as well as invertebrate groups. Current did impact sediment content and algae biomass, while variation in temperature and salinity was not sufficient between sampling stations to show an effect other the seasonal. Herbaceous and calcareous morphological biomass were the most abundant, while filamentous algae tended to grow epiphytically on these. Of all invertebrate groups found, polychaetes and molluscs (mainly tiny gastropods) were the most common. Echinoderms and decapods were relatively small in size both seasons.

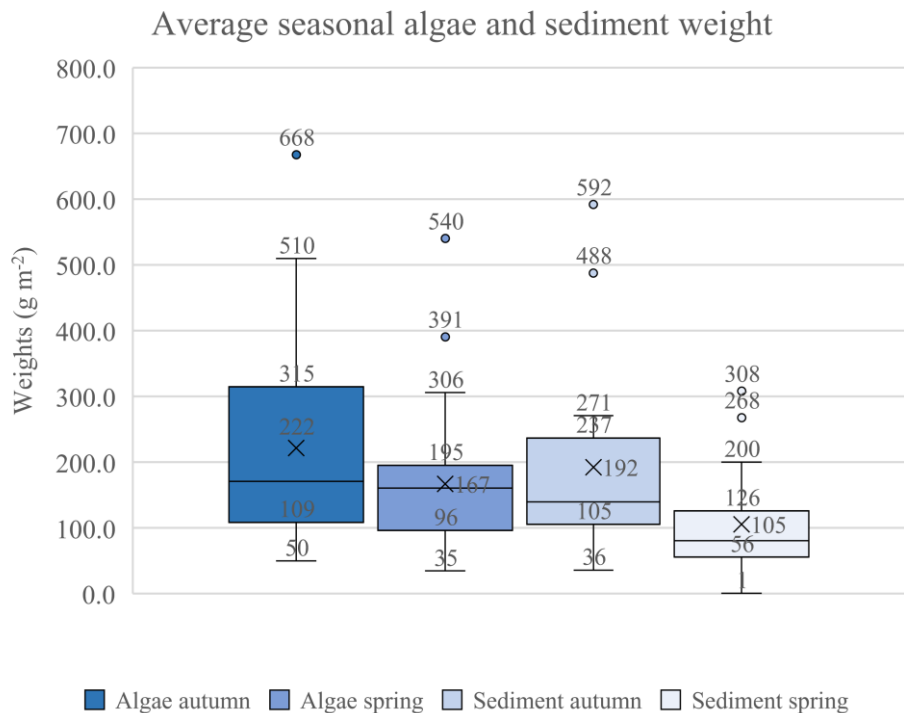
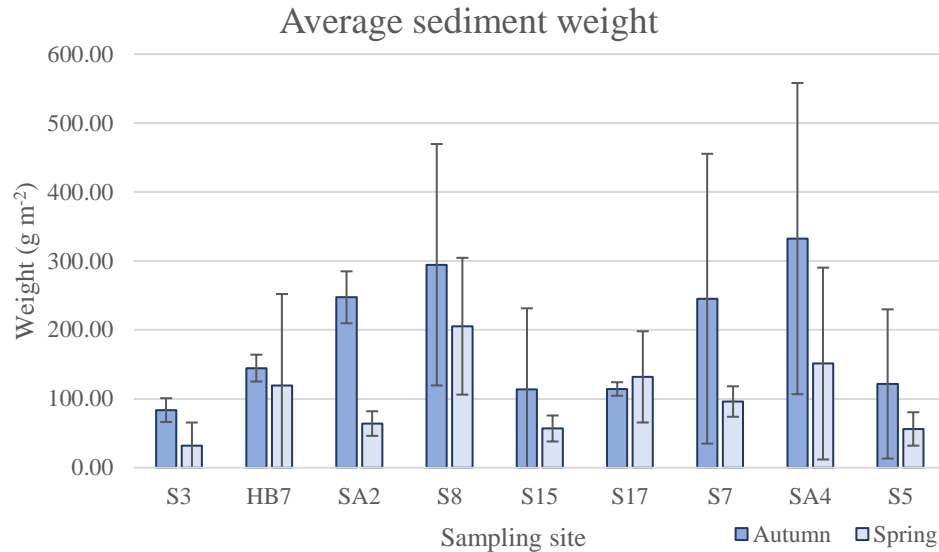


Figure 12: Box plots values calculated from average seasonal total algae and sediment content. The individual points above the boxes indicate outliers, the uppermost point representing the site with the highest weight in grams. An x in each box marks sediment content average, while the internal line is representing the median. The lower error bar represents the site with the lowest sediment content

Overall, the algae biomass and sediment content were higher in autumn than in spring, as shown in figure 12.

3.1 Sediment



	S3	HB7	SA2	S8	S15	S17	S7	SA4	S5
Autumn	a	a	a	a	a	a	a	a	a
Spring	b	bc	bc	c	bc	bc	bc	c	bc

Figure 13: Average sediment content per 1m² per sampling station seasonally. Error bars are standard deviation. Groups of means (Tukey's HSD) for algae biomass are displayed by site and season in accompanying table. Letters for groups of means are specific to each season; means may be equal for spring and autumn sites, but the Tukey groups of means were computed separately for each season.

Except for S17, all sites had higher sediment content in autumn (Figure 13). S8 and SA4 had intermediate current flow (Figure 10) and were considered 'protected' from wave exposure (table 2). These two stations had the highest sediment content in autumn and spring, respectively. S3 had the highest wave exposure and current flow, and the lowest sediment content. HB7 were second-highest current and SWM, yet sediment content was relatively high both seasons (Figure 13). The first of three HB7 samples from spring had no sediment but was instead full of unattached eggs. The third HB7 spring sample contained mainly coarse mollusc-shell based sediment. HB7 autumn samples had a mixture of sediment and crushed mollusc shells. A local source of mollusc shells could have provided the heavier material and was carried shorter distances by the strong flow before settling.

S7, SA2 and S17 experience low velocity currents and had higher sediment content, while S3 and HB7 had high wave exposure and current, and little sediment. S5 had low wave exposure and low sediment content. Sites with the highest sediment content experienced intermediate current velocity.

3.1.1 Sediment correlation

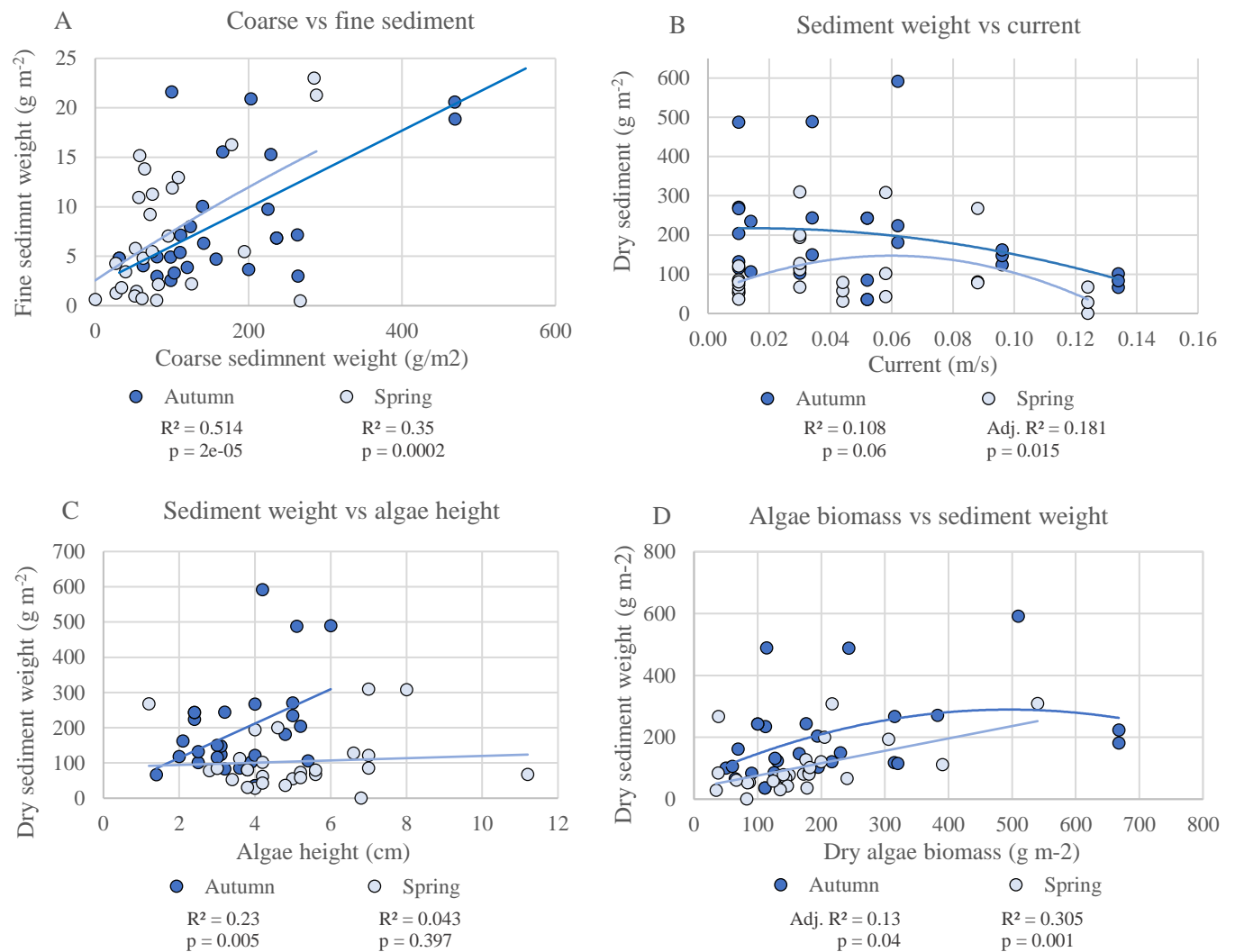


Figure 14: Scatterplots comparing A) Coarse sediment content to fine sediment content. B) Currents influence on sediment content. C) Turf algae height effect on dry sediment content. D) Algae biomass effect on sediment content. First or second-degree models were chosen based on lower AIC value.

Links between coarse and fine sediment were modelled using linear regression (Figure 14 A), resulting in positive relationships explaining 51.4% of the variation in autumn and 35% in spring. Sediment content displayed a concave (Linnaeus) Kützing relation to current speed (Figure 14 B) for both seasons. The autumn variables are, however, weakly associated according to the model. Algae height only significantly affected sediment content in autumn (Figure 14C), while algae biomass significantly explained sediment for both seasons (Figure 14D).

