

A Field Study on the Effects of Norwegian Aquaculture Farms on the Intertidal Rocky Shore Community



Ovidie Mari Lynge

Master of Science in Marine Biology



Department of Biological Sciences

University of Bergen

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Supervisors: Kjersti Sjøtun – Department of Biological Sciences, University of Bergen

Vivian Husa – Institute of Marine Research, Benthic Resources

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Abstract

The aquaculture industry has more than doubled since the early 2000s, and the growth is not predicted to stagnate any time soon. Norwegian salmonid aquaculture cages are usually open where waste is flushed from the cage by ocean currents, distributing nutrients and other compounds to the surrounding habitats. Nutrient enrichment can lead to eutrophication of the water masses, which again can have large ecological consequences on the habitat. This study examined if the intertidal communities around Bergen were affected by nearby aquaculture farms. This was done by examining data collected at rocky shores, and modeled values of change in dissolved inorganic nitrogen originating from aquaculture (Δ DIN) at each station retrieved from the NORWECOM model. In addition, three of the intertidal stations were resampled in summer to examine if there were differences in the results due to season. It was found that the intertidal animal community was influenced by Δ DIN, while the algae community was not. Biodiversity, species richness and functional group composition was not significantly driven by Δ DIN. The differences in station biodiversity, species richness, and functional group composition, were not significantly influenced by season, but the animal community, both during spring and summer, was influenced by Δ DIN, supporting my results from the main analysis. As grazing animals have been found to often prefer annual ephemeral algae, grazers have shown to aid as a tool for battling macroalgae blooms driven by nutrient enrichment. This could be the reason for the response in animal community, and not in algae community or biodiversity. More research is needed to figure out the ecological consequence of this change, but this study shows that the intertidal zone should be taken into consideration when deciding how the aquaculture industry should grow in the future.

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1. Introduction

1.1. The aquaculture industry

According to FAO's estimates, global fish production reached 179 million tons in 2018, almost half of this (46%; 82 million tons) originated from aquaculture (FAO, 2020). Aquaculture fish production has been increasing fast and has more than doubled since the early 2000s (yearly average in 1996-2005 was 34.2 million tons; FAO, 2020). With a growing human population, and per capita fish consumption, this increase is not expected to stagnate any time soon (FAO, 2020). In Norway, the rapid increase in aquaculture has led to a tenfold doubling since 1992 and a doubling since 2015, and it is now a large industry both considering economy and number of employers (Hjellnes et al., 2020; Olaussen, 2018).

Worldwide, aquaculture is an extremely diverse industry in terms of environment, species cultured, resource input level, and design and operation of the production system (Tidwell, 2012b, pp: 51, 2012a). In Norway, on the other hand, most aquaculture systems are marine, intensive, open production systems of finfish, usually the Atlantic salmon (*Salmo salar*). Concentrating on one species only, has led to Norway being the largest producers of Atlantic salmon (53% of total production in 2015) selling 1473950 metric tons salmonids grown from aquaculture in 2020 (Directorate of Fisheries, 2021; Hjellnes et al., 2020; Olaussen, 2018).

When the aquaculture adventure started in Norway in the 60s, it was completely un-regulated and everyone who wanted could join in. It was not until 1973 some regulations were formed when a permission was required to start a new farm (Aarset & Jakobsen, 2009). The environmental impacts have increased along with the sector's growth and in 2005 the first law focusing on a sustainable production was issued (Norges Sjømatråd & Sjømat Norge, 2021).

Monitoring of environmental conditions around the fish farms should be conducted in accordance with NS 9410:2016 (Directorate of Fisheries, 2018). MOM (Modelling-Ongrowing fish farms-Monitoring) was a mandatory monitoring program in Norway divided into MOM-A, MOM-B, and MOM-C, but it has since changed name to just A-, B-, and C-inspection. The A-inspection is voluntarily conducted by the fish farm itself and only looks on the sedimentation from the farm (Hansen et al., 2001). The B-inspection examines the benthic condition underneath and just besides the cages, and is mandatory for all to perform (Directorate of Fisheries, 2019). This inspection returns a number from one (very good) to four (very bad)

which refers to the ecological state of the site. The frequency of these inspections are dependent on the last results (Directorate of Fisheries, 2019). The C-inspection is more thorough and is used to determine how far from the cage impacts can be found (Directorate of Fisheries, 2017). The Directorate of Fisheries and the county council can demand this inspection in certain cases (Directorate of Fisheries, 2017).

Even though the B- and C-investigations aid in regulating each individual farm, there is only one indicator that is determining overall production growth in the different regions, the sea lice abundance (Olaussen, 2018). This works like a traffic light system, where green allows growth, yellow indicates a stable regional production, and red indicates that the production must be decreased. The amount of salmon lice found on wild salmon is the parameter deciding which color each region should have (Olaussen, 2018).

In the southern part of Vestland county a monitoring program called Marine Monitoring Hordaland is also applied, where the goal is to describe the environmental conditions in a variety of marine systems (Bye-Ingebrigtsen et al., 2019; Direktoratgruppen vanddirektivet, 2018). This is done by water sampling, benthic sampling and investigations of the intertidal zone (Bye-Ingebrigtsen et al., 2019). In addition, the Institute of Marine Research initiated a risk assessment of Norwegian salmon farming in 2010, which has been conducted every year since (Taranger et al., 2015). This year's assessment points to effects on wild salmon populations, emissions from net pens, capture and use of labrid fish as cleaner fish, and fish welfare as the risks of most concern (Grefsrud et al., 2021).

1.2. Impacts of aquaculture

The potential impacts of aquaculture are numerous, ranging from environmental, visual, and noise pollution, to animal welfare. How large ecological impact a farm has on the environment depends on many different factors, like “..the physical and oceanographic conditions of the site, seawater temperature and assimilative capacity of the environment, farm management (husbandry), farm size, stocking density, duration of farm operation, digestibility of the food, disease status, etc.” (IUCN, 2007).

1.2.1. Emissions of particulate and dissolved matter

Since most aquaculture farms in Norway are open, the surrounding water masses are continuously flushing the cages removing particulate and dissolved waste. Norwegian aquaculture alone is releasing amounts of nutrients that has been suggested to be equivalent to the sewage of almost twice the Norwegian population (~10 million people; Olausen, 2018). The particulate matter released is feces and feed-leftovers while the dissolved nutrients are mostly nitrogen and phosphorous released from the fish gills when eating, and some as urea (Grefsrud et al., 2021). The particulate matter is sinking quickly and mostly affects the seabed directly underneath the cage, while the dissolved nutrients are carried away and quickly diluted in the ocean (Jansen et al., 2018; Kutti et al., 2007; Valdemarsen et al., 2015).

In Norway, salmonid aquaculture accounts for 55% of total anthropogenic nitrogen emissions to the ocean (Selvik & Sample, 2018). From Rogaland and northwards along the coast, aquaculture is the main contributor of nutrients, while on the southern parts of Norway other sources like agriculture, industry, and sewage dominates (Grefsrud et al., 2021).

Many studies have shown severe effects of eutrophication caused by terrestrial derived organic pollution (e.g. Liu et al., 2010; Lotze et al., 2000; Ménesguen et al., 2010; Pang et al., 2010; Pinedo et al., 2015; Worm & Lotze, 2006). Fewer studies has been conducted on eutrophication derived from aquaculture, except for in the benthic environment, but the effects are thought to be similar and comparable (e.g. Dalsgaard & Krause-Jensen, 2006; Enell, 1987; Oh et al., 2015).

Since most open cages are placed in areas with high water flow, the short residence time of water leads to a quick dispersion of the dissolved matter. Due to this quick dispersion, nutrient enrichment was not detected beyond 100 meters from the cages in any of the studies around modern aquaculture systems discussed in Price et al. (2015). Jansen et al. (2018)'s model did however predict small elevations in ammonium levels up to 1000 meters from the cages. A lot of studies has taken it a step further and tried to use microalgae biomass as a proxy for higher nutrient levels around farms, but most have not found a significant difference (Price et al., 2015). This might be due to the generation time of microalgae usually being longer than the residence time of the water body, and thus the algae will not be in the high-nutrient area long enough for a response in growth. With large variations in effluents, both daily and interannually, it might be a better option to use macroalgae for monitoring nutrient release

from farms, since these are sessile and have a longer life time (Dalsgaard & Krause-Jensen, 2006).

1.2.2. Chemical releases - Medical treatments and antifouling

Different chemicals are used in the aquaculture industry for battling diseases and keeping the equipment clean. Nowadays salmon lice (*Lepeophtheirus salmonis*), a small ectoparasitic copepods, is seen as the biggest problem for the industry and a lot of different anti-sea lice methods exists. Another problem still battled is unwanted fouling of equipment submerged in the ocean.

A variety of anti-sea lice methods exists, both biological, physical, and chemical (Hannisdal et al., 2020). In Norway there has recently been a paradigm shift where chemical treatments were dominating (>81%) in 2012 – 2015, which then changed to a dominance of mechanical (>40%) and thermal treatments (>74%) in 2016 and 2017 (Overton et al., 2018). The chemical anti-sea lice agents are either distributed in the feed (e.g., Emamectin) or as bath treatments (e.g., azamethiphos and hydrogen peroxide; Hannisdal et al., 2020). These chemicals will inevitably enter the surrounding environment which leads to questions about the potentially damaging effects on non-target species. Several experiments and studies has been conducted, and while most have had promising results with no indications of negative effects on non-target organisms, others concluded with lethal or sublethal effects on e.g., sugar kelp and blue mussel (Canty et al., 2007; Escobar-Lux & Samuelsen, 2020; Grefsrud et al., 2021; Haugland et al., 2019; Parsons et al., 2020).

Antifouling, an undesirable growth of organisms, is a recurring problem in aquaculture, reducing water flow and increasing production costs (IUCN, 2007). A common way to deal with this problem is to use antifouling paint on the submerged structures. This paint was previously based on heavy metals (e.g., tin and chrome), nowadays it is usually with copper (IUCN, 2007). According to the Norwegian Environmental Agency ~85% of this copper is released to the environment and multiple studies have shown that copper can have unwanted effects on non-target species in, and around the cages (Fitridge et al., 2012; Guardiola et al., 2012; Skarbøvik et al., 2017). Nowadays, antifouling paints are less and less used, often replaced or combined with other biofouling management techniques, like in situ cleaning (J. Bannister et al., 2019).

However, in Norway, large amounts of copper is still used by the aquaculture industry every year (Skarbøvik et al., 2017).

The aquaculture cages in Norway are usually located close to the shore, and it is not unlikely that the effluents of nutrients and chemicals from the farm could have an impact on the intertidal zone and the community living there.

1.3. Intertidal zone

Often the intertidal zone has been defined as the zone within the tidal range, but it has been argued for it to not be this simple (Kaiser et al., 2011; Lewis, 1961). The exact definition of the intertidal zone has long been debated, but most agree on defining it by biological variables rather than physical ones (Lewis, 1961; Stephenson & Stephenson, 1949). Lewis (1961) proposed a general definition on the intertidal zone: “the marginal belt of marine life characterized by organisms which are adapted to or require alternating periods of exposure to air and of wetting by submersion, splash or spray.”. In the North Atlantic it is agreed on the lower boundary being where the uppermost laminarian algae occurs, the upper boundary though has been more debated (Lewis, 1961). This controversy has arisen due to there not being one dominating algae in the upper shore, instead multiple organisms have been considered (upper margin of fucoids or the junction of black lichens and barnacles; Lewis, 1961).

The intertidal zone and the community living there is highly variable depending on different environmental factors like wave exposure, substratum, slope, tidal range, etc. In the north-east Atlantic, the coastline is mostly dominated by rocky shores (Emery & Kuhn, 1982).

At rocky shores, especially, there tends to be a clear zonation from sea to land, where you can predict the community quite precisely depending on each species' tolerance to physical stress and competition (Hestetun et al., 2018; Lewis, 1968; Lubchenco, 1980; Stephenson & Stephenson, 1949). While the upper limit of a species often is decided by its ability to tolerate dehydration, and more variable temperatures and salinities, the lower limit is usually determined by the species ability to compete with other species for space and resources (Connell, 1961a, 1961b; Hestetun et al., 2018; Kaiser et al., 2011, pp: 174-176; Schonbeck & Norton, 1978, 1980). However, studies have shown that the upper limit of low-shore species

can also be determined by biological interactions (Burrows & Lodge, 1951; Southward & Southward, 1978).

As previously mentioned, the wave exposure-gradient is also an important driver influencing the intertidal community. Some algae species, often perennials, are more tolerant to wave action while annual species tend to be fragile and get easier damaged (Littler & Littler, 1980; Pihl et al., 1999; Sousa, 1979). This might lead to exposed sites having a much higher proportion of perennials compared to annuals, but at highly exposed sites the canopy of algae can be almost absent and the shore dominated by mostly animals (barnacles, mussels, and limpets) and small algae (Chapman, 1946; Lewis, 1968). Most species of algae and animals have “wave exposure preferences”, which can arise from both direct (e.g., tearing/dislodging by waves) and indirect effects (e.g., transport of reproductive stages, grazing-pressure, competition for space, or changes in environmental conditions due to reduced water movement; Lewis, 1968). For example, experiments have shown that on barnacle-dominated shores, high grazing pressure reduces the establishment of *Fucus* sp., at the same time the wave exposure is preventing the algae from persisting on the shore (Jonsson et al., 2006).

The intertidal zone is dominated by perennial canopy-forming macroalgae in the North Atlantic, usually from the family Fucaceae, which creates habitats for animals and other algae (Jenkins et al., 2008; Worm & Lotze, 2006). Even though perennial macroalgae often dominates the habitat in terms of biomass, the highest abundance of algae species in the community are usually annual and pseudo-perennial with large fluctuations in abundance, distribution and interannual variation (Kim, 2001).

At a sheltered site in the Northeast Atlantic the expected zonation of dominant algae, from high to low in the intertidal, is *Pelvetia canaliculata* – *Fucus spiralis* – *Fucus vesiculosus* – *Ascophyllum nodosum* – *Fucus serratus* – *Laminaria digitata* (Chapman, 1946; Hawkins et al., 2019; Hestetun et al., 2018). As we move further to the exposed end of the gradient, some algae species will become less and less common, e.g., *P. canaliculata*, *F. spiralis*, *A. nodosum*, while other might start to appear, e.g., *Himanthalia elongata* (Hawkins et al., 2019).

Nutrient enrichment due to anthropogenic sources like aquaculture, has the potential to dramatically alter the intertidal community, especially if the concentration becomes too high,

which is common to occur in areas with little water movement (Lotze et al., 2000; Worm & Lotze, 2006).

1.4. Impacts on the intertidal zone

Most shores in Norway are subject to a variety of anthropogenic stresses, e.g. nutrient and chemical pollution, and habitat destruction, etc. (Crowe et al., 2000).

Nutrient enrichment can change the macroalgae community composition in both the intertidal and subtidal zone, with a transition from dominance of slow-growing algae, to more fast-growing ones (Gorgula & Connell, 2004; Kraufvelin, Moy, et al., 2006; Liu et al., 2010; Ménesguen et al., 2010; Pedersen & Borum, 1996; Teichberg et al., 2008; Worm & Lotze, 2006). The fast-growing algae usually have short life-times, a filamentous or sheet-like form (=a high area to volume ratio), and thus responds quickly to excess nutrients by growth and reproduction (Littler & Littler, 1980). These fast-growing algae does not have the same habitat- or biogeochemical- functions as the perennials, and therefore the whole community might become severely altered (Valiela et al., 1997). It has also been shown that higher aquaculture effluent levels can lead to a less heterogenous macroalgae subtidal community (Haugland et al., 2021).

Another plausible direct effect of increased nutrients is an increase of suspension feeding organisms (e.g., bryozoans, hydroids, mussels, etc.), responding to the amplified levels of food (Cabral-Oliveira et al., 2013; Haugland et al., 2021; Worm & Lotze, 2006). There is also a possibility that large nutrient inputs can have indirect effects on the intertidal community. If the composition of algae changes, there is a large probability that the associated fauna will also be altered due to changes in food and/or habitat (Kraufvelin, Moy, et al., 2006; Valiela et al., 1997).