Sediment vs morphological algae biomass

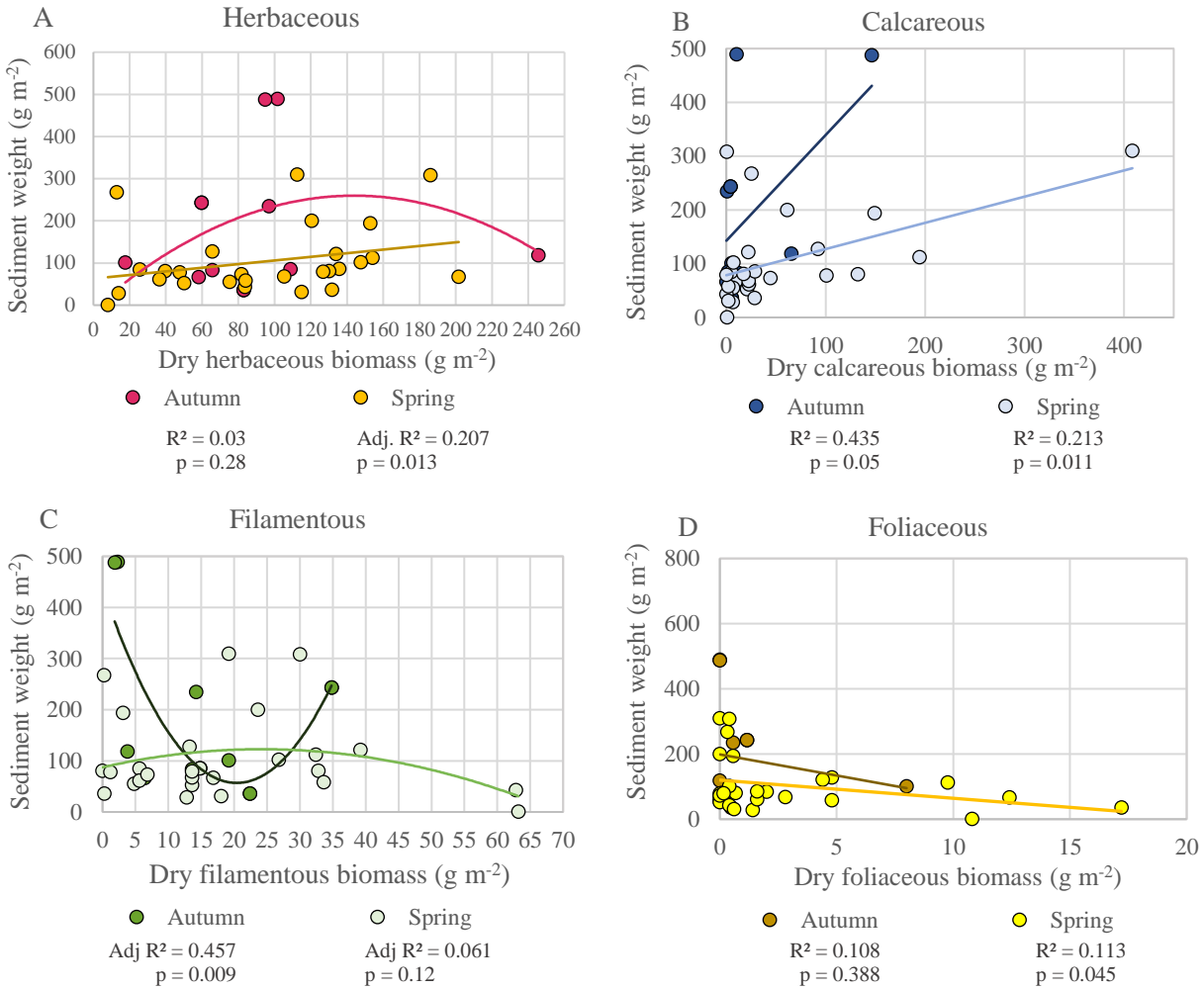


Figure 15: Scatter plots displaying A) herbaceous, B) calcareous, C) filamentous, D) foliaceous algae biomass against sediment content. First or second-degree regression was chosen based on the lowest AIC value.

Significant relations were found between sediment and morphological algae biomass (Figure 15). The autumn samples have missing data but were included as autumn biomass impacted sediment content as seen in figure 14 D. Sediment was significantly impacted by spring herbaceous algae (Figure 15 A), calcareous algae for both seasons (Figure 15 B), autumn filamentous algae (Figure 15 C) and spring foliaceous algae (Figure 15 D). The regression line was concave for filamentous algae in autumn. Both calcareous and filamentous algae could explain almost half of the sediment variation for autumn. Both herbaceous and calcareous algae had a positive response on sediment content in spring, while sediment behaved in a concave fashion for filamentous algae. Filamentous algae contribute to sediment increase in turf up until a certain point (6 g of algae biomass) before it begins decreasing with increased biomass.

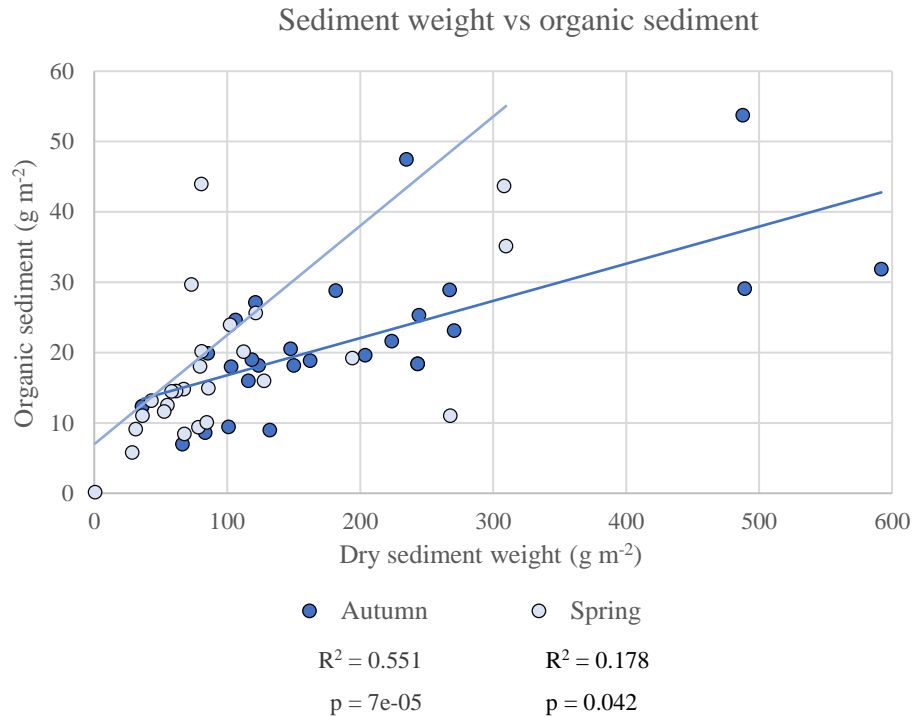


Figure 16: Scatter plot displaying organic content in relation to sediment content. Linear regressions were performed on data separately by season.

Organic content in sediment was positively related to sediment content (Figure 16). Neither algae biomass nor invertebrate biomass had any significant impact on organic material. Autumn experienced higher levels of organic matter, as well as a stronger correlation between sediment content and organic content.

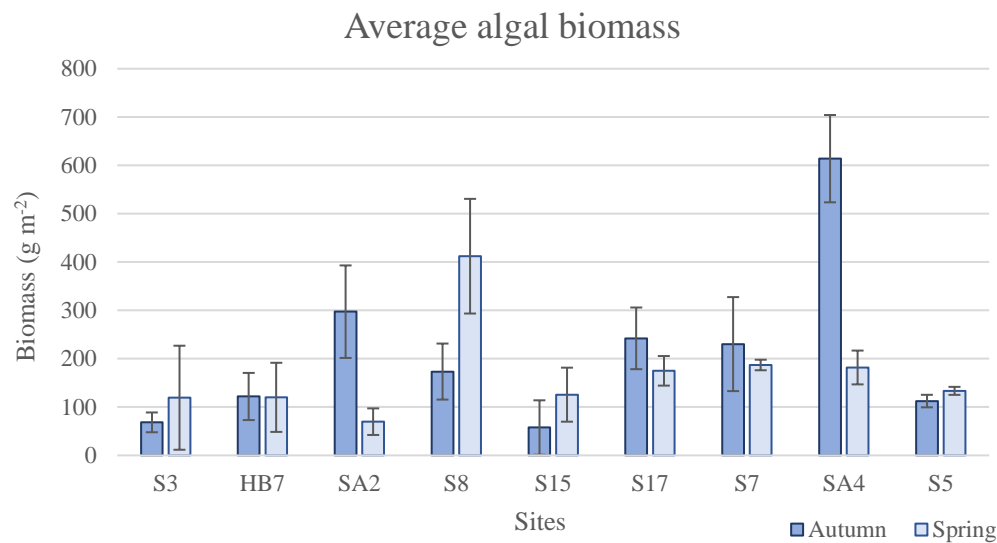
3.2 Turf algae

Sixty species of algae were identified, of which 38 were rhodophytes, 16 were phaeophytes, 5 were chlorophytes, and 1 was cyanobacteria. Rhodophytes were dominant for both autumn and spring, with a higher species count for autumn. Phaeophytes and chlorophytes were more common in spring. Rhodophyta had 13 unique species in autumn, and 4 in spring, and had 21 overlapping species. Phaeophytes had three unique species in autumn and 8 in spring, while five were found in both seasons. Of the Chlorophytes, there was one unique species for autumn and 3 in spring. They shared one identical species. Only one cyanobacterium was found overall, belonging to the genus *Lyngbya*.

Of the four morphological traits, the herbaceous type was the most abundant in terms of biomass (Figure 18), while species richness for herbaceous and filamentous groups were very similar. There are 23 herbaceous algae in total. 17 in autumn, 7 of them unique. 16 herbaceous species were counted in spring, 6 of them unique.

Filamentous algae had a total of 25 species, 17 in autumn with 5 unique species in autumn, 20 in spring, 8 of them unique and 12 in common.

There were overall six calcareous algae identified, all six were found in autumn and 4 found in spring. Calcareous algae had 2 unique species in autumn, none in spring and 4 in common. Five foliaceous algae were found in total, three in each season with *Ulva* sp. as the shared species.



	S3	HB7	SA2	S8	S15	S17	S7	SA4	S5
Autumn	a	abc	d	ad	ab	cd	bd	e	ab
Spring	f	f	f	g	f	f	f	f	f

Figure 17: Average dry algae biomass from each site. The error bars represent standard deviation. Groups of means (Tukey's HSD) for algae biomass are displayed by site and season in accompanying table. Letters for groups of means are specific to each season; means may be equal for spring and autumn sites, but the Tukey groups of means were computed separately for each season.