The question is if the effluents released from fish farms are large enough to induce a shift in the intertidal community or not, and if the intertidal zone can be influenced even without this community shift. A study assessing the ecological conditions of the macroalgae community in the Hardangerfjord, a Norwegian fjord with a very high aquaculture production, found little evidence of regional eutrophication in the macroalgae community (Husa, et al., 2014). In addition, a monitoring program has been conducted in former Hordaland County since 2013,

monitoring the water quality, soft bottom fauna, and macroalgae community in the fjords (Eilertsen & Tveberg, 2015). In the period 2016-2018 all stations investigated was categorized as in good or very good ecological condition (Bye-Ingebrigtsen et al., 2019). These investigations might suggest that the effluents released from Norwegian aquaculture in most cases are small enough, and/or are diluted quickly enough to not have a large impact on the surrounding habitat. However, these assessments have been done as sightings and by use of indices, and it cannot be disregarded that more thorough investigations and community analyses may reveal some impacts.

1.5. Aim of the study

With the desire to continue expanding the aquaculture industry, it is important to know the resilience of the ecosystems in subject to this production. There have been previous studies in the North Atlantic showing changes in macroalgae communities induced by emissions from nearby fish farms (Boyra et al., 2004; Hemmi et al., 2005; Rönnberg et al., 1992; Vadas et al., 2004). Most monitoring and studies conducted on impacts of cage-based aquaculture have focused on the benthic environmental conditions, especially in close proximity to the farm, and have not taken the intertidal zone into consideration (Carroll et al., 2003; Hansen et al., 2001; Keeley et al., 2019; Price et al., 2015; Valdemarsen et al., 2015; Wilson et al., 2009). In Norway it is mandatory for every fish farm to monitor the seabed using different parameters, but for now there is no requirements for the pelagic or the intertidal zone close by.

The aim of this study was to examine if intertidal communities on the western coast of Norway can be affected by nearby open aquaculture cages with salmon. This has been examined by conducting stratified random sampling during spring at rocky shore communities close to fish farms, and reference stations further away. In addition, predicted values of change in dissolved inorganic nitrogen induced by aquaculture farms was retrieved, before comparing the results using statistics. My hypothesis is that the intertidal communities at sites close to aquaculture cages are significantly influenced by nutrient enrichment originating from aquaculture farms. The results of this study may contribute to an increased knowledge on the environmental effects of salmon farming.

2. Materials and methods

All field work was conducted in near proximity of Bergen in the southern part of Vestland County, on the western coast of Norway. All stations (A1-3, C1-5) were sampled during spring low tide between the 4th and 20th of May 2020. In addition, one aquaculture station (A3) and two control stations (C4 and C5) were resampled between the 20th and 22nd of July, in order to investigate a possible change in impacts from the aquaculture farm on the intertidal stations due to season. Five of the sites examined were sheltered from the open ocean only by small islands (A1-2, C1-3) while the three others were further inland, in an open fjord locality (A3, C4-5; Figure 1).

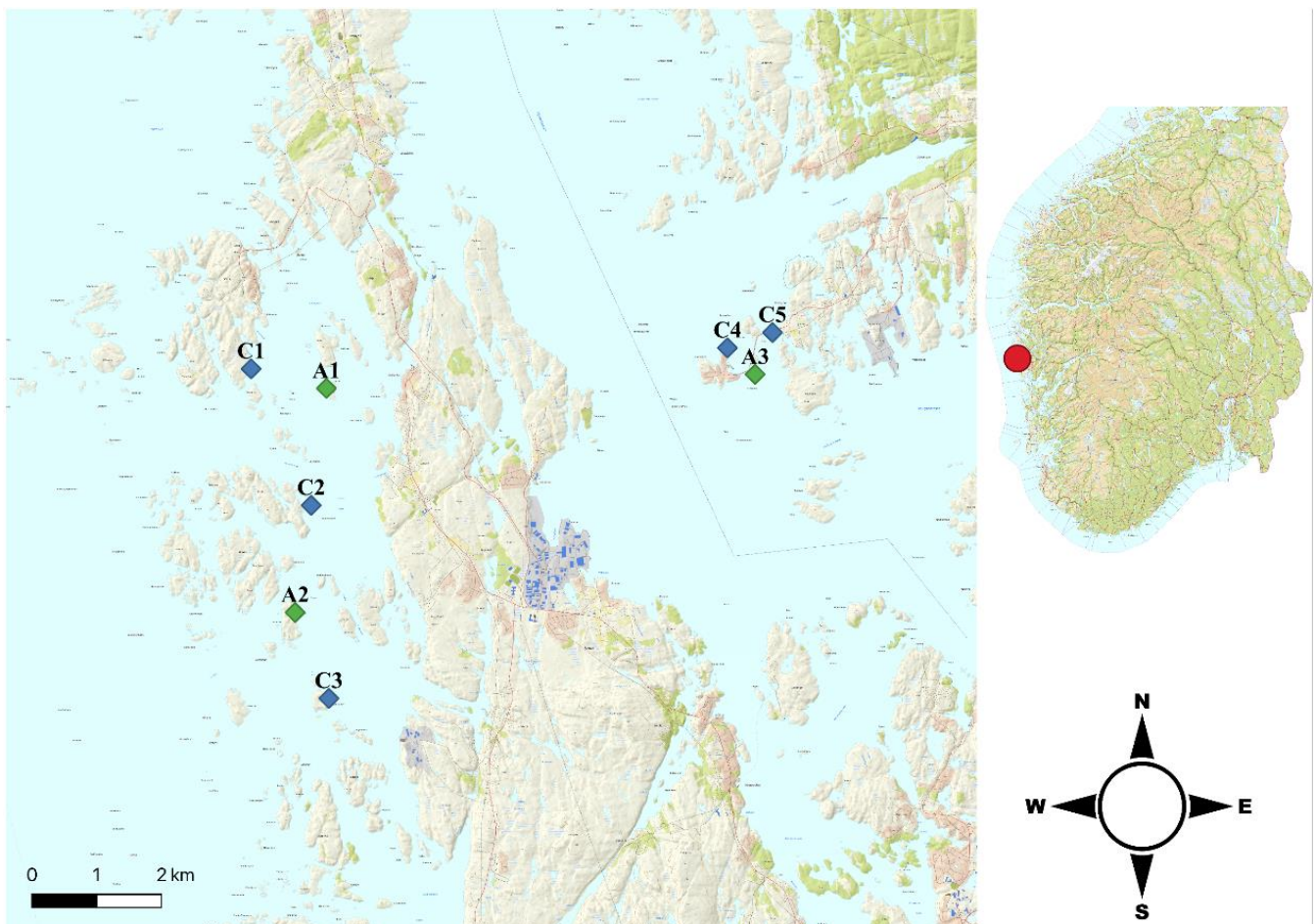


Figure 1 – Map of stations sampled. Green diamonds indicate aquaculture stations (A1-A3) and blue ones indicate control stations (C1 – C5). A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5. Map retrieved from Kartverket and modified with QGIS (N50 Kartdata, The Norwegian Mapping Authority, <https://kartkatalog.geonorge.no/metadata/n50-kartdata/ea192681-d039-42ec-b1bc-f3ce04c189ac>).

2.1. Locating the stations

Firstly, potential study farms were identified with the help of the Directorate of Fisheries' Aquaculture Map (Directorate of Fisheries, n.d.). Only open farms with salmonids in the southern part of Vestland County were looked at. For a farm to be considered for this study it had to be situated not more than ~300 meters away from shore, and be a high production farm in the full production phase. Due to problems with field activity during the covid-19 lockdown only farms relatively close to Bergen were considered. In the end, three farms that had comparable relative wave exposures, and that were situated in areas that were not too heavily impacted by human activity, were selected.

After identifying the fish farms, one aquaculture station and two control stations were found for each site (Figure 1 and 2). The aquaculture stations (A1-3) were placed at shores as close as possible to the net pens. The criteria for the control stations (C1-5) were that they had to be situated at least 300 meters away from the cage and have a similar degree of wave exposure as the aquaculture stations. All stations had to either be reachable by car or by a small boat from Bergen.

The relative wave exposure of each station was calculated using a simplified version of Baardseth (1970) cartographic measurements, taking the distance to nearby land (fetch) from the station into consideration. This method was also used by Armitage et al. (2014). Fetch is estimated by drawing straight lines from the station to nearest land with intervals of 10° on a map using a protractor (Figure 3; Scale 1:50000, The Norwegian Mapping Authority). The relative wave exposure of each station was then found by summarizing all lines, ending with a unitless number. A higher number indicated a higher exposure to waves. This method was conducted twice for each station to account for variations depending on the direction of the first line, and an average was found (Table 1).

A1



A2









Figure 2 – Pictures of all stations taken prior to sampling (A1-A3 and C1-C5). A1-3 stands for aquaculture station 1-3 and C1-5 for control station 1-5.

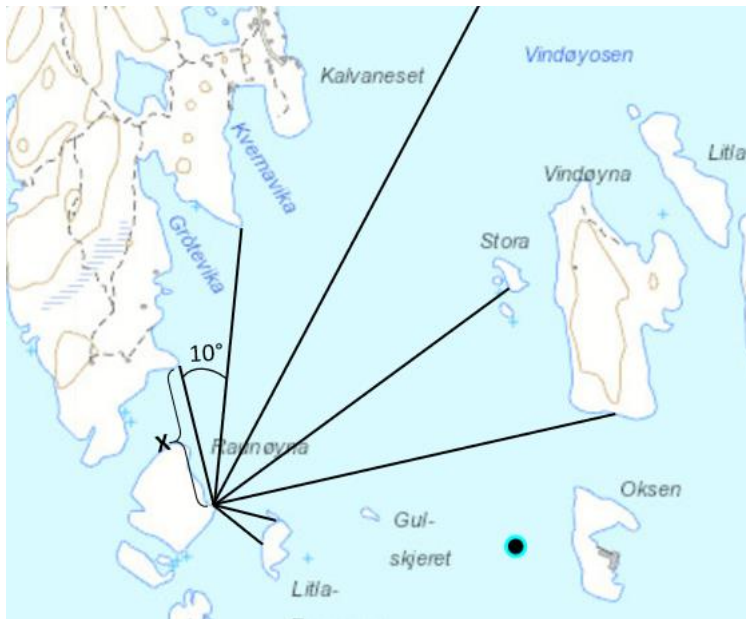


Figure 3 – Schematic drawing of how the relative wave exposure was calculated. X is the length of the line. Lines with 10° distance were drawn from the station to nearest land by hand on an analogue map. The lengths of all lines were added up which resulted in a unitless number where the higher number indicated a more wave exposed station. Digital map used in the figure from The Directory of Fisheries (Directorate of Fisheries, n.d.).

In field, small adjustments to some of the locations were made due to steepness and difficulties of reaching the predetermined locations. One control station was removed altogether leading to a total of five control stations instead of six as planned. The reason for this station’s removal was that the small island initially planned for a station did not have an upper tidal zone due to it being completely submerged during high tides.

Table 1 – Station overview with names, ID, the relative wave exposure calculated, total allowable biomass of fish and biomass at April-June 2020, and distance to aquaculture net pen for each station.

Station name	ID	Relative wave exposure	Total allowable biomass (tons) / biomass at April-June 2020 (tons)	Distance to net pen (m)
Aquaculture 1	A1	574	4680 / 3400	65
Aquaculture 2	A2	559	4680 / 3800	240
Aquaculture 3	A3	459	3120 / 3000	330
Control 1	C1	498	-	973
Control 2	C2	578	-	1440
Control 3	C3	442	-	1290
Control 4	C4	654	-	1940
Control 5	C5	309	-	1030

2.2. Field procedure

2.2.1. Prior to sampling at the station

At each station a 20 meter transect of the intertidal zone was confined and divided into three vertical zones based on dominating species, using two ropes with marks for every meter (Figure 4). The upper zone (barnacle zone) started under the *Verrucaria maura* zone and was separated from the middle zone where *Fucus vesiculosus* and/or *Fucus spiralis* started appearing, and the middle zone was separated from the lower zone by the upper limit of *Fucus serratus*. The lower boundary of *F. serratus* was also the lower boundary of the lower zone. In some stations there were no *F. serratus* and then the middle and lower zone boundary was set to the upper limit of *Himanthalia elongata*. In each zone three quadrants of 50 x 50 cm were placed randomly using an online number generator from 1-20 for the horizontal placement of frames. If the zones were wider than 50 cm the vertical position in each zone was decided in field by trying to subjectively cover all parts (e.g., upper, middle, and lower part of each zone). This method with sampling in different strata is termed stratified random sampling and is a common way of surveying the intertidal zone. The vertical zonation is an important environmental factor influencing the species in the intertidal zone and it is crucial that all major vertical zones are sampled, which this method ensures (Acharya et al., 2013). In total, nine quadrants were sampled at each station.



Figure 4 – Example of how the different vertical zones were divided. Lower boundary of the lower zone is the lower boundary of *F. serratus* – on this picture under sea level.

2.2.2. Levelling

To be able to compare different stations all sample squares were leveled. To do this a monocular and measuring rod was used. Firstly, the monocular got installed on a tripod at the station and adjusted to be leveled. When the monocular was installed, it was stationary at one place for all measurements at the station. The vertical highest and lowest point of all quadrants were measured by placing the measuring rod and noting down the height on the rod through the monocular (Figure 5). All numbers in each station could be compared to see which quadrant was placed highest in the intertidal, and the slope of the quadrant could also

be found. In this case the higher number meant lower in the intertidal zone. For us to be able to compare numbers from different stations, the height of the water was measured and the exact time measured was noted. Post hoc, all heights measured were transformed to distance from chart datum (the highest astronomical tide) using Kartverket's service "se havnivå" (<https://kartverket.no/til-sjos/se-havniva>), providing standardized vertical heights of all quadrants at all sites.



Figure 5 – Figure showing monocular and how the vertical height was measured. The measuring rod to the left is measuring the highest point on the quadrant, the one in the middle the lowest point, and the one to the right is measuring the water level. The black line indicates the view through the monocular.

2.2.3. Community analysis

Each quadrant was analyzed and coverage of sessile species and abundance of mobile species larger than three mm was recorded. This was done systematically, starting with the upper canopy species and working towards the understory, to make sure most macroscopic species were registered. To make it easier to estimate the coverage, another quadrant with a grid of 100 1% squares was placed on top. If a species had less than one percent coverage, the coverage was put as "+". Since this was a three-dimensional environment the total coverage in each quadrant often exceeded 100%. If a specimen was unable to identify in field, a sample

or a picture was taken for further examination back at the laboratory. Formaldehyde (4%, buffered with borax) was used to preserve the samples prior to examination. All species were identified to lowest taxonomic level possible using different literature (Burrows, 1993; Cornelius, 1995a, 1995b; Fletcher, 1987; Hayward, 1988; Irvine, 1983; Maggs & Hommersand, 1993; R. Nielsen & Lundsteen, 2019b, 2019a; Rueness, 1977). All nomenclature was checked in WoRMS (WoRMS Editorial Board, 2021).

2.3. Modelling of nutrients released from the cages

A coupled three-dimensional physical-chemical-biological ocean model NORWECOM (the NORwegian ECOlogical Model system) was used to model the surface dispersion of dissolved inorganic nitrogen (DIN) released from the aquaculture cages (Skogen et al., 1995; Skogen & Sjøiland, 1998). Based on nutrient concentration and ocean circulation, the model simulates nutrient dynamics, and primary and secondary production. The Institute of Marine Research performed the simulations using a similar method as described in Haugland et al. (2021) comparing one simulations with nutrient releases from fish farms and one simulation without. The model was run from 1st of February – 30th August 2016, with feed data from the same period and a horizontal resolution of 160 x 160 meters. The model provided us with an effluent map and individual predicted elevated nitrogen values (Δ DIN) for each station.