Total algae biomass was not consistently higher in spring or autumn (Figure 17), suggesting other factors than season to be the source of variation. SA2, S17, S7 and SA4 had higher biomass in autumn, SA4 the highest of them. S3, S8, S15 and S5 had higher biomass in spring. S8 had the highest biomass for this season. One of the Spring SA4 samples consisted mainly of *Desmarestia*

aculeata (Linnaeus) J. V. Lamouroux and had little sediment. Groups of means had to be computed separately since season is a structured variable, whereas sampling site is not (no a priori apparent structure to order them by). Rigorous use of multiple comparisons such as Tukey's HSD was applied to means of unstructured variables. Turf biomass for autumn ranged from 58 to 613 g m⁻² with an average of 213 g m⁻². Spring biomass was lower, ranging from 69 to 412 g m⁻² with an average of 169 g m⁻².

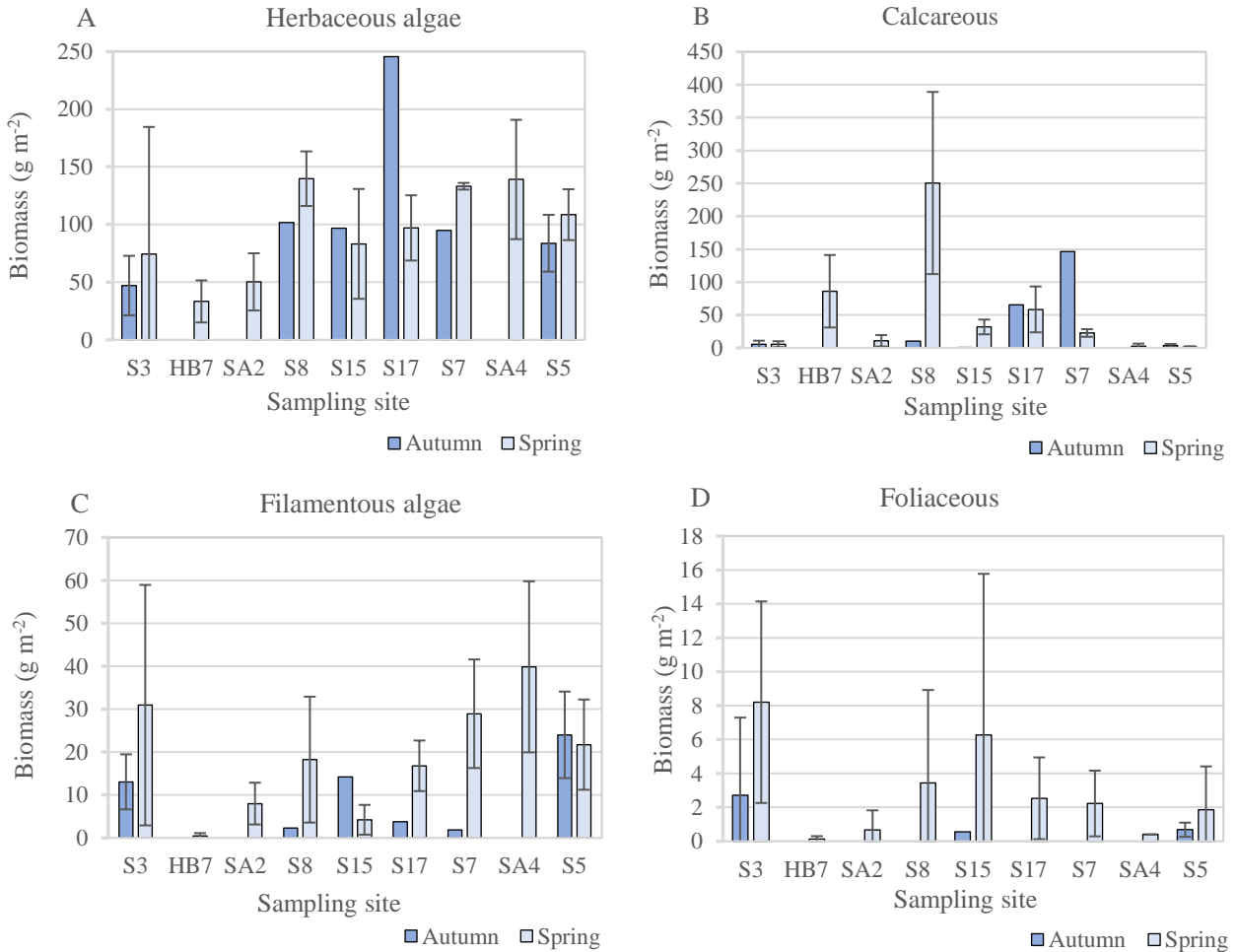


Figure 18: Total A) herbaceous, B) calcareous, C) filamentous, D) foliaceous dry algae biomass site wise. Three autumn samples (HB7, SA2 and SA4) are missing due to sample processing error. All autumn samples except S3 and S5 lack error bars because only one sample for each site was sorted into morphological types.

Herbaceous morphology was dominant in both seasons (Figure 18 A). Calcareous algae biomass varied greatly between samples and were often dominant in the samples they were found in (Figure 18 B). Filamentous algae mainly grew epiphytically and had in many cases completely

overgrown the erect algae (e.g. S3 and S7 in spring) (Figure 18 C). Foliaceous algae were rare and were mostly found in spring (Figure 18 D). *Delesseria sanguinea* (Hudson) J.V.Lamouroux 1813, is a semi-annual alga species that is reduced to only consist of the midrib in the fall. *Ulva* sp. was found both in the spring and the fall (See Appendix E).

3.2.1 Abiotic factors effect on algae biomass

Temperatures and salinity varied little between stations and was therefore not adequate to use for comparing effects on the ecosystem, other than the seasonal one. Instead current was influential on both biomass and species composition.

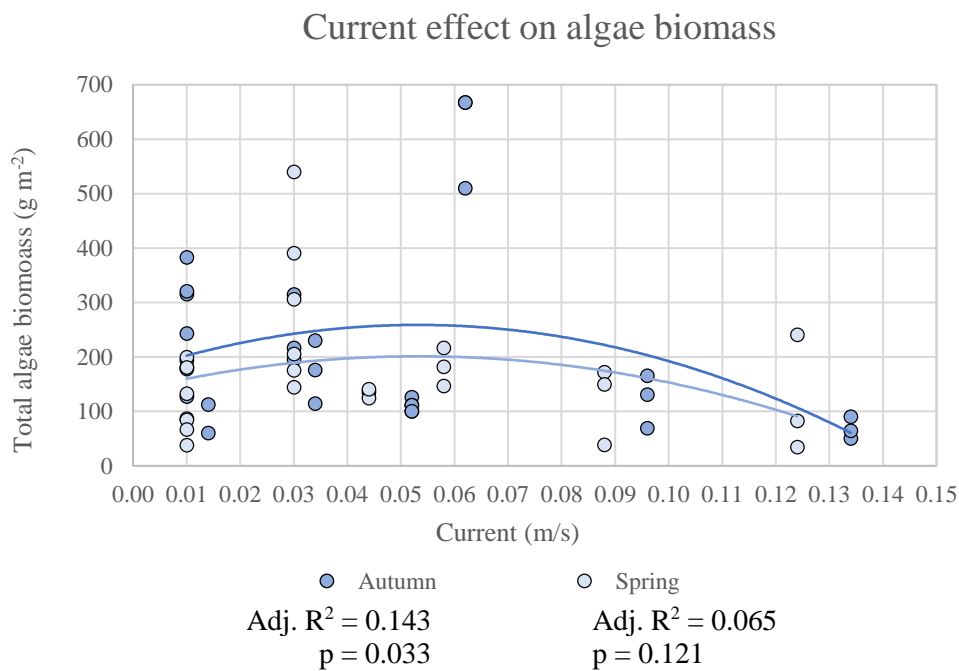


Figure 19: Scatter plot displaying currents effect on algae biomass. AIC value was used to select models.

The variation in biomass was greater and on average higher in the lower ranges of current speed. In areas with higher current speed biomass was reduced and data had less spread. Algae biomass only had a significant relationship with current in autumn.

Current vs morphological algae biomass

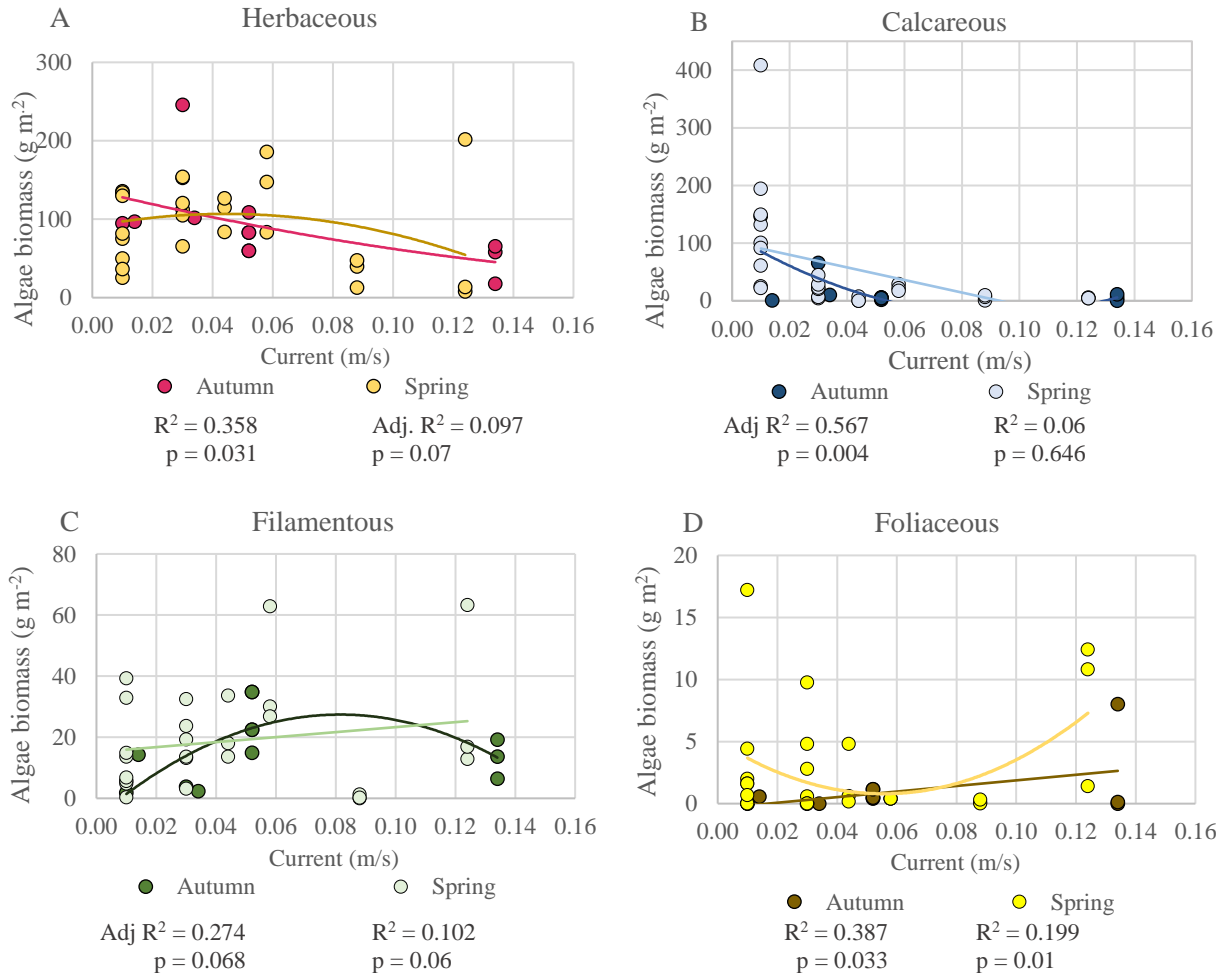


Figure 20: Scatter plots displaying currents effect on A) herbaceous, B) calcareous, C) filamentous, D) foliaceous algae. AIC was calculated to choose whether first degree or second-degree models best fitted the data.