2.4. Statistical analyses

All analyses was conducted in R using the packages *vegan*, *lme4*, *nlme*, *ggplot2*, *ggpubr*, *tidyverse*, and *dplyr* (Bates et al., 2015; Kassambara, 2020; Oksanen et al., 2020; Pinheiro et al., 2021; R project core team, 2021; Wickham, 2016; Wickham et al., 2019, 2021).

2.4.1. Preparation of the data sheet

When preparing the data set for statistical analyses some species were combined into genus or wider taxonomic groups due to the uncertainty if they were exclusively registered in one group. This was done for the genera *Littorina*, *Ceramium*, *Cladophora*, *Laminaria*, *Osmundea*, and *Porphyra*. In addition, all *Ulothrix* sp. and *Urospora* sp., *Mastocarpus stellatus* and *Chondrus crispus*, and all crustose corallines were combined in separate groups. All observations of “+” coverage of a species was changed to 1% coverage.

Two data sets were made from the original one: one with the spring data and one which included the resampled data from the three stations (A3, C4 and C5) at summer. The summer data was only used for assessing variations between seasons. The data sets were also divided into one with algae and one with animals.

2.4.2. Environmental variables

An overview of environmental variables available for the analyses can be found in Table 2.

Table 2 – Overview of available variables and explanation of what they include and how they were found.

Environmental variable	Explanation
Type	Aquaculture (A) or control (C). Depends on how close to the aquaculture cage the station was.
Zone	High, middle, low. Which zone in the intertidal the quadrant was in.
Height_mean (cm)	Mean height over chart datum of each quadrant.
Exposure	Relative wave exposure, or cartographic wave exposure, calculated for each station.
Slope	Slope of each quadrant.
Δ DIN (μ M)	Number extracted from the model for each station. Tells us how much excess dissolved inorganic nitrogen was predicted to be at each station due to the aquaculture cages.
East_West	East or West. Tells if a station was on the east or west side of a large archipelago (Figure 1). Stations that were east were situated in an open fjord and stations west only sheltered from the open ocean by small islands.
Distance_netpen (m)	Distance from station to aquaculture cages measured using the Directorate of fisheries' Aquaculture Map (Directorate of Fisheries, n.d.).

Type, Distance_netpen, and Height_mean were not used in the analyses due to them most likely being highly correlated to Δ DIN (first two) and Zone (last one).

Barentswatch (<https://www.barentswatch.no/fiskehelse/>) was used to check if there had been conducted any chemical treatments in the aquaculture cages the previous year before sampling, and to find sea surface temperatures around the cages.

2.4.3. Direct ordination

Multivariate analysis provides a method for separating systematic variation from noise in data sets with multiple response variables (Gauch, 1982). To examine the community structure at all stations and test if they were significantly affected by some of the environmental variables, a direct ordination was conducted.

Before the analyses, rare species were removed from the data set. A species was considered rare if it had less than 5% coverage or five individuals in less than three quadrants. The axis length of both the algae and animal data dictates that both most likely had unimodal responses. Based on this, a partial canonical correspondence analyses (CCA), with Zone partialled out since the dominating differences between zones were not of interest in this study, and since CCAs are known to work well with community data, was most likely the best ordination method (ter Braak & Verdonschot, 1995).

To find the minimal set of significant environmental variables that explained the data as well as the full set, forward selection was conducted. Before this the environmental variables were checked for correlation using the Variance Inflation Factors (VIF). A Hellinger transformation was used for the algae data and log transformation for the animals. At the end two ordinations were conducted, one with algae and one with animals. To find the significant influence each variable in the CCA had on the communities, an analysis of variance was conducted (ANOVA).

2.4.4. Univariate analyses

For the univariate analyses the rare species were not removed, and the whole data set was used.

Diversity and richness:

The Shannon Wiener's Diversity Index, and species richness was found for all quadrants and all stations. When finding one for each station all species data was first combined for each station. The combined data was used to create a table showing the diversity indices and richness.

To test if diversity or species richness was significantly affected by predicted elevated nitrogen values (Δ DIN) the quadrant data was used to create linear mixed effect models (LME) nested in zone and station, which were then tested with ANOVA.

Functional groups:

With the help of literature all species got assigned to a functional group (Appendix A). For the algae this was either annual, perennial, or unknown and for the animals grazer, predator, suspension feeder, scavenger, or omnivore. The data set was combined into functional groups and then divided into algae, mobile animals, and sessile animals. The combined station data was used to create bar plots of the cumulative coverage/proportion of each functional group at each station.

The reason for dividing into functional groups was that, according to literature, functional groups are often a good indicator of how a species might respond to nutrient enrichment, e.g., annual algae are thought to respond quicker than perennial algae and suspension feeding animals and grazers are also thought to have a positive response (Cabral-Oliveira et al., 2013; Christie et al., 2009; Díaz et al., 2012; Fowles et al., 2018; Haugland et al., 2021; Kraufvelin et al., 2010; Kraufvelin, Salovius, et al., 2006; Liu et al., 2010; Lotze & Worm, 2000; Lubchenco, 1978; Ménesguen et al., 2010; Menge et al., 1997; Oh et al., 2015; Pang et al., 2010; Pedersen & Borum, 1996, 1997; Teichberg et al., 2008; Valiela et al., 1997; Worm & Lotze, 2006).

When testing if Δ DIN had a significant impact on the proportion of functional groups at each station, the data with functional groups per quadrant was used. Empty rows were removed from the data set before analysis. For count data (mobile animals) a generalized linear mixed effect model (GLMM) with Poisson distribution was used, and for coverage data (sessile animals and algae) a linear mixed effect model (LME) was used. An ANOVA, nested in zone

and station, was then performed on the models. For algae and mobile animals, the interaction of functional group and Δ DIN was what was interpreted.

2.4.5. Comparison of A3, C4, and C5 spring and summer

To get a snapshot of if there were times of year when the effects of aquaculture was more visible, three stations (A3, C4, and C5) were resampled during summer. The same method as for the whole data set was conducted on only station A3, C4, and C5, and compared with separate analyses of the same stations at summer (A3H, C4H, and C5H). Thus CCAs, Shannon Wieners diversity indices, species richness, and functional group composition was compared, and tested for significance between spring and summer.

3. Results

3.1. Environmental conditions

In order to gain information on the nutrient effluents from fish farms, two model simulations, one with the three fish farms and one without, was compared looking at the concentration of dissolved inorganic nitrogen (DIN). From station A2 (Aquaculture station 2) the main effluents were in southern direction, but also extended towards north (Figure 6). Effluents from station A1 moved quite equally in all directions except in the western direction, where the effluents barely moved. From station A3 the dominant direction of effluents was towards north.

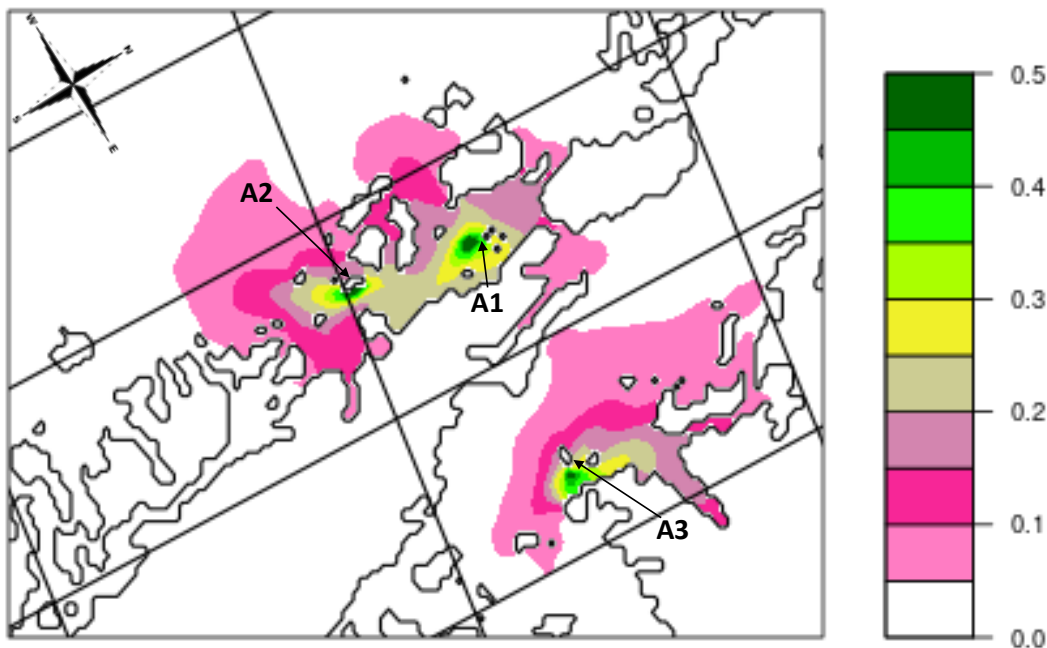


Figure 6 – Map showing predicted changes from the NORWECOM model in inorganic dissolved nitrogen (Δ DIN) at sea surface spreading from each of the aquaculture cages from May to August 2016. The unit of the gradient is increase in dissolved nitrogen (with fish farms) compared to natural circumstances (without fish farms), in μM DIN. The fish farms A1-3 are placed in the darkest green areas – the areas with the highest predicted inorganic nitrogen concentrations. A1-3 is aquaculture station 1-3.

All predicted elevated nitrogen (Δ DIN) values at each station were between 0.17 and 1.24 μM increase in nutrients compared to natural circumstances, with station C3 (Control station 3) and A2 having the lowest and highest value, respectively (Table 3). Mean Δ DIN for aquaculture stations was four and a half times higher than for control stations.

All fish farms had conducted a chemical treatment, either in form of bath treatment or feed treatment, less than a year before examination, but the station where this was closest in time to the examination was A3 where Azamethiphos was used in week 27 in year 2020 (Table 3).

The distance from net pens to the station, if the station was situated east or west of the archipelago, relative wave exposure calculated for each station, total allowable biomass, the actual biomass when examined and mean surface temperature at each aquaculture farm, and the mean slope of all quadrants sampled at each station have been combined in one table (Table 3).

Table 3 – Station overview containing information on change in nitrogen concentration (Δ DIN), distance to aquaculture net pen, if situated east or west of the archipelago, relative wave exposure, fish biomass, chemicals used, mean surface temperature, and mean slope of quadrants at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5. Δ DIN values were retrieved from the NORWECOM model, and chemicals and temperatures retrieved from www.barentswatch.no/fiskehelse. A2 was missing temperature data from week 35 and 36.

Station	Δ DIN (μ M; Delta in some plots)	Distance net pen (m)	East/West	Relative wave exposure	Total allowable biomass (tons) / biomass at April-June 2020	Chemical used/week number	Mean sea surface temperature February / August 2020 ($^{\circ}$ C)	Mean slope of quadrants, spring / summer (cm)
A1	1.05	65	West	574	4680 / 3400	Emamectin benzoate/week 9 and 10 - 2020	6.9 / 15.1	19 /
A2	1.24	240	West	559	4680 / 3800	Hydrogen peroxide/Week 42 - 2019	7.0 / 16.0	19 /
A3	0.68	330	East	459	3120 / 3000	Azamethiphos/Week 27 - 2020	7.0 / 14.4	17 / 16
C1	0.2	973	West	498	-	-	-	27 /
C2	0.19	1440	West	578	-	-	-	21 /
C3	0.17	1290	West	442	-	-	-	20 /
C4	0.2	1940	East	654	-	-	-	8 / 11
C5	0.33	1030	East	309	-	-	-	27 / 14

3.2. Direct ordination

In the ordination with algae data the algae community was significantly affected by wave exposure (ANOVA, $p = 0.042$) and if the station was east or west of the archipelago (ANOVA, $p = 0.001$) while the animal community was significantly affected by the wave exposure ($p = 0.033$), east or west of the archipelago (ANOVA, $p = 0.001$), and predicted elevated nitrogen values (Δ DIN; ANOVA, $p = 0.001$).

In the CCA conducted with algae data, station A3, C4, and C5 were associated with the east side of the archipelago, while station A1, A2, C1, C2, and C3 were in general associated with the west side (Figure 7). Examining the wave exposure gradient most stations were close to the center except for C5 which was associated with a lower wave exposure and C4 associated with a higher wave exposure than the mean.

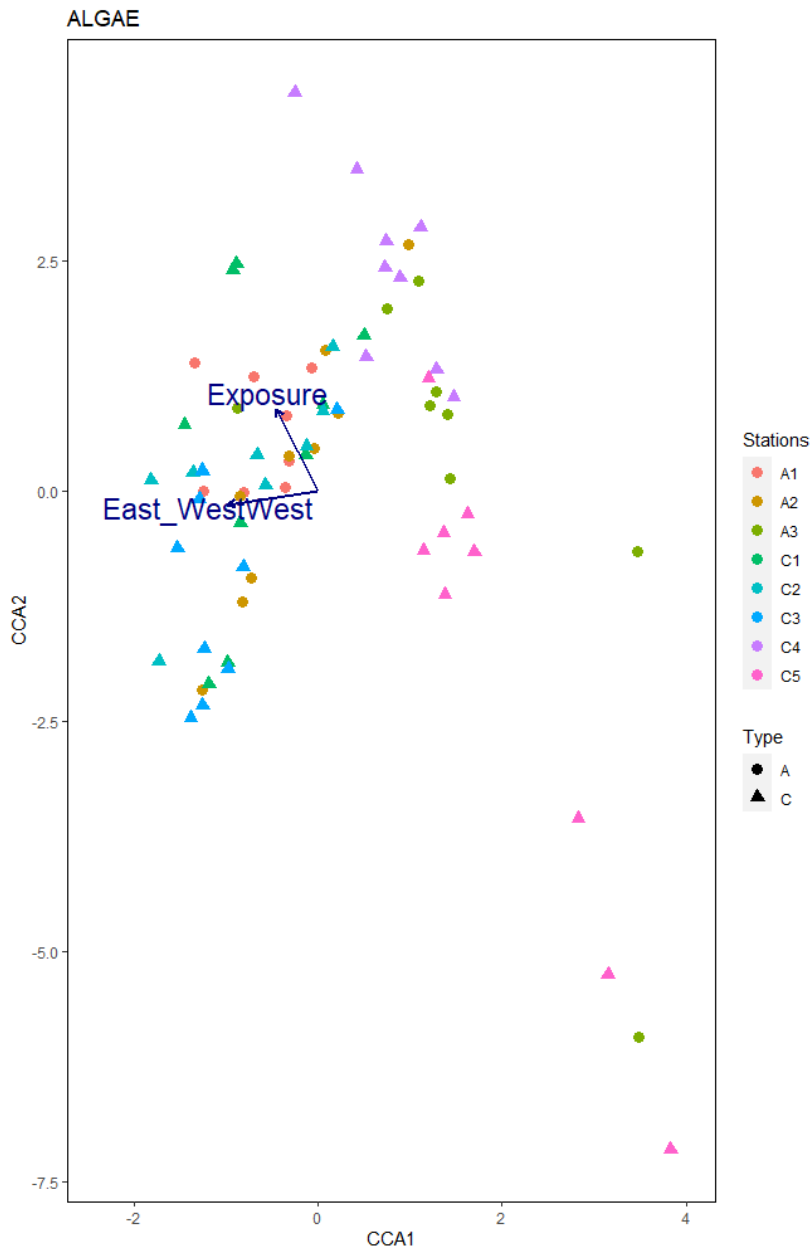


Figure 7 – Canonical correspondence analysis (CCA) of algae data from the different stations with zone partial out. In the CCA 8% of the inertia was explained by the constrained factors and 19% by the conditioned. Each point represents a quadrant, color indicates different stations, and symbol if it is an aquaculture station (A; circle) or control station (C; triangle). The East_West variable implies if the station is located on the east side (in an open fjord) or west side of the archipelago (only sheltered from the open ocean by small islands). Exposure is the relative wave exposure.