Autumn morphological biomass data have missing values (see Appendix D, Table D1), yet it was included as the current had a significant impact on total algae biomass (Figure 19). Figure 20 shows that all except spring calcareous, filamentous autumn, and foliaceous spring biomass were significantly influenced by current. While increasing current negatively impacted herbaceous and calcareous algae biomass, it had a positive effect on spring filamentous and autumn foliaceous algae.

3.3 Turf algae species composition

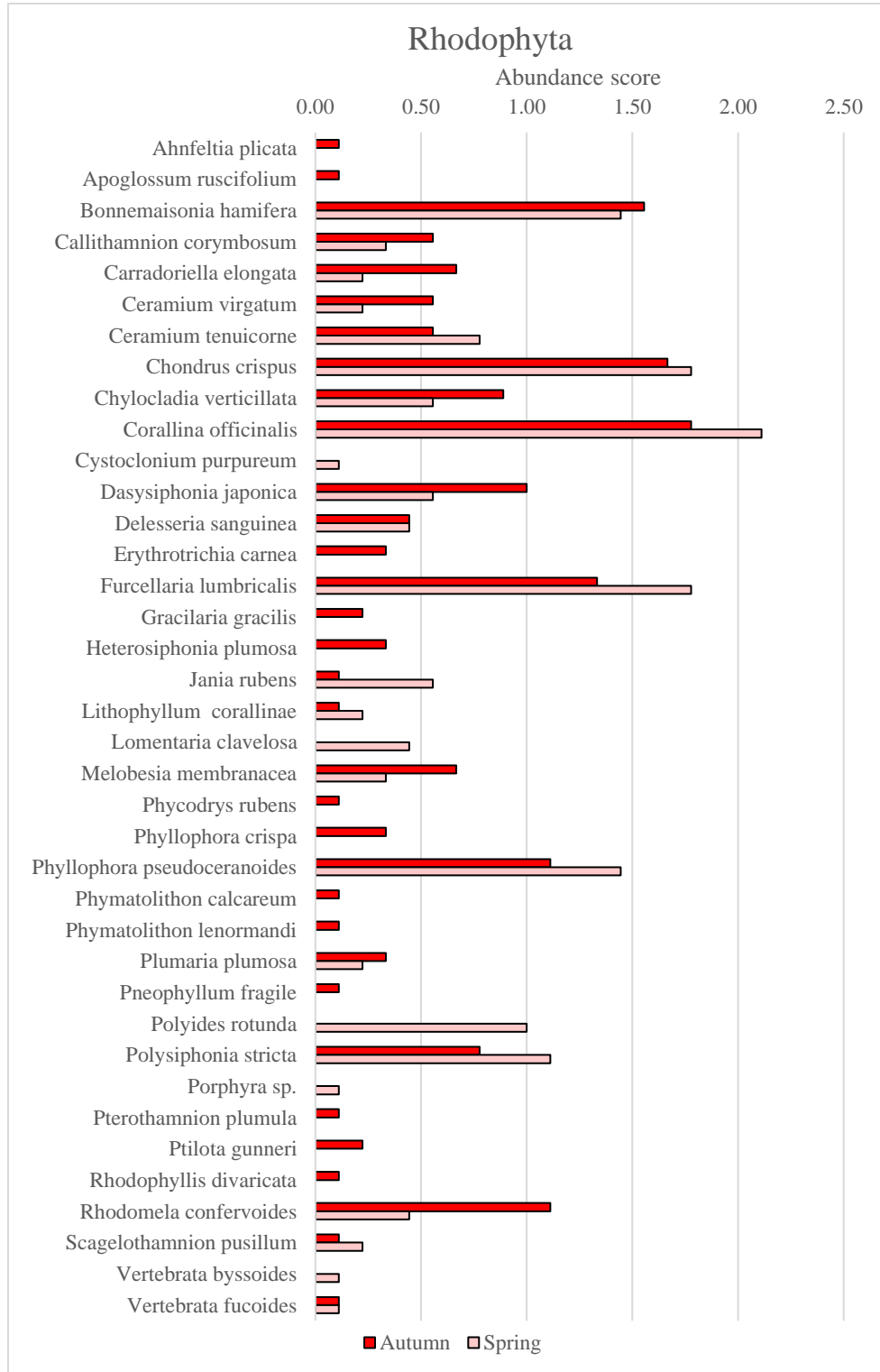


Figure 21: All identified red algae species in autumn and spring with average abundance score.

Both seasons contained 38 species of red algae in total, where 17 were unique to each season. *Bonnemaisonia hamifera* Hariot 1891, *Chondrus crispus* Stackhouse 1797 and *Corallina officinalis* Linnaeus 1758 all had an average abundance score above 1.5 for the autumn samples, although *B. hamifera* had an abundance score of 1.4 in spring. Overall *C. crispus* and *C. officinalis* were the most abundant algae, and both were more abundant in spring than in autumn. *C. crispus* spring score was 1.7, and *C. officinalis* had a score of 2.1. *Furcellaria lumbricalis* (Hudson) J.V.Lamouroux 1813 score was 1.7 in spring, and 1.4 in autumn (Figure 21).

Other high scoring Rhodophyta (between 1.5 and 1) were *Dasysiphonia japonica* (Yendo) H. S.Kim 2012 in autumn (1.0), *Phyllophora pseudoceranooides* (S.G.Gmelin) Newroth & A.R.A.Taylor ex P.S.Dixon & L.M.Irvine 1977 in autumn (1.1) and spring (1.44), *Polyides rotunda* (Hudson) Gaillon 1828 in spring (1.0), *Polysiphonia stricta* (Mertens ex Dillwyn) Greville 1824 in spring (1.1) and *Rhodomela confervoides* (Hudson) P.C.Silva 1952 in autumn (1.1) (Figure 21).

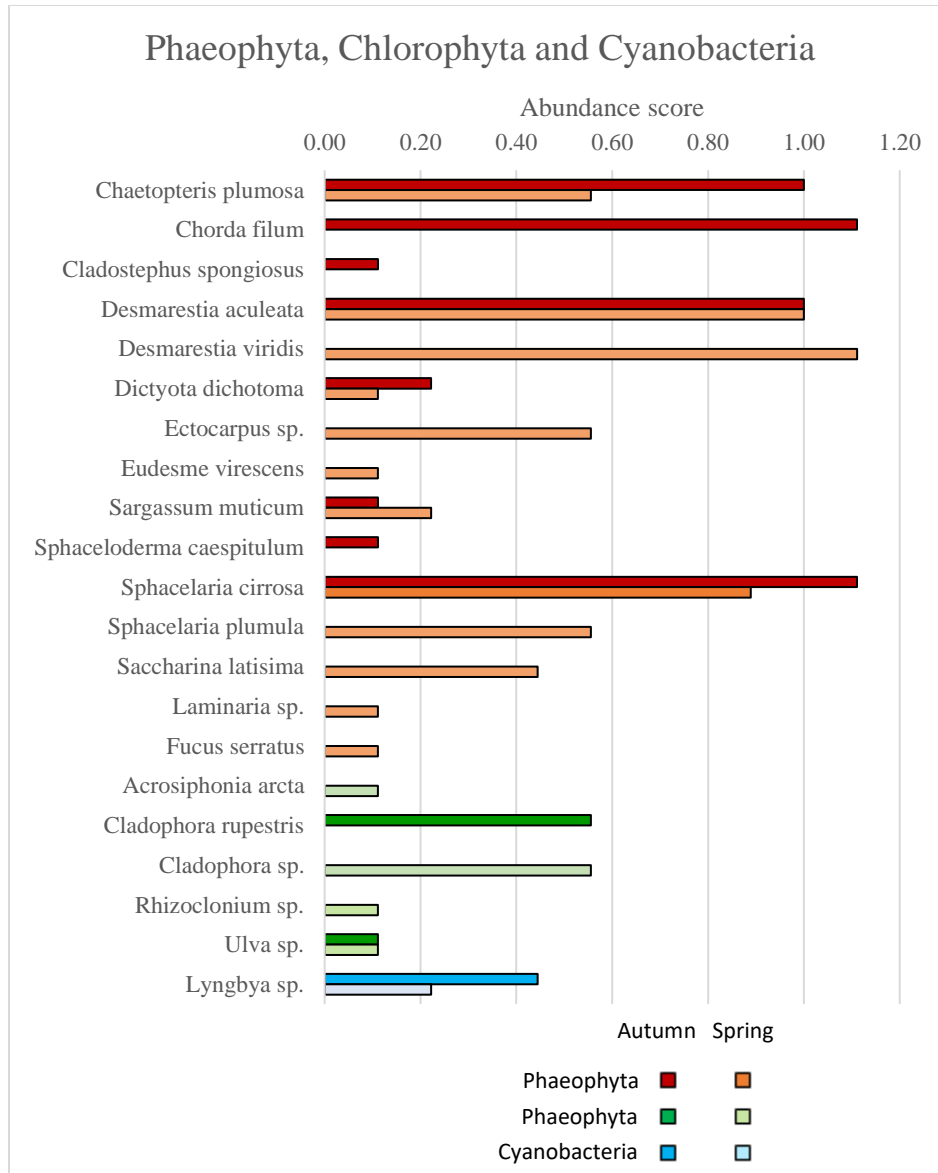


Figure 22: List of identified phaeophytes, chlorophytes and cyanobacteria with associated abundance number.