In general, aquaculture stations were associated with a higher Δ DIN value, while the control stations were associated with a Δ DIN closer to the mean, or lower (Figure 8). Station A1 was the station associated with the highest Δ DIN, station C2 and C3 were associated with a lower than mean Δ DIN, while the other control stations were associated with a mean Δ DIN. As in the algae CCA, station A3, C4, and C5 were associated with the east side of the archipelago, and the other stations more highly with the west side of the archipelago. The wave exposure gradient had a low impact on the stations and acted in the same direction as the East_West gradient.

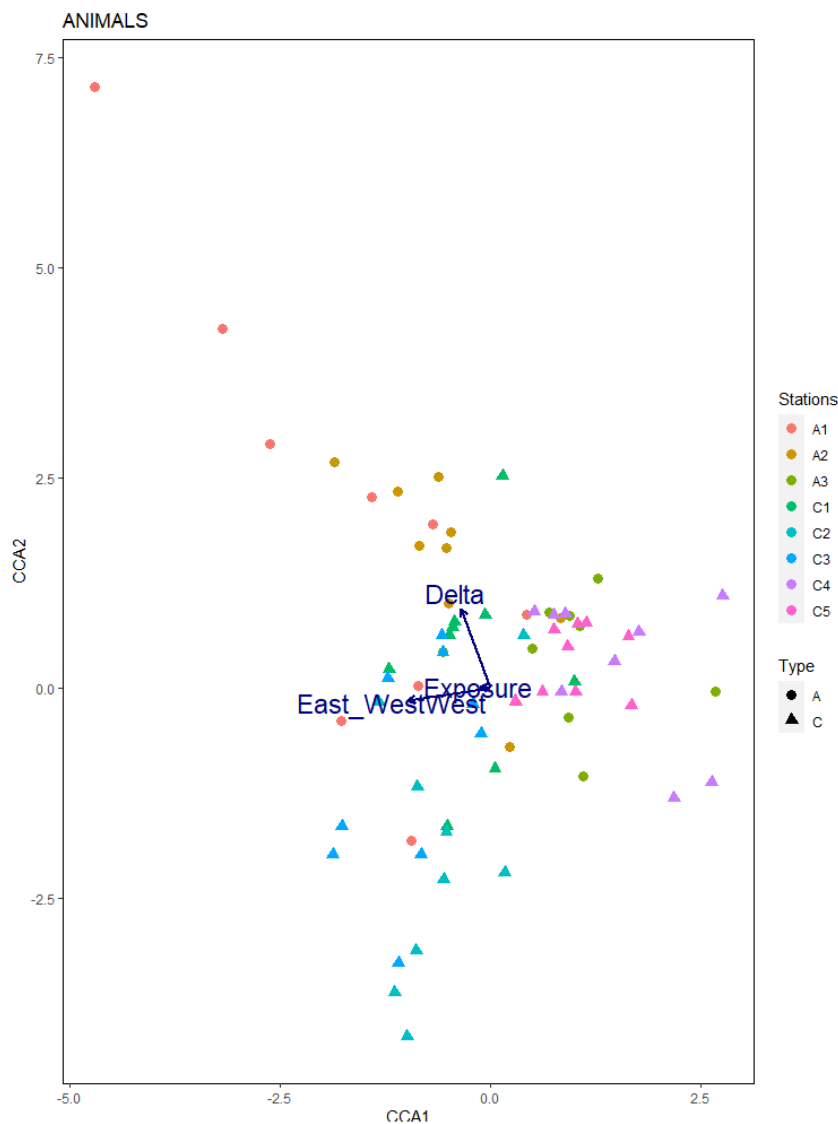


Figure 8 – Canonical correspondence analysis (CCA) of animal data from the different stations with zone partial out. In the CCA 14% of the inertia was explained by the constrained and 19% by the conditioned factors. Each point represents a quadrant, color indicates different stations, and symbol if it is an aquaculture station (A; circle) or control station (C; triangle). The East_West variable implies if the station is located on the east side (in an open fjord) or west side of the archipelago (only sheltered from the open ocean by small islands). Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Exposure is the relative wave exposure.

The algae taxa *Osmundea* spp. and *Urospora/Ulothrix* were associated with more wave exposed sites while *Fucus spiralis*, *Ulva fenestrata*, *Pylaiella littoralis*, *Cladophora* spp., and *Himanthalia elongata* were associated with more sheltered sites (Figure 9). *Osmundea* spp., *Pelvetia canaliculata*, *Cladophora* spp., *P. littoralis*, and *F. spiralis* were associated with the east side of the archipelago, while *H. elongata*, *Leptosiphonia brodiei*, *Dumontia contorta*, *Alaria esculenta*, *Spongonema tomentosum*, and *Porphyra* spp., were more associated with the west side.

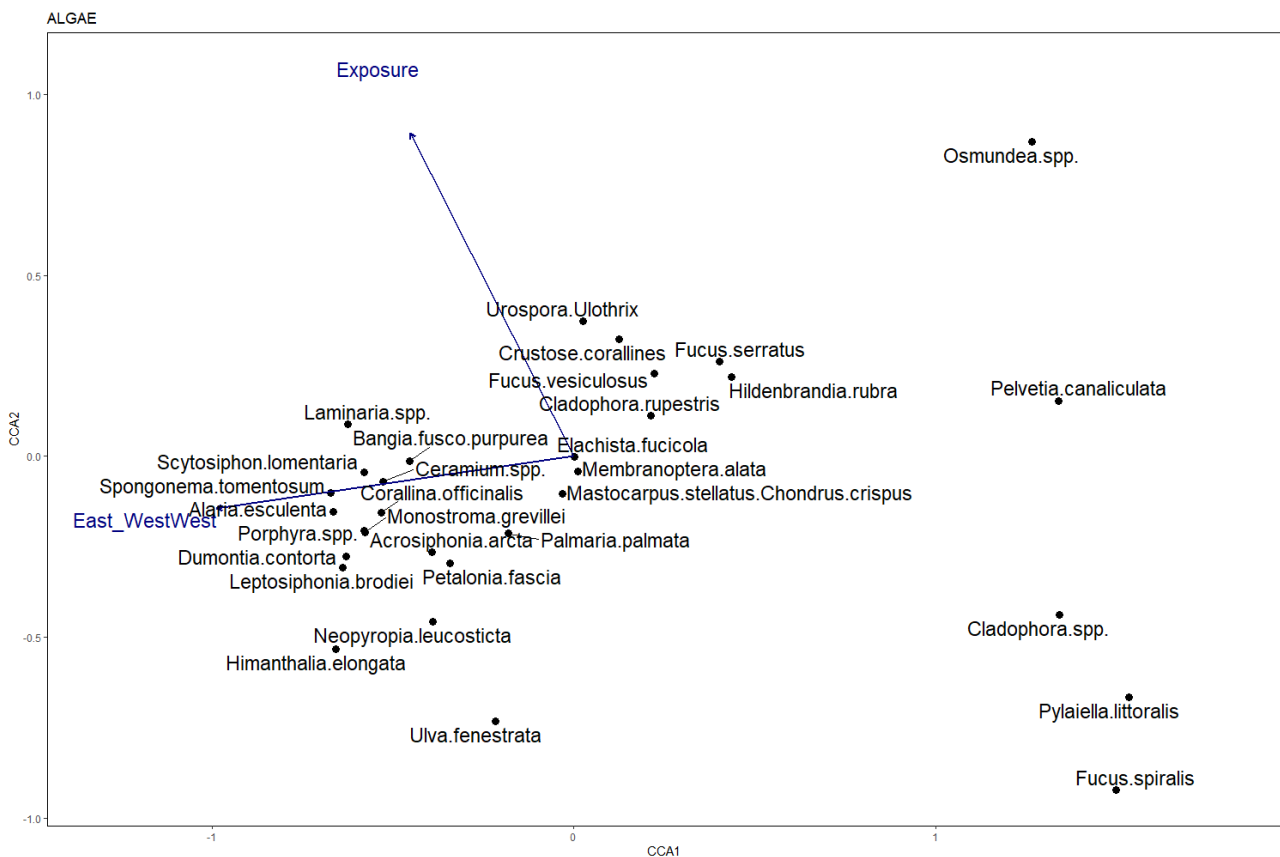


Figure 9 – A canonical correspondence analysis (CCA) of algae data with zone partial out, displaying species instead of stations. The East_West variable implies if the station is located on the east side (in an open fjord) or west side of the archipelago (only sheltered from the open ocean by small islands). Exposure is the relative wave exposure.

The animal taxa *Mytilus edulis* (bivalve) and *Metridium senile* (anemone) were associated with a higher Δ DIN, while *Alcyonidium hirsutum* (bryozoa), *Halichondria* (*Halichondria*) *panicea* (sponge), *Gammarus* sp. (crustacean), and *Nucella lapillus* (gastropod) were associated with a low Δ DIN (Figure 10). *Actinia equina* (anemone), *Idotea* sp. (crustacean), *M. edulis*, *M. senile*, and *Electra pilosa* (bryozoa) were associated with the west side of the archipelago while *Tritia reticulata* (gastropod) and *Spirorbis* (*Spirorbis*) *spirorbis* (annelid) were associated with the

east side. *Semibalanus balanoides* (crustacean) and *Patella vulgata* (gastropod) were centered in the plot.

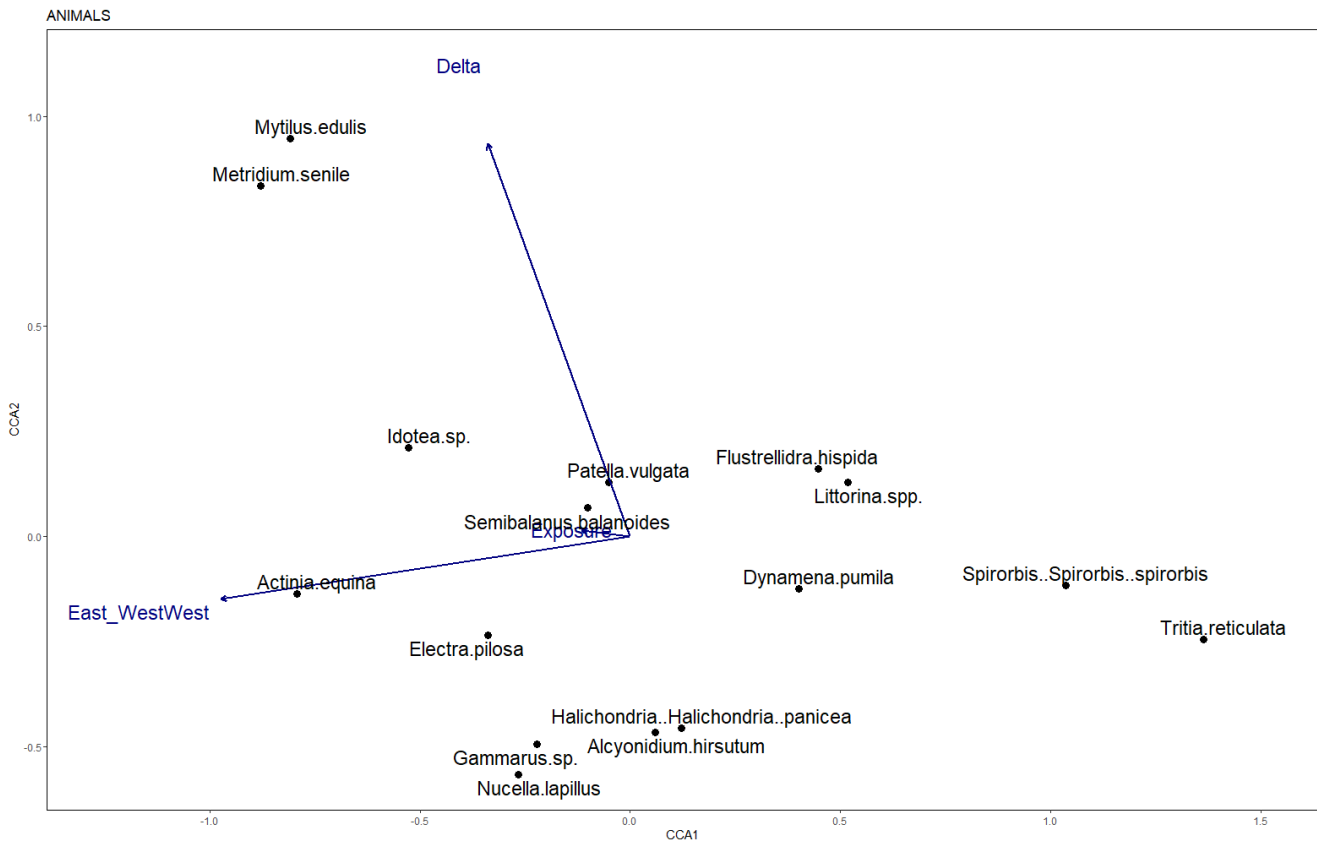


Figure 10 – A canonical correspondence analysis (CCA) of animal data with zone partial out, displaying species instead of stations. The East_West variable implies if the station is located on the east side (in an open fjord) or west side of the archipelago (only sheltered from the open ocean by small islands). Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Exposure is the relative wave exposure.

3.3. Diversity indices and richness

In order to examine if the biodiversity or species richness was affected by nearby aquaculture cages, the Shannon Wiener Diversity index and species richness was calculated for all stations and the results compared.

Station C1 had the highest Shannon Wiener diversity index (2.66) while station A2 and C5 had the lowest (2.20), while for species richness station C3 had the highest (44) and station C4 the lowest (28; Table 4). The mean Shannon diversity was 2.31 for the aquaculture stations and 2.43 for control stations, but the difference was not significantly influenced by Δ DIN (ANOVA, $p = 0.744$). Mean species richness for the aquaculture stations was 37 species and for control

stations 39 species, but nor this difference was significantly affected by Δ DIN (ANOVA, $p = 0.961$).

Table 4 – Diversity indices and species richness of different stations. Shannon indicates Shannon Wiener Diversity Index. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

Station	Shannon	Richness
A1	2.23	38
A2	2.20	41
A3	2.50	33
C1	2.66	41
C2	2.48	37
C3	2.56	44
C4	2.23	28
C5	2.20	43

3.4. Functional groups

Since functional groups can be a good indicator of how a species will respond to nutrient enrichment, all species got divided into functional groups and each stations composition of these groups were examined.

3.4.1. Algae

The largest cumulative coverage of an annual algae taxa at a station was *P. littoralis* (98%) at station C5 and for the perennial taxa crustose corallines (268%) at station C4 (Table 5). The lowest cumulative coverage of the second most dominant annual taxa was 5% of *P. littoralis* at station C4 and of perennial species 90% *Fucus serratus* at station C2. Station C4 also had the highest coverage of *F. serratus* (250%), which was the second most dominating species at the station.