Of the phaeophytes, *Chorda filum* (Linnaeus) Stackhouse and *Sphacelaria cirrosa* (Roth) C.Agardh scored 1.1 in autumn. In both sampling seasons, *Chaetopteris plumosa* (Lyngbye) Kützing 1843 in autumn and *Desmarestia aculeata* scored 1.0. Chlorophytas highest score was 1.1 in autumn for *Cladophora rupestris* (Linnaeus) Kützing, and *Cladophora sp.* which was only found in spring (Figure 22).

3.3.1 Algae species composition and abiotic factors

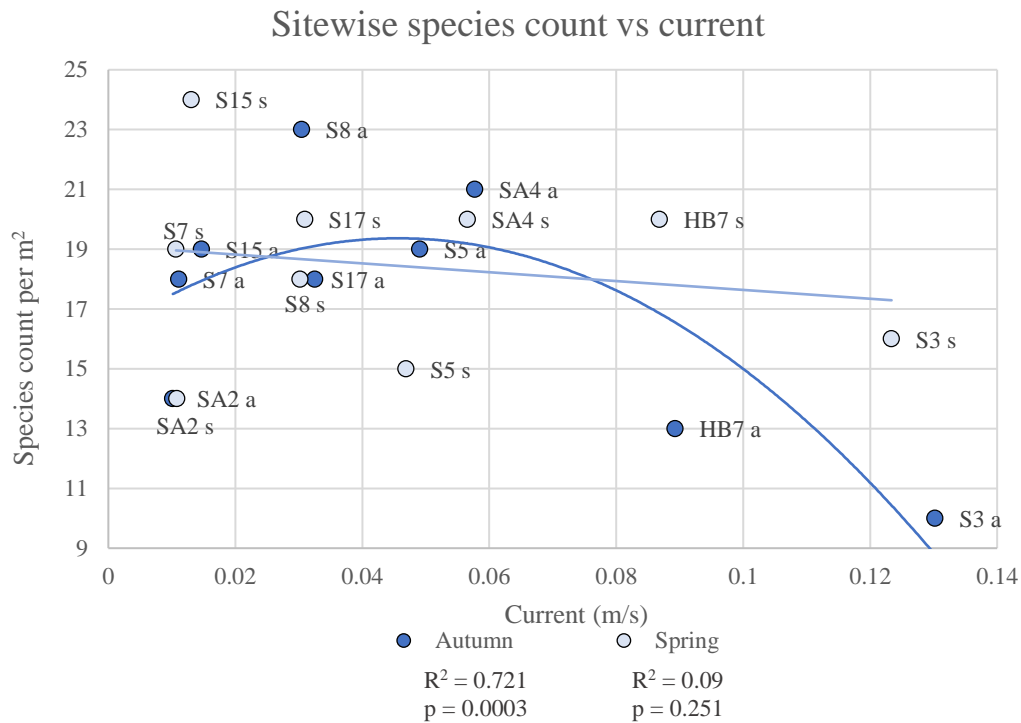


Figure 23: Average current plotted against species count for each individual site. Current was derived from the average five months prior to each sampling. a = autumn, s = spring. Based on AIC, a first order model was chosen to describe the relation between species count and current in spring, while a second order model was selected for the corresponding relation in autumn.

There was a somewhat inverse behaviour between species count and current. The latter had a significant effect on species count in autumn but not in spring. Autumn samples displayed a concave trend, indicating higher species richness in sites with intermediate current levels (Figure 23). S3 separated itself from the rest in terms of species composition and was also the site with the highest current exposure. Species richness was mostly higher in spring than in autumn for every site except for SA2, S8 and SA4.

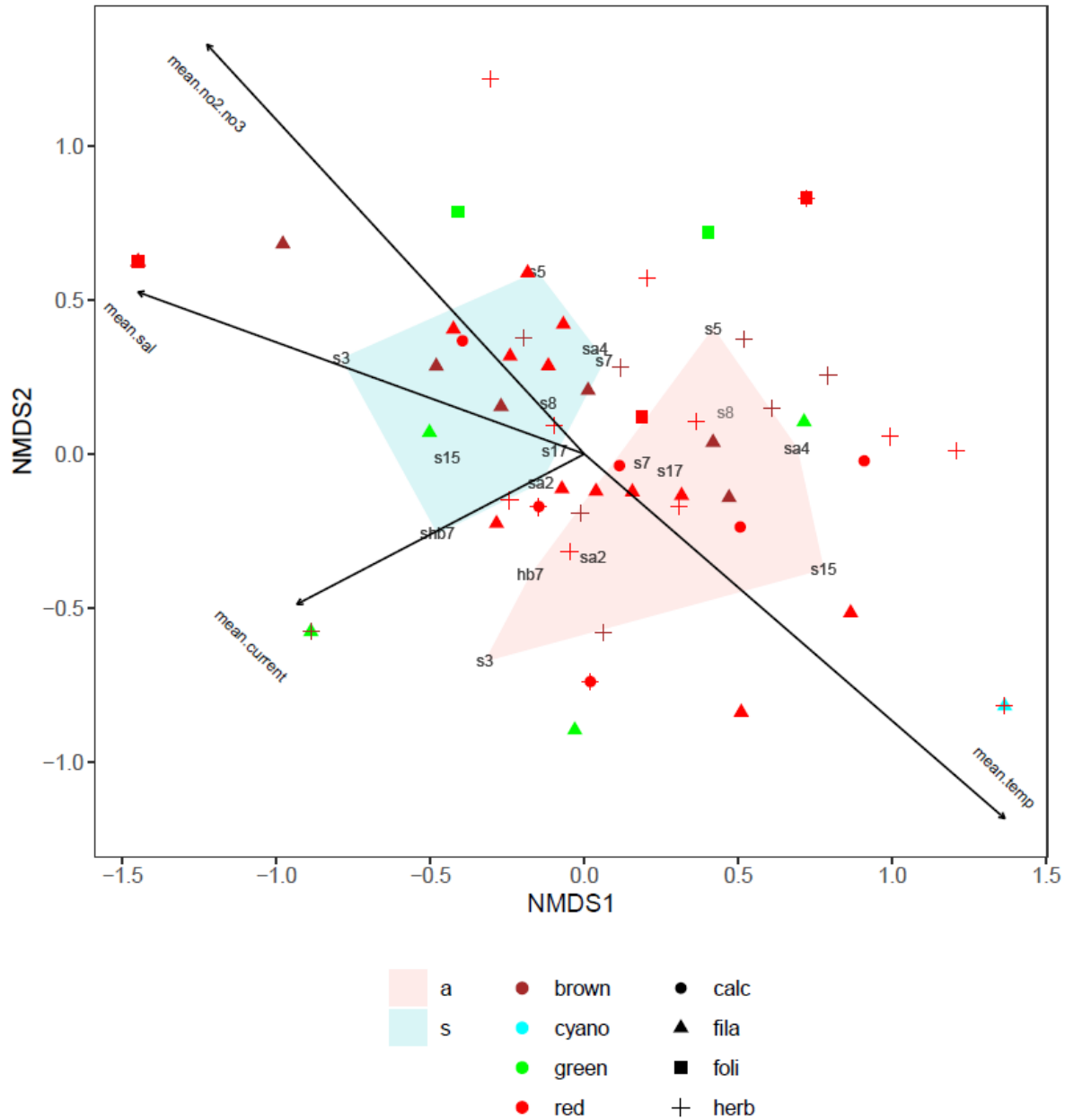


Figure 24: Non-metric multidimensional scaling of algae abundances for samplings in autumn 2018 and spring 2019. Species scores are plotted as shapes and site scores as text. Algal phylum and morphological type are indicated by colour (Phaeophyta=brown, Cyanophyta=blue, Chlorophyta=green, Rhodophyta=red) and shape (calcareous=round, filamentous=triangle, foliaceus=square, herbaceous=cross). Observations for each season are delimited by coloured polygons (a = autumn = red, s = spring = blue). Mean (average of the five months prior to sampling) salinity, current, temperature and nitrogen values were fitted onto the ordination and displayed here as vectors.

Observations by season (Figure 24) did not overlap and show significant differences, indicating that the sites discriminate clearly by season. Although mean current, salinity, temperature and nutrients fit significantly with the ordination, they do not closely follow its main axes. Mean nutrients followed the mean temperature vector. There were only one set of nutrient data per

season, causing this effect. Temperature and salinity point in opposite directions, suggesting they follow a common pattern likely attributable to seasons. Adjusted R-square for the effect of season on algae species abundances variation was 9.1%. Current behaves differently than temperature and salinity as indicated by a vector somewhat perpendicular to the latter.

Nutrient means were discriminated by season which resulted in two identical vectors with opposite directions when fitted onto the ordination. A first set comprising chlorophyll, nitrate, nitrogen species, phosphorus, and oxygen displayed a positive relationship with spring, while nitrite, ammonium and total nitrogen together with temperature varied positively with autumn. This data was supplied by Lars-Johan Naustvoll along with the relevant nutrient data yet was not included in the figure as they aligned perfectly either with nitrogen species or temperature vectors.

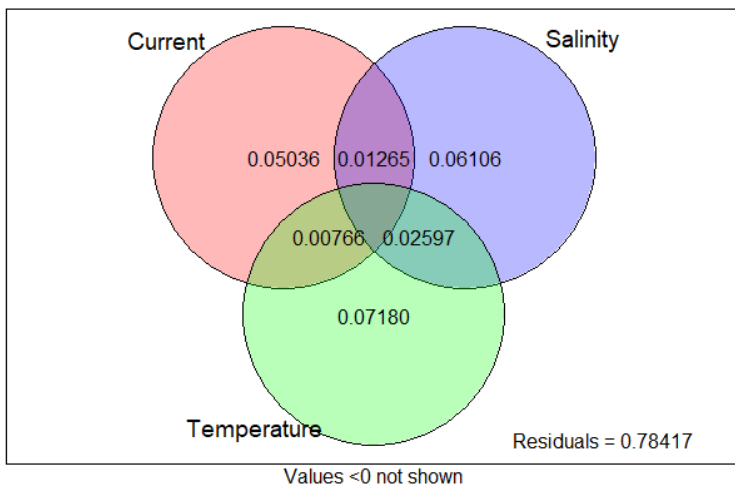


Figure 25: Venn diagram showing R-squared values for current, salinity and temperature effect on algae species composition. The overlapping areas indicate shared contributions to observed variation.

Current, temperature and salinity for both seasons explain a combined 21.5 % of the variation observed in algae species composition (Figure 25).