Table 5 – Overview of the two dominating algae taxa in each functional group, as well as their cumulative coverage in percentage. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

Station	Functional group	Dominating species #1	Cumulative coverage #1 (%)	Dominating species #2	Cumulative coverage #2 (%)
A1	annual	<i>Bangia fuscopurpurea</i>	16	<i>Spongonema tomentosum</i>	13
A2	annual	<i>Spongonema tomentosum</i>	13	<i>Elachista fucicola</i>	12
A3	annual	<i>Pylaiella littoralis</i>	50	<i>Bangia fuscopurpurea</i>	37
C1	annual	<i>Urospora/Ulothrix</i>	64	<i>Acrosiphonia arcta</i>	43
C2	annual	<i>Ceramium spp.</i>	40	<i>Elachista fucicola</i>	16
C3	annual	<i>Spongonema tomentosum</i>	28	<i>Porphyra spp.</i>	15
C4	annual	<i>Elachista fucicola</i>	17	<i>Pylaiella littoralis</i>	5
C5	annual	<i>Pylaiella littoralis</i>	98	<i>Elachista fucicola</i>	10
A1	perennial	<i>Crustose corallines</i>	112	<i>Laminaria spp.</i>	110
A2	perennial	<i>Himanthalia elongata</i>	141	<i>Corallina officinalis</i>	137
A3	perennial	<i>Fucus vesiculosus</i>	217	<i>Crustose corallines</i>	214
C1	perennial	<i>Fucus serratus</i>	184	<i>Crustose corallines</i>	145
C2	perennial	<i>Crustose corallines</i>	162	<i>Fucus serratus</i>	90
C3	perennial	<i>Himanthalia elongata</i>	185	<i>Corallina officinalis</i>	108
C4	perennial	<i>Crustose corallines</i>	268	<i>Fucus serratus</i>	250
C5	perennial	<i>Fucus vesiculosus</i>	139	<i>Fucus serratus</i>	106

The coverage of perennial taxa was around 85% of the algae coverage at most stations (Figure 11). Station C1 had the lowest proportion of perennials with just below 75%, while station C4 had the highest with over 95% coverage. Δ DIN was not significantly driving the difference in functional group composition (ANOVA, $p = 0.700$).

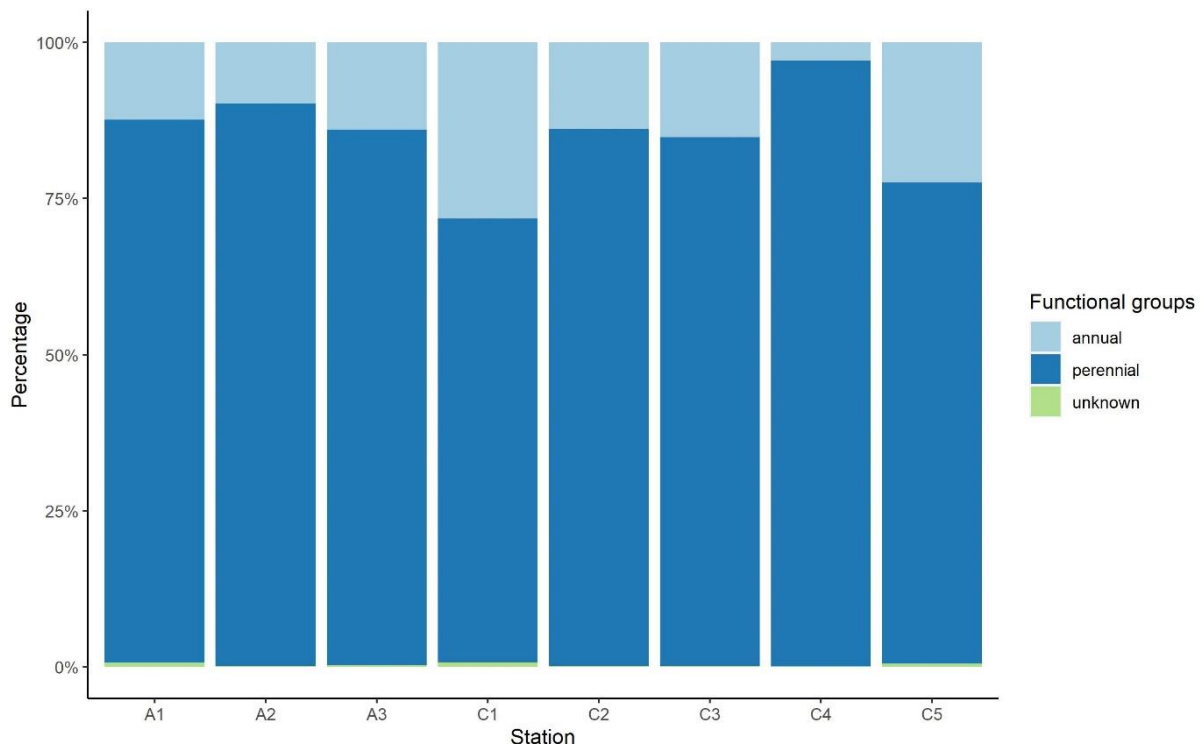


Figure 11 – Proportion of annual and perennial algae coverage at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

3.4.2. Suspension feeders

At all stations most of the suspension feeder coverage was by *S. balanoides* with the highest cumulative coverage at station C5 (577%) and lowest at A3 (152%; Table 6). The second most dominant species varied between stations. The lowest cumulative coverage of the second most dominant suspension feeder was at station A2 with 6% of *E. pilosa*.

Table 6 – Overview of the two dominating species of sessile suspension feeding animals along with their respective cumulative coverage at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

Station	Functional group	Dominating species #1	Cumulative coverage #1	Dominating species #2	Cumulative coverage #2
A1	suspension feeder	<i>Semibalanus balanoides</i>	459	<i>Metridium senile</i>	36
A2	suspension feeder	<i>Semibalanus balanoides</i>	554	<i>Electra pilosa</i>	6
A3	suspension feeder	<i>Semibalanus balanoides</i>	152	<i>Dynamena pumila</i>	33
C1	suspension feeder	<i>Semibalanus balanoides</i>	354	<i>Dynamena pumila</i>	12
C2	suspension feeder	<i>Semibalanus balanoides</i>	389	<i>Halichondria (Halichondria) panicea</i>	25
C3	suspension feeder	<i>Semibalanus balanoides</i>	356	<i>Halichondria (Halichondria) panicea</i>	16
C4	suspension feeder	<i>Semibalanus balanoides</i>	181	<i>Spirorbis (Spirorbis) spirorbis</i>	31
C5	suspension feeder	<i>Semibalanus balanoides</i>	577	<i>Flustrellidra hispida</i>	15

Station C5 had the highest coverage of suspension feeders (618%) and A3 the lowest (212%; Figure 12). Δ DIN was not significantly affecting the amount of suspension feeders at different stations (ANOVA, $p = 0.382$).

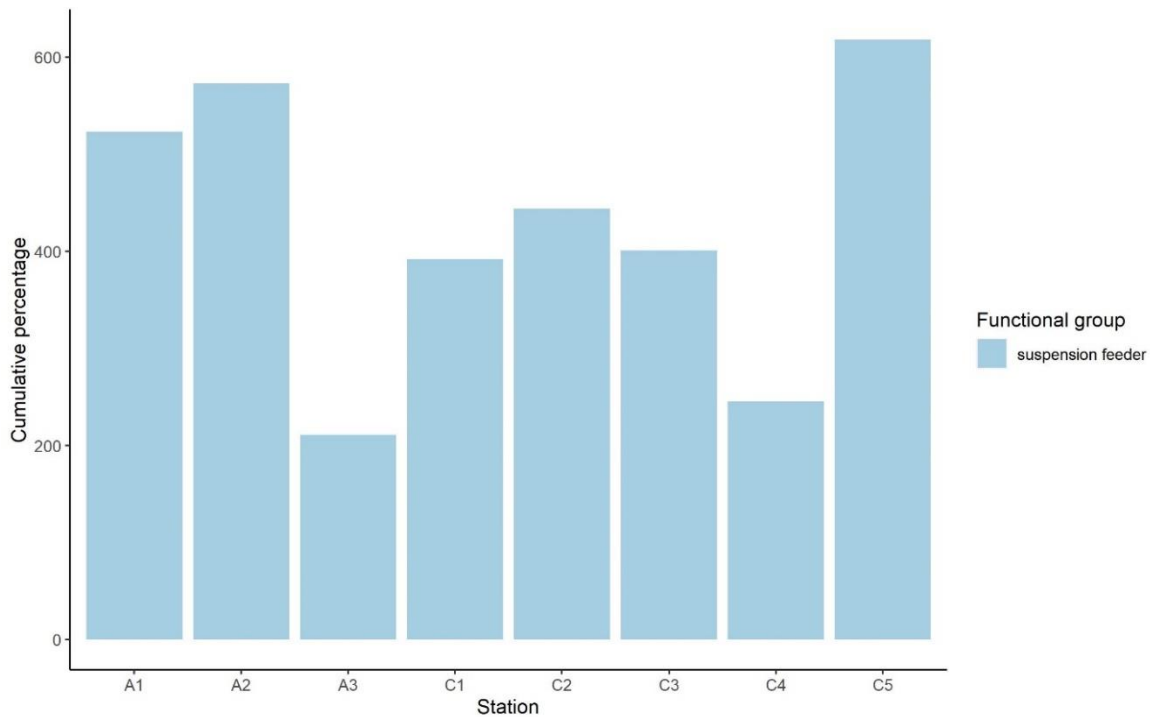


Figure 12 – Cumulative percentage coverage of all sessile suspension feeding animals at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

3.4.3. Mobile animals

The grazing taxa with highest abundances were *P. vulgata* and *Littorina* spp. (Table 7). The highest cumulative abundance of *P. vulgata* was at station A1 (119 individuals) with the lowest abundance observed at station C1 (43 individuals), while C4 was the station with most *Littorina* spp. found (350 individuals) and C3 having the lowest abundance (16 individuals).

The only omnivore taxon found was *Gammarus* sp. with the highest abundance observed at station C2 (40 individuals) and lowest at A1 (zero individuals). *N. lapillus* was always the dominant predator species with abundances ranging from 291 (station C2) to one individual (station A2), and *T. reticulata* was the only scavenger species, only found at station C4 (four individuals) and C5 (two individuals).

Table 7 – Overview of the two most dominating taxa in each functional group of mobile animals, along with their cumulative abundance at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

Station	Functional group	Dominating species #1	Cumulative abundance #1	Dominating species #2	Cumulative abundance #2
A1	grazer	<i>Patella vulgata</i>	119	<i>Littorina</i> spp.	14
A2	grazer	<i>Patella vulgata</i>	87	<i>Littorina</i> spp.	48
A3	grazer	<i>Littorina</i> spp.	130	<i>Patella vulgata</i>	89
C1	grazer	<i>Patella vulgata</i>	43	<i>Littorina</i> spp.	20
C2	grazer	<i>Patella vulgata</i>	56	<i>Littorina</i> spp.	41
C3	grazer	<i>Patella vulgata</i>	80	<i>Littorina</i> spp.	16
C4	grazer	<i>Littorina</i> spp.	350	<i>Patella vulgata</i>	70
C5	grazer	<i>Littorina</i> spp.	62	<i>Patella vulgata</i>	45
A1	omnivore	-	-	-	-
A2	omnivore	<i>Gammarus</i> sp.	11	-	-
A3	omnivore	<i>Gammarus</i> sp.	4	-	-
C1	omnivore	<i>Gammarus</i> sp.	4	-	-
C2	omnivore	<i>Gammarus</i> sp.	40	-	-
C3	omnivore	<i>Gammarus</i> sp.	5	-	-
C4	omnivore	<i>Gammarus</i> sp.	3	-	-
C5	omnivore	<i>Gammarus</i> sp.	2	-	-
A1	predator	<i>Nucella lapillus</i>	29	<i>Calliostoma zizyphinum</i>	1
A2	predator	<i>Nucella lapillus</i>	1	-	-
A3	predator	<i>Nucella lapillus</i>	13	-	-
C1	predator	<i>Nucella lapillus</i>	12	-	-
C2	predator	<i>Nucella lapillus</i>	291	-	-
C3	predator	<i>Nucella lapillus</i>	40	<i>Asterias rubens</i>	1
C4	predator	<i>Nucella lapillus</i>	4	<i>Calliostoma zizyphinum</i>	2
C5	predator	<i>Nucella lapillus</i>	16	-	-
A1	scavenger	-	-	-	-
A2	scavenger	-	-	-	-
A3	scavenger	-	-	-	-
C1	scavenger	-	-	-	-
C2	scavenger	-	-	-	-
C3	scavenger	-	-	-	-
C4	scavenger	<i>Tritia reticulata</i>	4	-	-
C5	scavenger	<i>Tritia reticulata</i>	2	-	-

All stations were highly dominated by grazing animals, except C2 where predators dominated (Figure 13). Station C4 had the highest proportion of grazing animals (827 individuals). The differences in mobile animal functional group composition were not significantly affected by Δ DIN (ANOVA, $p = 0.739$).

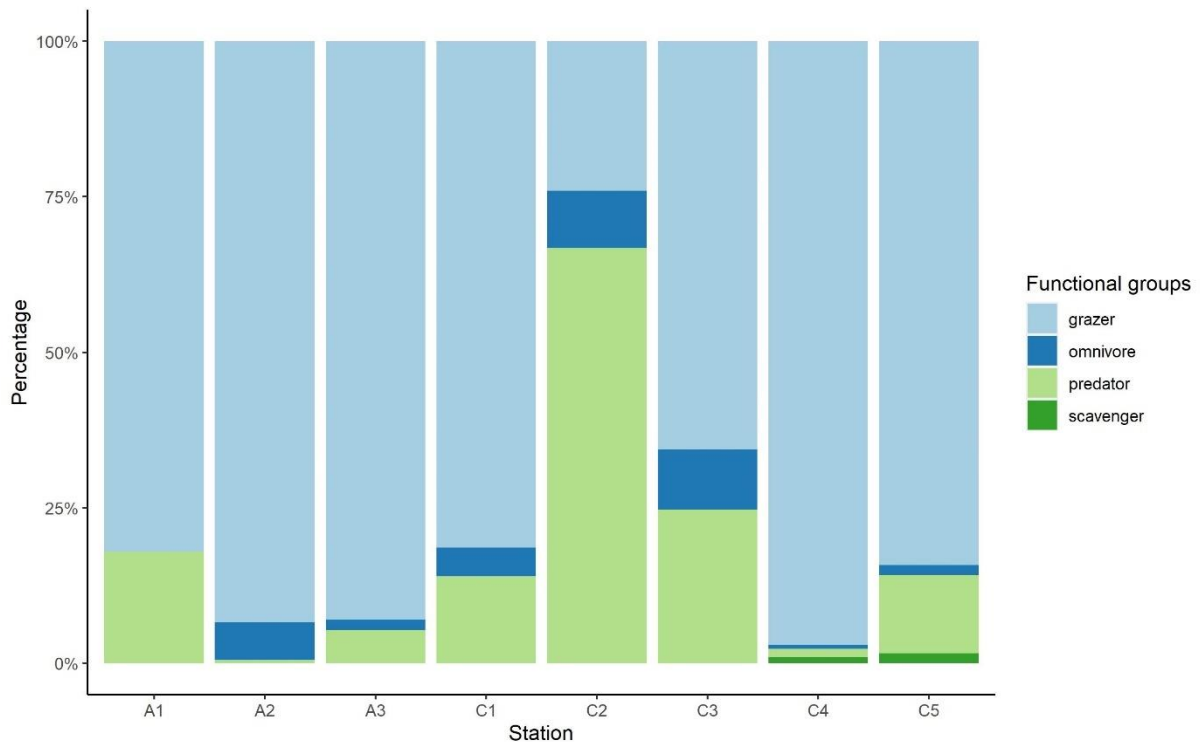


Figure 13 – Proportion of mobile animals counted in each functional group (grazer, omnivore, predator, scavenger) at each station. A1-3 implies aquaculture station 1-3 and C1-5 implies control station 1-5.

3.5. Comparison of station A3, C4, and C5 spring and summer

To get an insight into if there were large variations in the intertidal community between spring and summer, especially in accordance with aquaculture effluents, three stations were resampled and the data analyzed.

3.5.1. Direct ordination

The differences in algae community of both spring and summer data from the stations on the east side of the archipelago was not significantly affected by any of the environmental factors tested (Δ DIN, relative wave exposure, and slope of the quadrants), and the results from the analyses are not shown. The differences in animal data though were significantly affected by

the environmental factors. Δ DIN was slightly less significant for the spring data (ANOVA, $p = 0.012$) than for the summer data (ANOVA, $p = 0.007$). In addition, slope (for spring data: ANOVA, $p = 0.008$, and summer data: ANOVA, $p = 0.034$) had a significant impact on both spring and summer data, and in addition wave exposure was also affecting the summer animal community (ANOVA, $p = 0.001$).

Station A3 was associated with a higher Δ DIN than station C4 and C5 in the spring CCA (Figure 14). The quadrants from station C5 sampled in spring had in general a steeper slope than the mean, while C4 was associated with a more gentle slope.

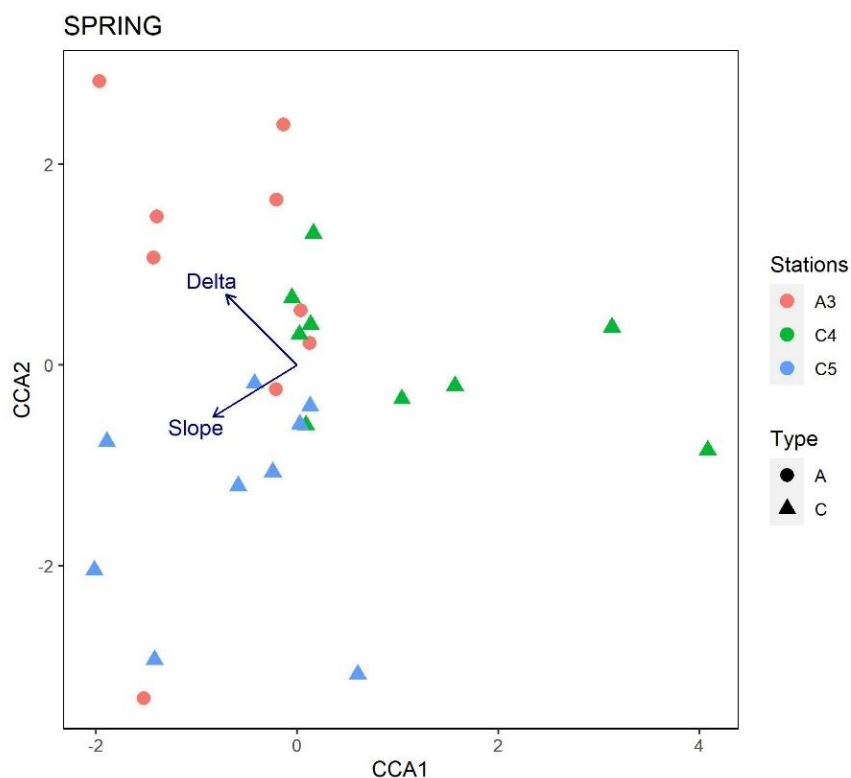


Figure 14 – Canonical correspondence analysis (CCA) of animal data from the eastern stations sampled during spring with zone partial out. 17% of the inertia was explained by the constrained factors and 39% by the conditioned factor. Each point represents a quadrant, color indicates different stations, and symbol if it is an aquaculture station (A; circle) or control station (C; triangle). Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Slope was the slope of the quadrants.

The animal community during summer at station A3H was associated with a higher Δ DIN than the community at the control stations C4H and C5H (Figure 15). The slope environmental gradient works in approximately the same direction as Δ DIN, thus the quadrants at A3H was also associated with a steeper slope than the control stations. C5H was associated with a lower relative wave exposure than the two other stations.

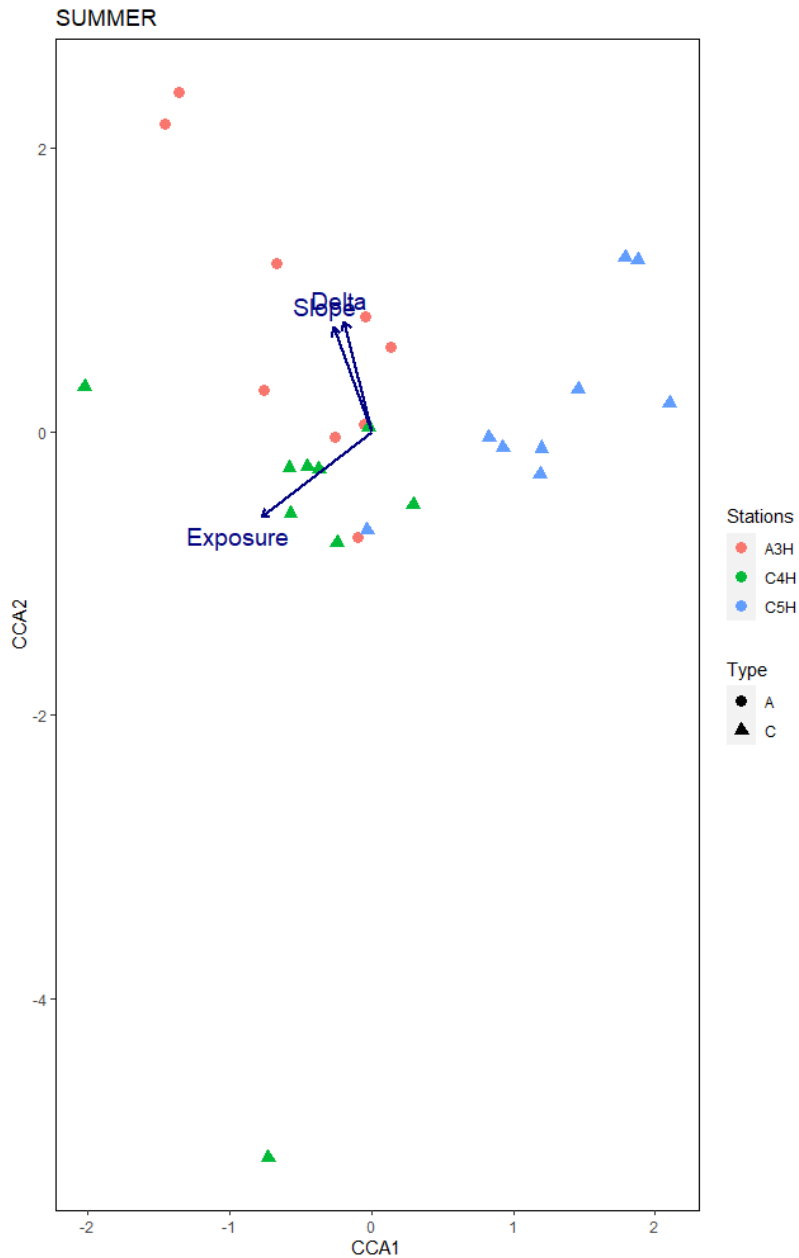


Figure 15 – Canonical correspondence analysis (CCA) of animal data from the eastern stations sampled during summer with zone partial out. The constrained factor accounted for 30% of the inertia and the conditioned for 37%. Each point represents a quadrant, color indicates different stations, and symbol if it is an aquaculture station (A; circle) or a control station (C; triangle). Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Exposure was the relative wave exposure and Slope was the slope of the quadrants. The H in the station name indicates that the data was collected in summer.

From the CCA of animal data from spring, *Idotea* sp. stood out as the species most associated with a high Δ DIN, while *E. pilosa* and *T. reticulata* were associated with a lower than mean Δ DIN (Figure 16). *Dynamena pumila* (hydrozoa) had also a stronger association with Δ DIN than

the mean. Considering the slope environmental gradient *S. balanoides* was associated with a steeper slope and *E. pilosa* and *A. hirsutum* with a more gentle slope than the mean.

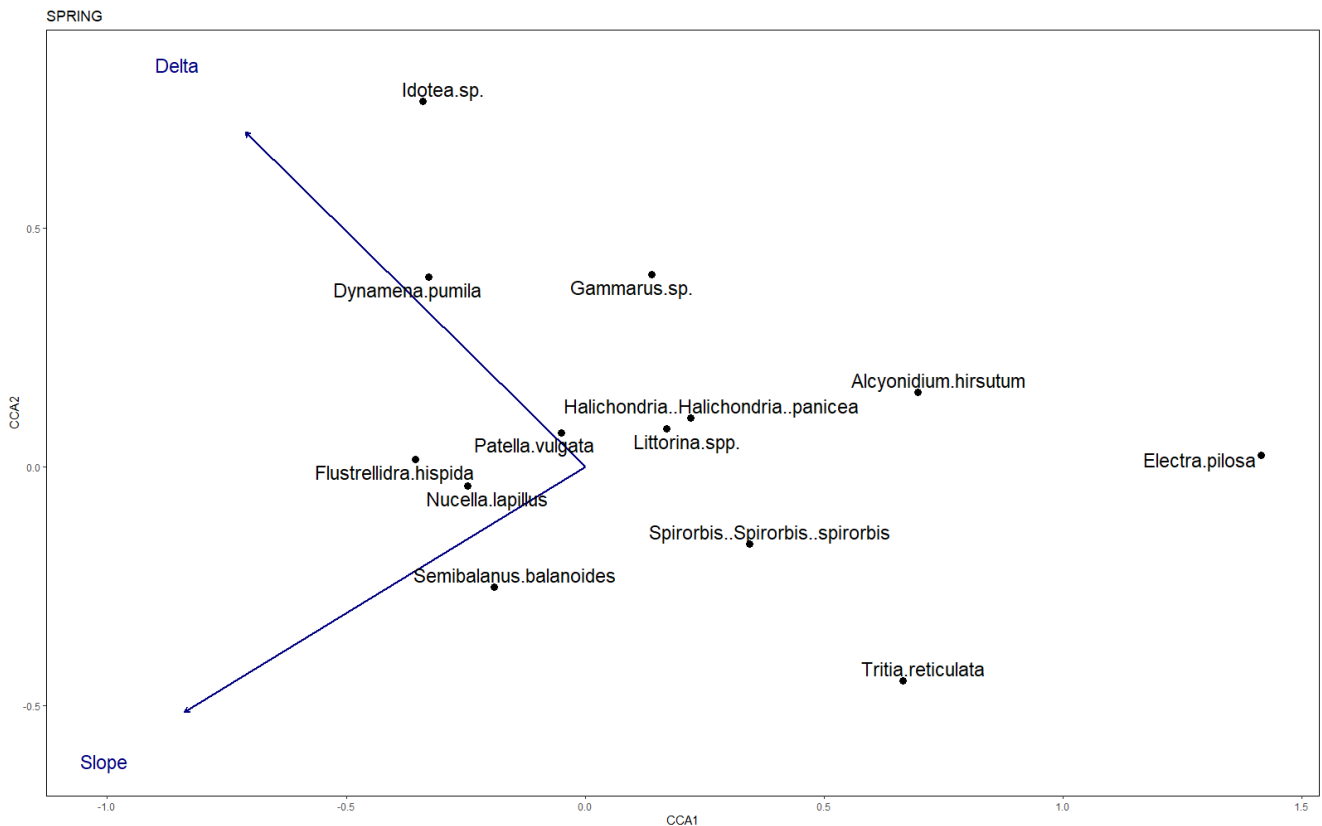


Figure 16 – Canonical correspondence analysis (CCA) of animal data from the eastern stations sampled during spring with zone partial out, displaying species instead of stations. Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Slope is the slope of the quadrants.

In the CCA of animal data collected in summer, *D. pumila* and *Membranipora membranacea* (bryozoa) were associated with a higher Δ DIN and slope than the rest of the species, while *Steromphala cineraria* (gastropod) with lower values (Figure 17). *Pagurus* sp. and *S. cineraria* were associated with a higher relative wave exposure than the rest of the animal community.

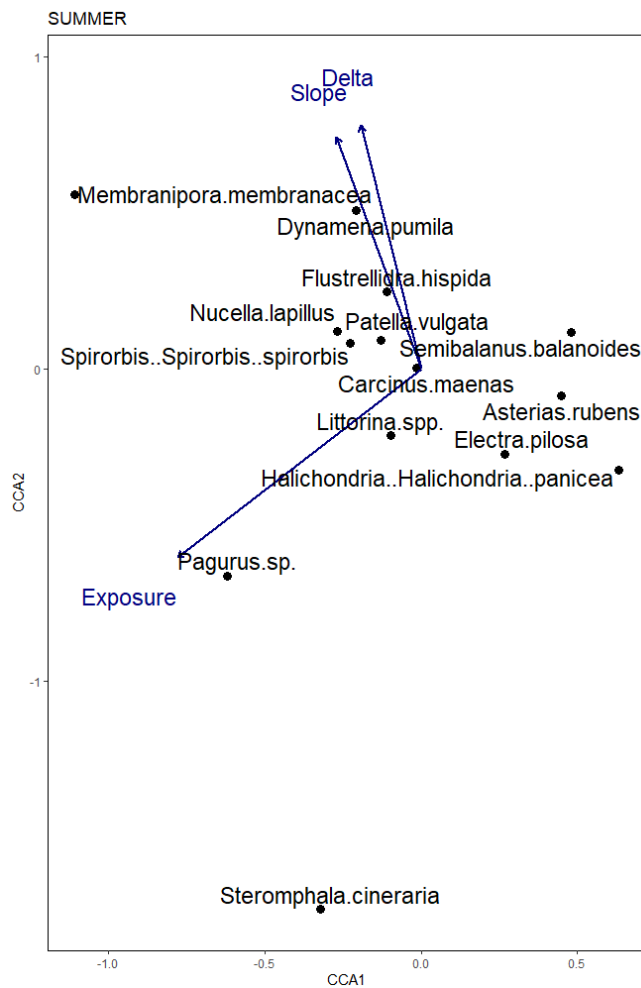


Figure 17 – Canonical correspondence analysis (CCA) of animal data from the eastern stations sampled during summer with zone partial out, displaying species instead of stations. Delta represents change in dissolved inorganic nitrogen (Δ DIN) induced by aquaculture. Exposure is the relative wave exposure and Slope is the slope of the quadrants.

3.5.2. Diversity indices and richness

Station A3 had the highest Shannon diversity (2.50) and C5 the lowest (2.20; Table 8). The highest species richness was 43 species and was found at station C5, while 28 species was the lowest and was found at station C4. The Shannon Diversity indices and species richness were not significantly different between spring and summer (ANOVA, $p = 0.549$ and ANOVA, $p = 0.587$, respectively).

Table 8 – Shannon Wiener’s Diversity Index and species richness comparing spring and summer data. A3 implies aquaculture station 3 and C4-5 implies control station 4-5. A3 and A3H is the same station, but the H in the station name indicates that the data was collected in summer while name without H was sampled in spring.

Station	Shannon	Richness
A3	2.50	33
A3H	2.44	38
C4	2.23	28
C4H	2.27	33
C5	2.20	43
C5H	2.33	36

3.5.3. Functional groups

At all stations the coverage of algae consisted of between 75 and 100% perennial algae (Figure 18). Station C4H had the largest proportion perennials and C5 the lowest. The largest difference between one station during spring and summer is station A3 where the proportion of perennials were lower than during summer (A3H). The two control stations had a similar composition during both spring and summer. The differences in algae functional group composition were, however, far from significantly influenced by season (ANOVA, $p = 0.0693$).