3.4 Invertebrates

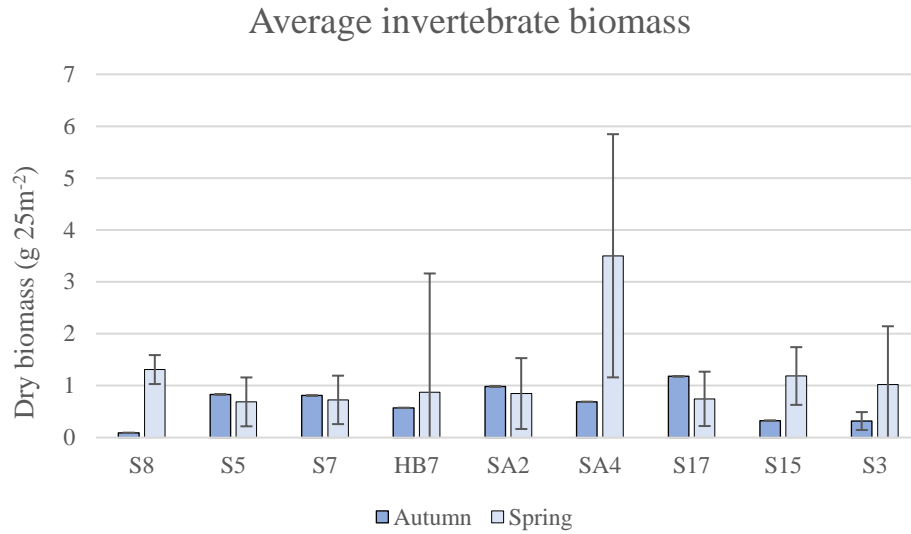


Figure 26: Average dry invertebrate biomass per 1m² for each sampling station. Error bars are standard deviation. Missing data from autumn samples result in single values for affected sites. Therefore, no standard deviation was obtained with the exception of S3. This biomass represents an area of 25cm².

Of all sites, SA4 had the highest invertebrate biomass. On average, the spring samples had higher invertebrate biomass than the autumn samples. S8, HB7, SA4, S15 and S3 had higher spring biomass, SA4 quite significantly so (Figure 26). Fan worms, a large polychaete, along with larger specimens of echinoderms, decapods and gastropods make up the larger portion of the spring samples, especially SA4. The main invertebrate components of the autumn samples were polychaetes, and some smaller gastropods, decapods and echinoderms (see Appendix C).

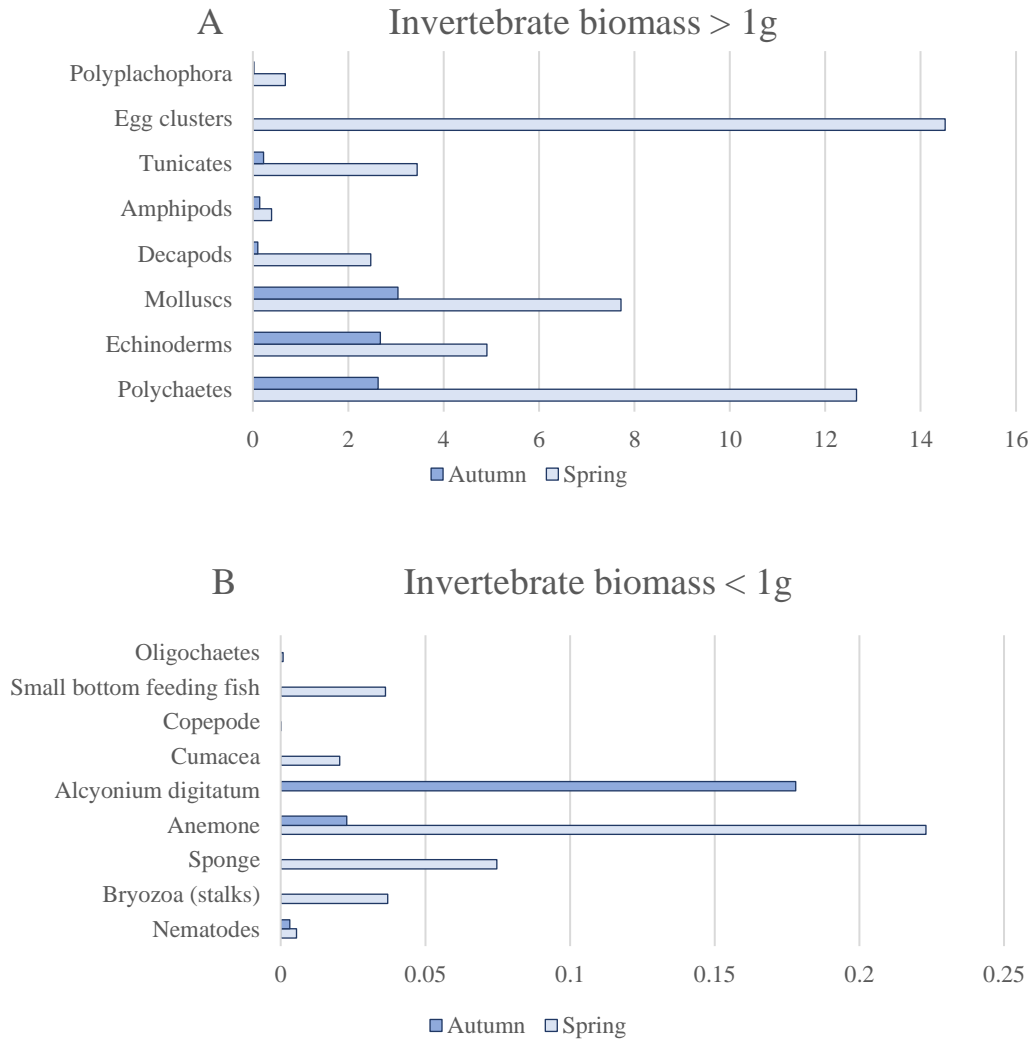


Figure 27: Total dry invertebrate biomass from all nine sites season-wise. A) Biomass close to or more than 1g. B) Biomass less than 1g. Attempts to calculate averages for invertebrate biomass rendered chart unreadable.

All organisms (except *Cumacea*) had higher biomass in spring than in autumn. Polychaetes, molluscs, echinoderms and decapod individuals were significantly larger in spring. Four samples from spring contained sea hare, which was grouped with other molluscs. One of the spring samples from site HB7 contained an abundance of sea hares. This sample also contained large quantities of unattached eggs from an unknown source, while in other samples eggs were found attached to the vegetation. Eggs were found in 4 of the spring samples.

Polychaetes had the highest biomass in spring with a total of 12.8 g. This group consisted of polychaetes in tubes in autumn and fan worms, serpulids (tubes of CaCO_3) and bigger free-living polychaetes in spring. A small amount of ampharetidae (tubeworms) was also included in this

group. Molluscs, (sea hare included) in spring had the second-largest biomass of 7.8 g followed by echinoderms with 4.9 g (Figure 27 A). The echinoderms group consisted mainly of sea stars (larger in spring) but also some small urchins.

In autumn, molluscs had the highest biomass (3 g), consisting of small turiform, lenticular and trochoid shelled gastropods. Echinoderms and polychaetes both had total biomass of 2.8 g in autumn (Figure 27 A).

Decapods had much higher biomass in spring than in autumn. Included in this group are shore crabs (*Carcinus maenas*) and great spider crabs (*Hyas* sp.), which were small in autumn and larger in spring. Hermit crabs were also found in spring. Polyplacophora were rare, while amphipods were numerous yet very small, which is why the biomass was so low for these two groups. Amphipods included a few caprellidae (skeleton shrimp) along with the more prevalent *gammaridae* and *hyperiid*ae.

Oligochaetes, tubeworm, copepod (see Appendix “red thing”), cumacea (hooded shrimp), sponge and bryozoa stalks were exclusively found in spring (Figure 27 B). Sponges were very small or rare, which explains their low biomass. *Alcyonium digitatum* (soft coral) was the only group only found in autumn. Only one individual of the bottom-feeding fish (*Myoxocephalus scorpius* (Linnaeus, 1758)) occurred, likely because it failed to escape the sampler. It was included, although it is a vertebrate organism (See Appendix D table 3 and 4)

For the effect of season on invertebrate biomass adjusted R-squared was < 1. Sieve size had an effect of 3.9% ($p=0.003$). Adjusted R-squared was insignificant for sites effect on invertebrate communities. Abiotic factors had no apparent effect on invertebrate biomass measures. Neither did algae morphology biomass.

3.5 Research question summary

1: Algae and invertebrate composition were partially explained by seasonality, but only algae was explained by abiotic factors.

2: There was a positive relation between turf biomass and height on sediment weight in autumn.

3: Calcareous and filamentous algal morphological types affected sediment weight in autumn.

4: There was no correlation between organic sediment content and algae biomass.

5: There was no correlation between fauna biomass and algae biomass, or any other parameter for that matter.

4 Discussion

The aim of this study was to describe turf mats along the Skagerrak coastline in terms of algae biomass, morphology, sediment content and invertebrate weights, along with identifying dominant algae species and invertebrate groups. Further, abiotic factors were linked to the aforementioned data to investigate whether they cause trends or variations.

Recent reports indicate that turf mat systems have seen a dramatic increase globally (H. Christie et al., 2019; Gorgula & Connell, 2004; Wernberg et al., 2019), prompting a need to understand their physical and ecological trends. Ultimately this study will aid in making predictions and mitigating adverse effects the loss of complex landscape that kelp forests provide will have (Jackson, 2009). Turf mats around the world have certain similarities but also differences, making “turf” an umbrella term encompassing a variety of systems that are physiologically similar yet ecologically different. Even within the same ecoregion, there are differences in species, sediment content, biomass.

This is the first in-depth study focusing on turf along the Norwegian Skagerrak coastline. This discussion will highlight how different abiotic factors impact turf communities, as well as examining the relationships found between the components within samples.

4.1 Turf and abiotic factors

In recent times the environmental factors influencing kelp-turf shifts have become more favourable for turf, with increasing temperatures, higher nutrients levels and low grazing pressure driving the shift along the Norwegian coastline (Filbee-Dexter & Wernberg, 2018).