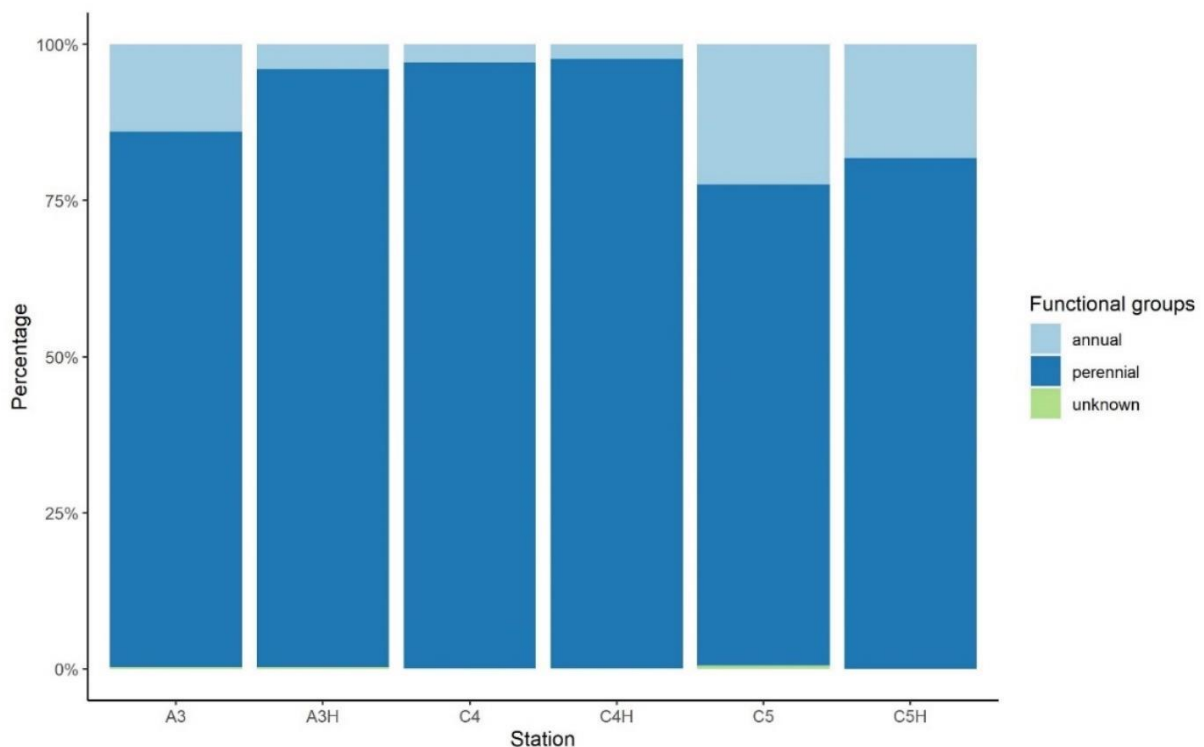


Figure 18 – Stacked bar plot comparing percentage coverage of annual and perennial algal species at each station sampled spring and summer. A in the station name indicates aquaculture station and C control station. A3 and A3H is the same station, but the H in the station name indicates that the data was collected in summer while name without H was sampled in spring.

The coverage of sessile animals, suspension feeders, was between 618 and 211 cumulative percentage at all stations where station C5 had the highest and A3 the lowest (Figure 19). Station A3 had only 1% less coverage during spring than summer (A3H), C4 7% less than C4H, and C5 161% less than C5H. These differences in cumulative coverage of sessile animals were not significantly influenced by season (ANOVA, $p = 0.307$).

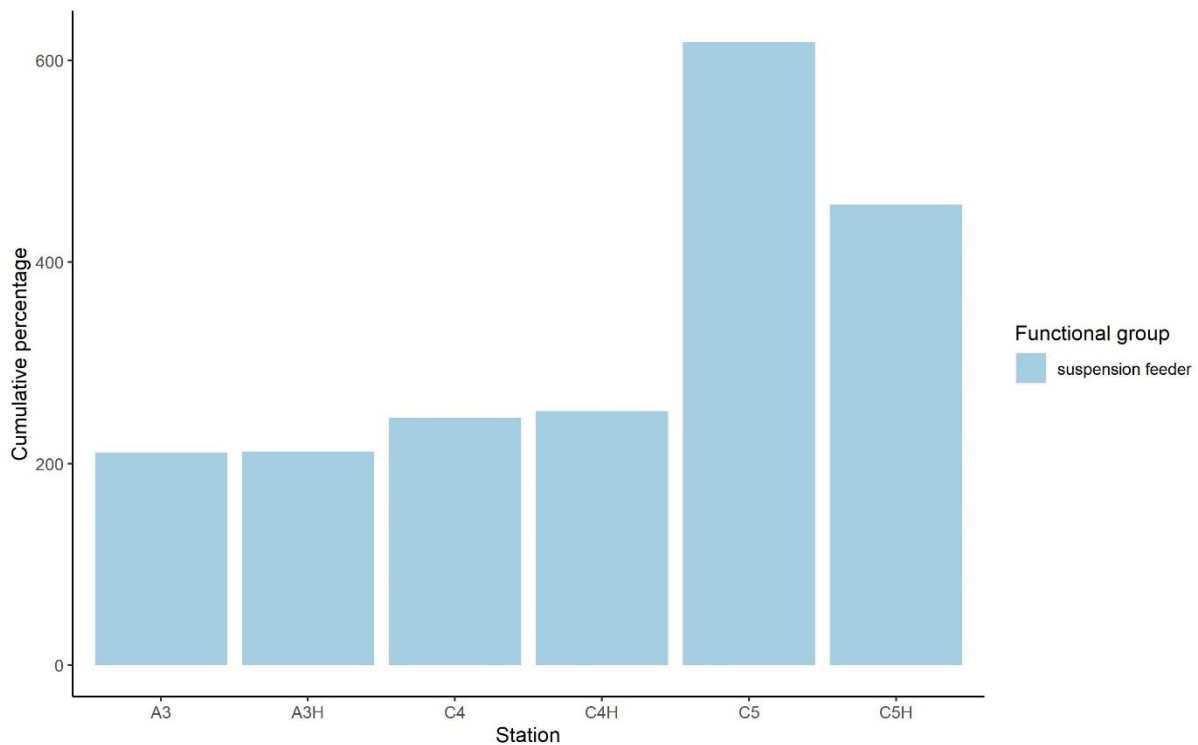


Figure 19 – Cumulative percentage coverage of all suspension feeding animals at each station. A in the station name indicates aquaculture station and C control station. A3 and A3H is the same station, but the H in the station name indicates that the data was collected in summer while name without H was sampled in spring.

At all stations the dominating mobile animal functional group was grazers (between 80% and 95%) and the second most dominating group was predators (Figure 20). Station C5 and C5H had an almost similar mobile animal composition, while the other two stations had some variations between spring and summer. On station A3 ~ 95% of the mobile animals was grazers while A3H had around 80% grazers, while C4 had over 95% grazers and C4H had ~ 90%. The mobile animal functional group composition was not significantly influenced by season (ANOVA, $p = 0.586$).

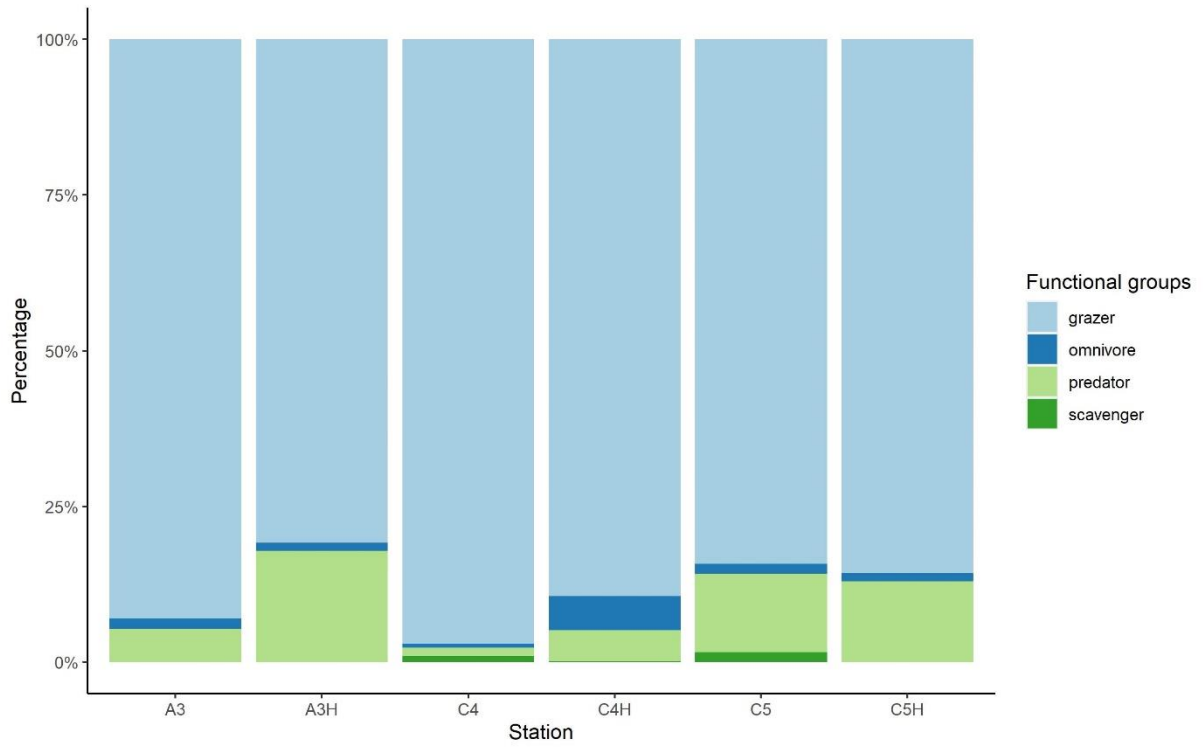


Figure 20 – Proportion of mobile animals counted in each functional group (grazer, omnivore, predator, scavenger) at each station. A in the station name indicates aquaculture station and C control station. A3 and A3H is the same station, but the H in the station name indicates that the data was collected in summer while name without H was sampled in spring.

4. Discussion

The results showed that the intertidal community at stations around aquaculture farms was influenced by relative wave exposure and geographical position in accordance to the archipelago. The animal community was in addition affected by simulated change in dissolved inorganic nitrogen originating from aquaculture (Δ DIN). The results of algae and animal community at the stations are thus discussed separately.

4.1. Environmental conditions

Not all factors influencing a community are physical. Biological ones like interspecific and intraspecific competition can also have large effects on the communities. However, the interactions these factors have with nutrient enrichment are difficult to measure in field studies and was thus not tested in this study.

Dissolved inorganic nitrogen (DIN) values on the western coast of Norway, especially during spring and summer, are usually quite low (Husa, Kutti, et al., 2014). If I assume that the nutrient values measured in the Hardangerfjord by Husa, Kutti, et al. (2014) are representable for west of Bergen, and add the predicted DIN values retrieved from the model, all stations would still have nutrient concentrations that according to The European Framework Directive are categorized as very good (Table 3; Aure & Johannesen, 1997; Direktoratgruppen vanndirektivet, 2018). The area sampled is therefore not categorized as eutrophicated based on the estimated nutrient concentrations, but that does not necessary mean that the intertidal community is unaffected by the nutrient effluents originating from aquaculture.

In this study I have focused on DIN originating from the aquaculture farms, but as mentioned in the introduction, large amounts of particulate organic matter (POM) is also released from aquaculture farms (Grefsrud et al., 2021). Since these nutrients are bound to feces or feed, they sink faster to the seabed than the dissolved nutrients, and are thus believed to have a smaller impact on the surrounding communities not situated directly underneath the farm (R. J. Bannister et al., 2014; Kutti et al., 2007; Valdemarsen et al., 2015). R. J. Bannister et al. (2016) predicted, using a model, that 75% of the POM originating from fish farms are dispersed shorter than 500 meters away from the cages. Since all aquaculture stations sampled were situated not more than 300 meters away from the cages, they were most likely also influenced by elevated POM concentrations. I only tested the impact of DIN on the community, as this

was what was retrieved from the NORWECOM model, and as this was the variable most likely to affect the macroalgae, which had the highest focus in this study. Especially the suspension feeders might have been more influenced by the organic nutrients than the inorganic ones. If there is a correlation between amount of DIN and POM on each station, as I assume, my results might not have become so different by including POM values.

Since each aquaculture farm had only conducted one chemical treatment, and I only had three different aquaculture farms, it was not possible to test if there were any significant difference in the intertidal community induced by the chemicals used (Table 3).

Azamethiphos is used in feed treatments and is therefore bound to the feed, most of it will sink quickly to the seabed and most likely not have a large impact on the intertidal zone. The two other chemicals, hydrogen peroxide and Emamectin benzoate, are used as bath treatments where the treatment water is released into the ocean following the currents after treatment, and thus might have a larger impact on the organisms living in the intertidal zone (Canty et al., 2007; Haugland et al., 2019). The results did not show any signs of impacts from these chemicals on the aquaculture stations, and it is therefore reasonable to assume that the chemical treatments on the farms did not have a substantial impact on the community. To be certain that the intertidal zone is not affected by these bath treatments a more thorough research focusing on this topic should be conducted.

4.2. Species communities

4.2.1. Algae communities

The algae community was not significantly influenced by predicted elevated nitrogen values (Δ DIN), but both degree of wave exposure and geographical position in accordance to the archipelago were altering the community. Most stations were clustered in the middle of the ordination indicating they had similar wave exposure, but station C5 (Control station 5) was associated with a lower one and station C4 with a higher (Figure 7) – which can also be seen by looking at the relative wave exposure for each station (Table 3). Station C5, C4, and A3 (Aquaculture station 3) had an association with the east side of the archipelago, while the other stations were more associated with the west, as would be expected from the locations of each station (Figure 1).

Earlier studies have shown a higher abundance of annual ephemeral algae as a response to nutrient enrichment in eutrophicated areas (Fowles et al., 2018; Kraufvelin et al., 2010; Liu et al., 2010; Ménesguen et al., 2010; Oh et al., 2015; Pang et al., 2010; Pedersen & Borum, 1996, 1997; Teichberg et al., 2008; Valiela et al., 1997). In this study no response in the algae community induced by nutrient enrichment was found, and there are multiple factors that can explain this. First of all, the nutrient output from the fish farms might not have been large enough, or were too quickly diluted, to create a response in the intertidal community. In the Institute of Marine Research's risk assessment they concluded that the risk of regional eutrophication in Norway, caused by salmonid farms, were low (Grefsrud et al., 2021). During an aquaculture cycle, nutrients are continuously released into the environment, but the flumes are larger during summer when the fish grows and eats more, and at the largest in the period before harvesting. And in addition, there is a period of fallowing before the net pens are restocked which also gives the community some time to recover before the new cycle.

Secondly, established rocky shore communities have been described as resilient to environmental stressors, and experiments have shown that the communities can tolerate high nutrient levels for many years, before a sudden community shift might occur (Bokn et al., 2002; Kraufvelin, Moy, et al., 2006; Worm & Lotze, 2006). One plausible explanation for this resistance in the algae community is that large perennial algae (such as *Fucus* spp. or kelps) can resist a higher wave action than the ephemeral algae, and might even detach annual algae by whiplashing at stations with relatively high wave exposure (Bokn et al., 2002; Kiirikki, 1996; Kraufvelin et al., 2010; Littler & Littler, 1980; Lubchenco & Menge, 1978; Pihl et al., 1999; Sousa, 1979).

Another explanation for the lack of response in the algae community could be the grazers in the community. Many studies have shown that grazing fauna prefers fragile, ephemeral algae, usually annuals, over perennials for consumption (Christie et al., 2009; Lotze & Worm, 2000; Lubchenco, 1978). Due to this feeding preferences these organisms can hinder large amounts of annual algae to establish on the shore, and can even work as a counteractive force of eutrophication (Hillebrand, 2003; Kraufvelin, Salovius, et al., 2006; Lotze et al., 2000; Lotze & Worm, 2000; Lubchenco & Menge, 1978; Worm et al., 2006; Worm & Lotze, 2006).

According to the CCA, *Osmundea* spp. was associated with a high wave exposure and with the east side of the archipelago (Figure 9). Previously these species have been described as

common on rocky shores ranging from exposed to moderately sheltered (Pizzolla, 2003). *Osmundea* spp. were only recorded at station C4, the most exposed station and situated on the east side, which is most likely the explanation for this response (Table 3).

The algae taxa *Fucus spiralis*, *Pylaiella littoralis*, and *Cladophora* spp. were highly associated with both low wave exposure and east of the archipelago. *F. spiralis* is known to thrive in more sheltered areas, which corresponds to my results (Figure 9; Hawkins et al., 2019; Lewis, 1961). *P. littoralis* and *Cladophora* spp. are both filamentous algae and, as mentioned previously, ephemeral algae can usually withstand a lower wave exposure than more sturdy perennial algae, which might explain the preference for a lower wave exposure (Bokn et al., 2002; Kiirikki, 1996; Kraufvelin et al., 2010; Littler & Littler, 1980; Lubchenco & Menge, 1978; Pihl et al., 1999; Sousa, 1979). *Ulva fenestrata* is also an ephemeral alga which might explain the association with a lower wave exposure.