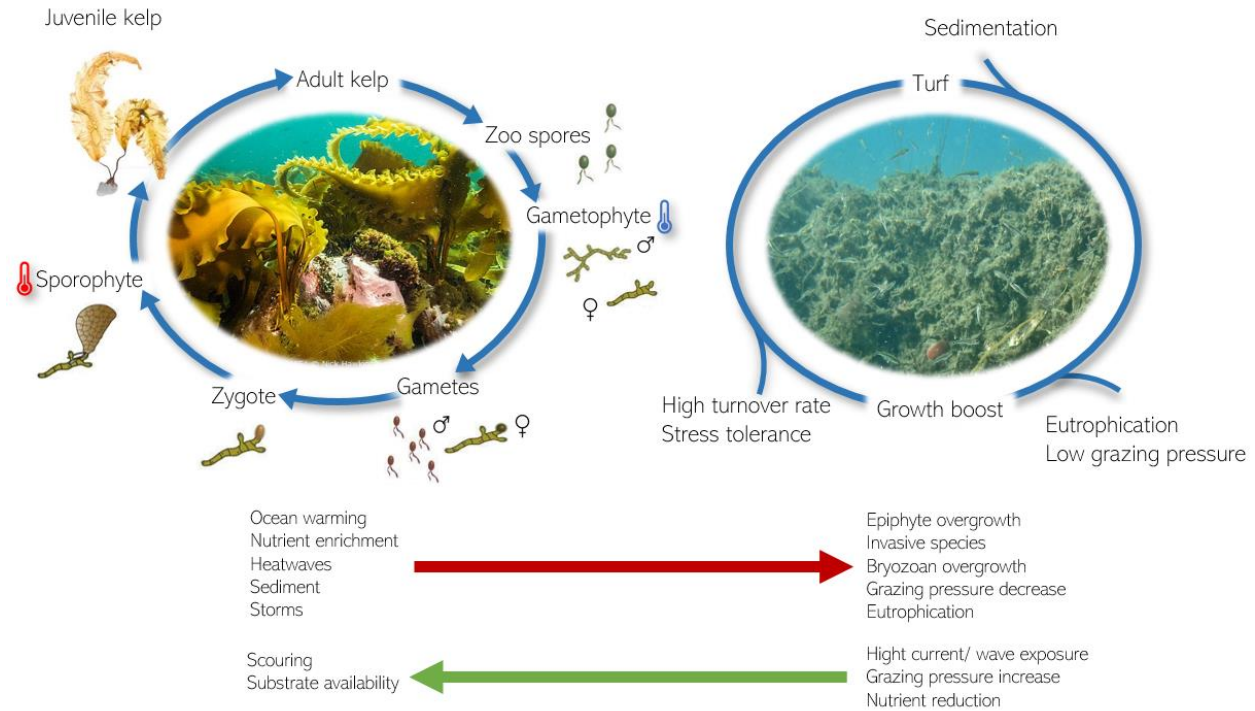


Figure 28: Overview of the influencing factors of kelp forest and turf mat shifts. The cycle on the left is the life cycle of *Saccharina latissima*. On the right are feedback loops and factors maintaining turf state. The red arrow signifies what primary factors that push a system towards turf on the left side of the red arrow. The secondary factors (resulting from primary factors) are listed on the right side of the red arrow. The green arrow signifies factors that can push a turf habitat towards kelp forest growth. On the right side of the arrow are the primary factors, and left side are secondary. Scouring by sediment or kelp fronds can harm turf algae when there are high levels of water movement. The blue thermometer icon signifies that this life stage is more tolerant of high temperatures, while the red indicates that high temperatures can have fatal consequences for this life stage.

Adult *Saccharina latissima* grows rapidly in winter and spring and slows down in summer and autumn time, with peak recruitment happening in winter (Andersen, 2013). Although diebacks and recoveries of kelp forests is a regular occurrence, fewer areas are experiencing such recoveries (H. Christie et al., 2019; Scheffer et al., 2001).

The combination of the abiotic factors, along with the consequences of overfishing and invasive species creates a positive feedback loop on the turf system (Filbee-Dexter & Wernberg, 2018; Moy & Christie, 2012). The indirect effects of these factors further complicate finding the key stressors that contribute to kelp forest declines. For example, increasing temperatures causing both kelp tissue weakening and bryozoan overgrowth results in brittleness, which make kelp more vulnerable to grazing and aberration (Burek et al., 2018; Krumhansl et al., 2014; Wernberg et al., 2010). Additionally, nutrient pollution and temperature shock can cause growth and reproduction limitations (Wernberg et al., 2019), while the boosted ephemeral algae overgrow

and smother the kelp (Filbee-Dexter & Wernberg, 2018). The surviving individuals experience lower genetic variation followed by lower fecundity (O'Brien & Scheibling, 2016)

Moy and Christie (2012) found that the Norwegian west coast experience less kelp loss than the Skagerrak coastline due to it being more wave-exposed, as kelp outcompetes turf in environments with higher water velocity. Sampling sites with low current speeds had turf biomass extending from 38 to 667 g m⁻², while in sampling sites with higher current, algae biomass ranged from 37 to 240 g m⁻². Although current speed only ranged from 0.01 to 0.14 m/s, this indicates that water current has a significant impact on algae biomass. This is in accordance with Gowan et al., (2014) findings in Australia, where lower-level currents were linked to higher levels of turf biomass. Where biomass is concerned, Airoidi & Virgilio (1998) recorded turf weight ranging from 7.8-120 g m⁻² in Livorno, which is similar to the findings of this study. Few studies of turf have included this parameter, making it difficult to compare.

Most turf species have annual lifecycles, blooming when ocean water warms up in spring, and nutrient and light is readily available (Airoidi & Virgilio, 1998). At the end of the growth season, biomass will naturally be higher than at the beginning of the growth season. Yet, algae biomass did not show consistently higher biomass autumn between sites. This variation could be explained by local differences in grazing pressures, nutrient concentration and water velocity (Boaventura et al., 2002; Pihl et al., 1999).

Through the sampling period, water temperatures remained below *Saccharina latissima*'s threshold of 20°C (Lüning, 1990), yet the sampled area likely remained in turf state after this threshold was reached during the heatwave in 2018 (Filbee-Dexter et al., 2020). Elevated temperatures have a negative effect on turf algae biomass as well, yet because turf consists of more temperature tolerant species with higher thresholds, they can persevere through heatwaves. *Chondrus crispus* and *Heterosiphonia japonica* can, for example, tolerate up to 30 °C (Bjærke & Rueness, 2004; Kübler & Davison, 1993).

Turf habitats tend to be more dominant near urban areas where anthropogenic activities cause higher sedimentation and nutrient levels in the water column (Eriksson et al., 2002; Gorgula & Connell, 2004). *Saccharina latissima* stores absorbed winter nutrients for growth during the warmer, nutrient-depleted summer season when phytoplankton blooms utilize most of the

available nutrients (Daniel & Hain, 2012). When excess nutrients are available in times where they normally are a limiting factor, turf can increase their growth rate and outcompete kelp (Burek et al., 2018). This may explain the high biomass in some of the spring samples. Nutrients levels were not measured at each individual sampling station in Skagerrak, yet one can assume that nutrient levels will be higher near populated areas and by river outlets, benefitting turf population (Connell & Irving, n.d.). Still, S8's high average of 412 g m^{-2} in spring and 173 g m^{-2} in was not caused by being close to an urban population (Figure 2), nor were there any river outlets adding nutrient-rich water nearby. On the other hand, S8's modelled current measure was on the lower end of the spectrum, which favours turf.

Rainy autumn seasons causes higher levels of terrestrial nutrients runoff, adding nutrients to the marine environment. This in combination with the effect current has on the different sampling stations can explain some of the site-wise variation in algae biomass for autumn (Campbell et al., 2014; Moy & Christie, 2012; Sogn Andersen et al., 2019).

4.2 Sedimentation and turf algae

Turf collects large amounts of sediment, yet sediment content varies between regions and seasons (Airoldi et al., 1995; Christie et al., 2019). Airoldi & Virgilio (1998) found that higher levels of sediment to reduce turf productivity by smothering them. In this study, however, algae biomass and sediment content had a positive correlation, especially in spring. Airoldi & Virgilio (1998) also theorized that higher levels of sediment resulted in decreased biomass, possibly due to scouring by suspended sediment in combination with water motion. As the current level at the Skagerrak sites were relatively low, scouring by sediment is likely not an issue for turf there. Additionally, the levels of sediment along the Skagerrak coastline samples were relatively low in comparison to other turf sites around the world (average $192 \text{ g m}^{-2} \pm 136 \text{ g}$ in autumn and $104 \text{ g m}^{-2} \pm 82 \text{ g}$ in spring). Airoldi & Virgilio (1998) found in their sediment Livorno survey that the *Polysiphonia setcea* dominated turf mats trapped an average of $32.5 \text{ g m}^{-2} \text{ d}^{-1}$, although this did not indicate how much sediment this turf can hold. Filbee-Dexter et al. (2016) found on average 2 kg m^{-2} sediment in their Nova Scotia turf sites.

In order to find an accurate explanation for sedimentation, many factors have to be taken into account, such as particles density, grain size and sediment source (Cheng, 1997). These factors were not considered in this study. Yet, comparing modelled current speed with sediment content showed that sediment content was higher in areas with intermediate current flow. Once sediment particles are suspended by adequate water flow, they remain suspended until the flow is reduced, for example by obstacles such as turf. First, the larger and denser particles settle, followed by settlement of particles of reducing size. Higher current will additionally wash away sediment, while low current reduces transport of sediment to an area (Southard, 2006). None of the sampling sites are exposed to extreme high current.

Higher turf biomass average in autumn contributed somewhat to increased sediment entrapment. Tebbett & Bellwood (2020) similarly found that algae biomass did not impact sediment content but linked it to proximity to urban areas. Nevertheless, biomass alone explained only ca 10% of the high autumn sediment content, indicating that there are other factors at play, especially in this season. Another explanation for high sediment content in autumn is heavy seasonal rainfall causing runoff from land, while storm waves cause coastal erosion and increase sediment in the water column available for turf entrapment (Airoldi et al., 1995).

Anthropogenic coastal erosion causes large quantities of sediment to be added to nearby coastal ecosystems (Hanson & Lindh, 1993). This, in combination with turfs' tendency to amass sediment, prevents spores from kelp from settling on their preferred rocky substrate (Airoldi et al., 1995). Kelps have been observed attached to the turf itself using a trade-off for a larger holdfast to ensure survival, yet they are 20% more likely to dislodge (Feehan et al., 2019).

4.3 Turf algae morphology and sediment

Initially, filamentous turf was suspected to be the main contributor to sediment accumulation in the turf samples. This theory proved to be somewhat true for autumn, where it explained 46% of the variation. Admittedly, missing data for autumn morphological algae biomass made the sample size too small to make any accurate claims. Calcareous algae influenced sediment content significantly both seasons (44% autumn and 21% in spring), as did herbaceous in spring (21%).

Despite its low biomass, foliaceous algae influenced sediment content in spring, which is when it was most abundant (11%).

Of the morphological types, herbaceous had the highest dry biomass ($90 \text{ g m}^{-2} \pm 55 \text{ g}$), followed by *Corallina officinalis* ($22 \text{ g m}^{-2} \pm 43 \text{ g}$). Filamentous algae ($16 \text{ g m}^{-2} \pm 11 \text{ g}$) were found growing epiphytically on both *Corallina officinalis* and herbaceous algae. Connell et al., (2014b) categorized calcareous algae as a separate habitat, although in their case there were larger coralline barrens rather than the mosaic turf found in this research.

Epiphytic algae growth increases the surface area of erect algae, which may cause an amplification of sediment settlement in turf mats. In contrast, Airoldi (1998) observed that filamentous dominated turf mats, with no erect herbaceous algae, accrued large amounts of sediment in their study site near Livorno. In Western Australia (Gorgula & Connell, 2004) and along the east Canadian coastline (Filbee-Dexter et al., 2016), turf consisted of a mix of morphological types similar to the sites along the Skagerrak coastline. The overgrowth of epiphytic filamentous algae indicate a lack of grazers (Boaventura et al., 2002), further reinforcing the top-down effect overfishing on higher trophic level fish has on coastal ecosystems. Reduced grazing pressure allows filamentous algae to overgrow erect algae, and an increase in nutrient concentration can amplify this effect significantly (Jessen et al., 2013).

Turf height ranged from 1.2 to 11.2 cm, with an average of 4.4 cm, which is consistent with the research of Connell et al. (2014). Site to site variation can likely be attributed to variation in species composition, current, nutrients and variations in light quality as a result of depth. The height of the algae only influenced sediment content significantly in autumn, when the turf biomass was at its peak at the end of the growth season, and there was more sediment available in the water column. This supports Tebbett & Bellwood (2020) findings where increasing sediment content was also linked to the algae length.

4.4 Species composition

Species variation between samples can partially be attributed to the characteristic mosaic patchiness within a turf system. The fitted environmental variables in figure 24 showed that the environmental factors could not wholly explain species variation in terms of colour clade and

morphological type in the samples. Instead, a more accurate explanation could have been achieved by taking sampling depth and light quality into account (Norderhaug et al., 2015).

Site scores for the algae community composition showed a clear separation between seasons as well as their pattern following an axis. This composite axis includes temperature, nutrients and salinity while current appears as an orthogonal vector to these. Therefore, it appears that species abundances are a result of a two-dimensional gradient. Both temperature and salinity were largely affected by season, while current had no seasonal pattern. For the latter, species richness of turf mats decreased with elevated stress levels.

Sites in closer proximity to urban populations generally had higher species richness, yet this did not account for the variation entirely. Unsurprisingly, site S3 was most exposed to current and was farthest from any urban areas, and scored lowest on species richness, especially in autumn. This site also had low turf biomass and sediment content which likely is a result of the accumulated effect of current exposure and nutrient availability (Moy & Christie, 2012; Norderhaug et al., 2015).

While the Skagerrak samples were dominated by either a *Chondrus crispus/Bonnemaisonia hamifera*, *Corallina officinalis*, and in one sample *Chorda filum* (S17 in autumn), they were not mutually exclusive turf mats but had overlaps. The *C. filum* dominated site contained *Furcellaria lumbricalis*, which is also a long chord like algae, indicating that this sight had abiotic factors that catered to an elongated physiology. Also common in the *C. crispus/B. hamifera* sites were *Furcellaria lumbricalis* and *Phyllophora pseudoceranooides*. Conversely, Isaeus (2004) observed one dominant species, *Vertebrata fucoides* (Hudson) Kuntze 1891, in turf sites along the open coasts of Öland and Gotland.

Burek et al. (2018) found turf to be species-rich in Nova Scotia, Canada. Some species found there are similar to the Norwegian Skagerrak coastline species (*Rhodomela confervoides*, *Bonnemaisonia hamifera*, *Porphyra* sp., *Phyllophora pseudoceranooides*, *Chondrus crispus* and *Corallina officinalis*). In contrast turf sites along the Livorno shoreline, Italy (Airoldi, 1998), have been found to be monospecific.

Moy & Christie (2012) investigated turf along the west coast of Norway and found a similar composition of dominating species to the Skagerrak species. At the same depth species in this research were found, the herbaceous *Chondrus crispus*, *Corallina officinalis*, *Furcellaria lumbricalis*, and the filamentous *Dasysiphonia japonica* and *Bonnemaisonia hamifera* were identified. In contrast *Carradoriella elongata* was also dominant in their samples while they were only a common species in the nine Skagerrak sites. The reverse was true for *Phyllophora pseudoceranoides*.

Chondrus crispus reproduce by fragmentation (Collén et al., 2014), allowing it to maintain foothold in sedimented surfaces. It is found in the northwestern and northeastern Atlantic and surrounding waters such as the North Sea under tall kelp canopies forming dense patches. This species is also affected by increasing ocean temperatures, but have a higher heat tolerance (21 °C optimum temperature) than *Saccharina latissima* (Collén et al., 2014), making it more adapted to ocean warming. *Phyllophora pseudoceranoides* tolerate higher temperatures still, preferring 3-25 °C (Molenaar & Breeman, 1994).

Rare individuals of juvenile *Saccharina latissima* were found in the Skagerrak spring samples, while none were found in the autumn samples. Due to turfs ability to regain space rapidly by vegetative reproduction and high growth rates (Airoldi, 1998), they force kelp recruits to attach to turf itself. As Feehan et al. (2019) observed in the southernmost extent of kelp forests in the Northwest Atlantic, turfs attached kelp have slower growth and reproduction abilities, as a trade-off for stronger holdfast is required for attachment. Even then, kelp is 2-4 times more likely to detach.

Variation in community composition could partially be explained by the accumulation of current, salinity and temperature. Salinity influences species composition and distribution in for example estuaries (Schubert et al., 2011), yet as the variation in salinity was too low between the stations it would not have had an impact on turf species composition. It is likely that the effect salinities appear to have is caused by seasonal variation, as it behaved similarly to nutrient concentration and opposite of temperature. As previously mentioned, temperature and nutrient concentration does affect species composition. Alterations in temperatures will favour species with specific temperature thresholds (Sjøtun et al., 2015), as observable by seasonal variation in species

composition while species count did not differ in quantity. Further, species richness tends to increase with increase nutrient concentration (Kraufvelin et al., 2010).

4.5 Organic sediment content.

Organic content in sediment was not found to correlate with algae biomass or invertebrate biomass. It did, on the other hand, correlate positively with total sediment content. This can be sourced back to microorganism such as bacteria living of particulate and dissolved organic matter in-between sediment particles, thereby forming a positive relationship (Seiter et al., 2004; Thiel, 1982). Tebbett & Bellwood (2020) found organic content and sediment to be similarly linked, where the amount of sediment correlated positively with organic matter.

4.6 Invertebrates associated with turf

Dry invertebrate biomass did not correlate with algae biomass, similar to what Miller et al., (2009) found in their analysis in Californian turf sites. Conversely, the Californian invertebrate biomass was higher in turf then in folios algae assemblages, which made turf on an area-specific level a net heterotrophic system. Miller argues that this is caused by turf offering a physical structure that macrofauna such as amphipods prefer. Their abundance can also be explained by the abundance of the food source epiphytic algae provide (Hay et al., 1990). As food availability for invertebrates is higher during the spring bloom, it is expected that the biomass would also be higher for this season.

Amphipods were numerous in the Skagerrak samples, which is similar to what Shelamoff et al. (2020) found in South Australia. Other invertebrates appeared to be rather small in size (see Appendix C). Because turf offers 10 cm instead of shelter instead of kelps 2 meters or taller, higher trophic levels disappear from these areas as mainly smaller organisms are able to utilize this habitat (Hacker & Steneck, 1990) and move around the tangled turf site (Dommasnes, 1969).

Airoldi et al. (1996) observed a low abundance of grazers at the Livorno turf study site most of the year. It is expected that kelp loss and turf takeover results in the loss of mid trophic level fish, which reduces food availability for higher trophic levels and reduce pressure on lower trophic

levels, tipping the systems out of balance (Dijkstra et al., 2019). Schools of small fish were observed above turf mats in the Skagerrak region, mirroring Airoidi's findings.

Shelamoff et al. (2020) tested abiotic factors influence on kelp and turf fauna in southern Australia. They found that light availability explained 46% of the variability in secondary production, while sediment accumulation explained 25% when they investigated kelp patch size. Interestingly, when they investigated the same in turf algae mats, they found that they support extremely productive epifauna communities as well as secondary production, potentially increasing food resources for higher trophic levels. This further complicates finding consequences of turf take-over. A conclusion that can be drawn is that turf in different ecoregions support different invertebrate groups, thereby impacting higher trophic levels differently.

4.7 The future of turf research

Shelamoff et al. (2020) found in their study that Australian turf can support high levels of secondary productivity, as epifaunal richness had a positive relationship with algal species richness. Miller et al. (2009) in contrast found that secondary production decreased when investigating the same on Naples Reef, California. The uncertainty of how turf takeover will impact ecosystems in different ecoregions makes ramifications harder to predict.

It would be beneficial for conservation work and mitigation efforts to find appropriate categories for turf systems with similar drivers and assemblages, such as monospecific vs species-rich turf mats. Finding common solutions to similar turf system issues would be made easier by grouping turfs in categories, separating them by different invertebrate composition, trophic links, nutrient cycling and habitat function. Further, it would explain the effects these would have on the different region's ecosystem services.

Skagerrak turf held three different types of algal mats, herbaceous, *Corallina officinalis*, and in one case, *Chorda filum* dominated (S17). Other than the included temperature and current, nutrient concentration gradients, light and depth of sampling site are important factors for variance in species composition along this portion of Skagerrak coastline (Norderhaug et al., 2015). Future research should include these parameters as well.

Kelp bed recoveries have been observed despite the kelp forest ecosystem being red-listed in 2011 (Norderhaug, 2011). At the current rate of eutrophication, water darkening, increased ocean warming and heat waves will increasingly favour turf in the future (Aksnes et al., 2009; Frigstad et al., 2013; Moy et al., 2009).

4.8 Sources of error

While collecting turf samples, a CTD and a Secchi disk could have been used for collecting additional environmental information for each sampling station, to include visibility/light quality and nutrient content variation between stations. Having this data would give another proxy for understanding variation between stations.

Sediment weight could depend on local geographical differences, such as underwater boulders or other physical barriers. A larger number of replicates from each site could help determine the effect of wave action and currents on sediment accumulation. On the other hand, the workload would have been significantly higher in the field and the lab.

The initial miscommunication about the lab processing approach caused some missing values in the data for algae abundance in the October 2018 samples (See Appendix C).

By counting individuals in addition to weighing individual groups of fauna, a more accurate picture of the ecosystem assemblage could have been achieved. Identifying the invertebrates at a species level would also create a clearer picture of species composition and richness.

A larger sampling size would show trends in the data more clearly, yet this would also increase laboratory work time substantially.

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5.1 Environmental data

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