I would have expected *Pelvetia canaliculata* to also be associated with a lower wave exposure, but it was only found at one station (A3) which might explain these results (Hawkins et al., 2019; Osland, 1985). Another species that came out associated with a stronger wave exposure than predicted was *Cladophora rupestris* (Figure 9; Johannessen & Svensen, 2017). Both *P. canaliculata* and *C. rupestris* were associated with the east side of the archipelago however, which might have been less wave exposed than the cartographic wave exposure calculated suggested. This will be more thoroughly discussed in the limitation chapter further down in the discussion.

Alaria esculenta and *Himanthalia elongata* were expected to be associated with the more exposed side of the gradient (Hawkins et al., 2019; Lewis, 1961, 1968; Lubchenco, 1980; Osland, 1985). All the stations in this study had an intermediate wave exposure, thus all stations should be within *A. esculenta* and *H. elongata*'s wave exposure-niche. Both species were, however, more associated with the west side of the archipelago (Figure 9). This might indicate that the stations on the west side in reality were more wave exposed than the cartographic wave exposure calculated suggested.

4.2.2. Animal communities

The animal communities were significantly driven by predicted elevated nitrogen values (Δ DIN), whether stations were situated on the east or west of the archipelago, and the relative wave exposure, where wave exposure had the smallest impact. The animal community at station A1 was highly associated with a higher predicted Δ DIN, while the one at A2 was somewhat less associated (Figure 8). Station C2 and C3 were associated with a lower predicted Δ DIN. Station C4, C5, and A3 were more highly associated with the east side of the archipelago than the other stations. The wave exposure gradient and east west gradient were in the same direction in the CCA, thus the stations associated with the west side of the archipelago were also, in general, associated with a higher wave exposure.

According to my results, *Mytilus edulis* (bivalve) and *Metridium senile* (anemone) were associated with a higher Δ DIN (Figure 10). This was not surprising as both species are suspension feeders, which have shown to respond to the increased production arising from nutrient enrichment (Cabral-Oliveira et al., 2013; Haugland et al., 2021; Menge et al., 1997; Worm & Lotze, 2006). In addition, *M. edulis* has been documented to feed on particles originating from aquaculture (Lander et al., 2012, 2013; MacDonald et al., 2011).

The taxa *Nucella lapillus* (gastropod), *Gammarus* sp. (crustacean), *Alcyonidium hirsutum* (bryozoa), *Halichondria (Halichondria) panicea* (sponge), and *Tritia reticulata* (gastropod) were associated with a lower Δ DIN (Figure 10). It has previously been shown that predators like *N. lapillus* can have an increased abundance with a higher nutrient concentration due to bottom-up control, and this is therefore a bit surprising (Menge et al., 1997, 1999; Worm & Lotze, 2006). My results, however, is most likely influenced by station C2's very high abundance of *N. lapillus* compared to the other stations. *N. lapillus* is also known to thrive in a relatively exposed habitat, which fits with my results as it was associated with a higher wave exposure (Johannessen & Svensen, 2017). Kraufvelin, Salovius, et al. (2006)'s study showed that the abundance of gammarideans was positively correlated with nutrient addition, but this was not detected in my results. *H. panicea* is known to prefer a more exposed location due to the higher water flow and less interspecific competition (Crowe et al., 2000; Johannessen & Svensen, 2017). In this study *H. panicea* was associated with the mean wave exposure of stations, but as mentioned previously, all stations examined had an intermediate wave exposure which might explain the result. *H. panicea* and *A. hirsutum* are suspension feeders

and, as mentioned in the last section, this group has been known to respond positively to nutrient enrichment (Cabral-Oliveira et al., 2013; Haugland et al., 2021; Menge et al., 1997; Worm & Lotze, 2006). It is therefore conflicting with previous research that these species were associated with a low Δ DIN, but suspension feeders are a large heterogenic group and different species might have different feeding preferences, which could be an explanation for some suspension feeders being associated with a high Δ DIN and some with a low (Bougrier et al., 1997; Cucci et al., 1985; Lesser et al., 1992; Troost et al., 2009).

The species *Actinia equina* (anemone), *M. senile*, and *M. edulis* were associated with the west side and a higher wave exposure, while *T. reticulata* and *Spirorbis (Spirorbis) spirorbis* (annelid) were mostly associated with the eastern side of the archipelago and with a lower wave exposure (Figure 10). *A. equina*, *M. senile*, and *M. edulis* are all suspension feeding animals which might get a higher supply of food in more wave exposed areas (Cabral-Oliveira et al., 2013; Haugland et al., 2021; Menge et al., 1997; Worm & Lotze, 2006). Since *S. spirorbis* also is a suspension feeding organism, I assumed it to be associated with a higher wave exposure and the west side of the archipelago, but in this case it was not.

Tritia reticulata is a scavenger feeding on decaying algae which tends to gather in more sheltered areas (Crowe et al., 2000). This could explain the association with a lower exposure.

Semibalanus balanoides (crustacean) and *Patella vulgata* (gastropod) were centered in the plot indicating that these species were common on all sites, as they are in most places in Norway (Figure 10; Johannessen & Svensen, 2017). *S. balanoides* is also known to have a slight preference for more wave exposed sites, as most of my sites were (Bertness et al., 1991; Lewis, 1961, 1968; Osland, 1985).

4.3. Biodiversity and richness

The differences in total biodiversity and species richness between stations were not very large (Table 4). C1 was the station with the highest Shannon Wiener diversity index at 2.66, while station A2 and C5 had the lowest at 2.20. Station C3 had the highest number of species (44) while station C4 had the lowest (28). The difference in diversity indices and species richness was not significantly driven by predicted elevated nitrogen values (Δ DIN).

The p-values from the analyses conducted were far from significant indicating that the variation in diversity indices and species richness between stations, were caused by noise or natural variation. Due to previous studies I expected to find a less diverse community at stations subject to larger nutrient effluents (Haugland et al., 2021; Howarth et al., 2011; Pihl et al., 1999; Worm et al., 1999; Worm & Lotze, 2006). In certain cases, however, the biodiversity have been shown to be higher at nutrient induced stations (Hillebrand, 2003; Kraufvelin, Moy, et al., 2006; K. J. Nielsen, 2003). While Williams et al., (2013) found no effect of nutrient on seaweed diversity, so there are a lot of factors that can amplify and reduce each other's influence on the rocky shore biodiversity. An explanation for my results not showing an influence of Δ DIN on the biodiversity or species richness, could be that other factors are camouflaging the influence or, more likely, that the nutrient enrichment in the ecosystem was too small to have a significant impact.

4.4. Functional group composition

4.4.1. Algae

At most stations the algae biomass was dominated by perennials, and around 85% of the algae coverage was of perennial species (Figure 11). Predicted elevated nitrogen values (Δ DIN) did not, however, have a significant impact on the differences in algae functional group composition. In a natural situation, without large stressors, the intertidal zones in the North-East Atlantic Ocean are usually dominated by perennial coverage (Worm & Lotze, 2006). The largest cumulative coverage of an annual algae species was of *Pylaiella littoralis* at station C5 (98%), while for any perennial taxa the highest coverage was of crustose corallines at station C4 (268%; Table 5). Station C4 also had the highest cumulative coverage of *F. serratus* (250%), which was the second most dominating algae at the site.

A higher concentration of nutrients and eutrophication have, as previously mentioned, been shown to cause a shift in the algae community due to the annual, ephemeral algae's quick responses and can in extreme cases lead to a dominance of annual algae (Fowles et al., 2018; Kraufvelin et al., 2010; Liu et al., 2010; Ménesguen et al., 2010; Oh et al., 2015; Pang et al., 2010; Pedersen & Borum, 1996, 1997; Teichberg et al., 2008; Valiela et al., 1997). As the algae community and the algae functional group composition was not significantly influenced by Δ

DIN, the dominance of perennial algae was as expected. The difference in functional group composition between stations was thus caused by other factors or natural variation.

4.4.2. Sessile animals

Semibalanus balanoides was the dominating suspension feeding animal at all stations, with the highest cumulative percentage found at station C5 (577%) and the lowest at station A3 (152%; Table 6). C5 had the highest cumulative percentage of all suspension feeding organisms as well (618%), while A3 had the lowest coverage of suspension feeders – 212% (Figure 12). Predicted elevated nitrogen values (Δ DIN) was, however, not significantly influencing the amount of suspension feeders at the stations.

Since some suspension feeding taxa were found to be associated with high Δ DIN in the ordination analysis (Figure 10), I expected to find a significant difference of suspension feeders in the functional group analysis. This was however not detected in this study, which might be due to suspension feeders being a large and heterogenic group where different species have different feeding habits, like what to ingest and digest and what to not (Bougrier et al., 1997; Cucci et al., 1985; Lesser et al., 1992; Troost et al., 2009). This could lead to different responses to aquaculture effluents between species, and thus no clear trend in suspension feeding coverage between stations induced by predicted elevations in nitrogen (Δ DIN).

Another factor that could have hindered us from finding a response in suspension feeding fauna induced by Δ DIN, was that the sampling of epiphytic suspension feeders was not thorough enough with the sampling method used. This will be more discussed in the limitation section in the end of the discussion.

4.4.3. Mobile animals

Most stations were dominated by grazers, except station C2 which was dominated by predators (Figure 13). Most stations also had predators as the second most dominating functional groups, except A2 where it was omnivores and C2 where it was grazers. The domination of predators at C2 was due to the especially high amount of *N. lapillus* (291) found at the station, and the low proportion of predators at A2 was due to the low number of *N.*

lapillus (one; Table 7). The differences in mobile animal composition between stations were not significantly influenced by the predicted elevated nitrogen values (Δ DIN).

Since the animal community was found to be significantly affected by Δ DIN in the ordination, I also expected to find a significant difference in the mobile animal composition at the station induced by Δ DIN. This result might indicate either that the composition of mobile animal functional groups at a station was not the best indicator when investigating changes in intertidal communities, or that the taxa inside each group were too diverse and could not successfully be analyzed together in one group.

The highest number of individuals of one grazing species group was either *Patella vulgata* or *Littorina* spp. (gastropod) on all stations (Table 7). Station A1 had the highest number *P. vulgata* (119 individuals) and station C4 was the station with the highest amount of *Littorina* spp. (350 individuals; Table 7). The lowest number of *P. vulgata* was found at station C1 (43 individuals) and lowest number of *Littorina* spp. at C3 (16 individuals).

Multiple studies have found increases in grazers due to nutrient enrichment, most likely since they respond to the excessive growth of preferred food material and they can, as previously mentioned, even work as a counter-active force to nutrient addition (Christie et al., 2009; Díaz et al., 2012; Hillebrand, 2003; Kraufvelin, Salovius, et al., 2006; Lotze & Worm, 2000; Lubchenco, 1978). With this in mind I expected a higher abundance of grazers at stations with higher Δ DIN, but this trend was not visible in my results. However, the stations with the highest number of *Littorina* spp., C4 and A3, was also the stations with the especially low numbers of suspension feeders, mostly *S. balanoides* (Figure 12 and Table 6). Previous research has shown that feeding by grazing intertidal gastropods is less efficient with large amounts of barnacles (Little et al., 1988; Underwood, 1979). Díaz et al. (2012) also concluded after a mesocosm experiment that *Littorina littorea* originating from non-enriched mesocosms had a negative co-variation with barnacles, supporting my result. There was no visible relationship between *P. vulgata* and barnacles, however, as expected if the grazing is less efficient with large amount of barnacles (Little et al., 1988; Underwood, 1979).

The dominating predator species in this study was *N. lapillus* at all stations. Station C2 had 291 individuals while at A2 only one individual was found (Table 7). Station C2 had the highest relative wave exposure of all stations situated on the west side of the archipelago (Table 3).

N. lapillus is, as previously mentioned, known to thrive in mildly exposed areas and this could be an explanation for the high abundance (Johannessen & Svensen, 2017). Predators have previously been shown to be influenced by nutrient enrichment due to bottom-up control providing the fauna with food, but this trend was not visible in this study (Menge et al., 1997, 1999; Worm & Lotze, 2006).

4.5. Comparison of spring and summer

4.5.1. Direct ordination

The ordinations of algae data at stations A3, C4, and C5 during the spring and summer analyses were not significantly constrained by any of the environmental conditions (slope, wave exposure, Δ DIN) and these CCAs are not discussed further. The animal data from spring was significantly influenced by Δ DIN and the slope of each quadrant, while the animal data from summer was significantly influenced by Δ DIN, slope, and the relative wave exposure.

Station A3 (+ A3H) was associated with a higher Δ DIN than station C4 (+ C4H) and C5 (+C5H) both in the spring and summer animal CCAs (Figure 14 and 15). This was as expected since the aquaculture station was situated closer to the farms than the control stations. In the spring CCA the animal community at station C5 was associated with a higher slope and the animal community at C4 with a lower one (Figure 14). Pictures from the two stations and the mean slope of the quadrants indicates that station C5 was quite steep while station C4 was quite gentle (Figure 2 and Table 3).

In the summer CCA, A3H was more highly associated with a steep slope than C5H (Figure 15). This can be explained by the quadrants having a different placement in the second investigation, and the mean difference between upper and lower edge of quadrants at station C5 changed from 27 cm in spring to 14 cm in summer (C5H), making A3H the station having the steepest slope of quadrants during summer (Table 3). In summer, the animal composition also became significantly affected by wave exposure where the animal community at station C4H was associated with a higher wave exposure, the one at A3H was in the middle of the CCA, and the one at C5H was associated with a lower wave exposure (Figure 15). This was in accordance with the relative wave exposure calculated for each station (Table 3).

In the CCA of animal data from spring, *Idotea* sp. (crustacean) was associated with a high Δ DIN, and in addition *Dynamena pumila* (hydrozoa) was associated with a higher than mean Δ DIN (Figure 16). On the other side of the gradient *Electra pilosa* (bryozoa) and *T. reticulata* were associated with a lower than mean Δ DIN. *Idotea* sp. is a grazer and could be responding positively to a higher Δ DIN due to higher amounts of, and maybe more favorable, food (Christie et al., 2009; Kraufvelin, Salovius, et al., 2006; Lotze & Worm, 2000; Lubchenco, 1978). Both *D. pumila* and *E. pilosa* are suspension feeders so it is reasonable to think that they would be associated with a high Δ DIN, but in this case *E. pilosa* was surprisingly associated with the opposite end of the gradient.

In accordance with the slope gradient, *S. balanoides* was associated with a steep slope, and *E. pilosa* and *A. hirsutum* with a gentle slope (Figure 16). These results fit well with previous knowledge of that *S. balanoides* is thought to thrive in steeper slopes due to less competition for space by other organisms that are not able to stick to the steep rock, and *E. pilosa* and *A. hirsutum* are usually epiphytes on perennial algae and thus prefers an algae surface to stick to (Best & Thorpe, 1986; Lewis, 1968; Tyler-Walters, 2005).

In the CCA with summer animal data, *D. pumila* and *Membranipora membranacea* (bryozoa) were associated with a higher than mean Δ DIN and slope (Figure 17). The Δ DIN association was as expected due to them both being suspension feeders, but the slope association was a bit surprising as they are also mainly found on algae (Cabral-Oliveira et al., 2013; Haugland et al., 2021; Menge et al., 1997; Rossi et al., 2000; Rowley, 2004; Worm & Lotze, 2006).

Steromphala cineraria (gastropod) was associated with a very low Δ DIN and slope, compared to the other animals (Figure 17). *S. cineraria* is known to thrive between stones and algae in the lower intertidal zone, which could explain the association with a gentle slope since steeper walls often supports low level of algae and rocks (Hawkins et al., 2019; Johannessen & Svensen, 2017; Lewis, 1968). Since this species feeds on algae it is contradictory that it was associated with a low Δ DIN (Johannessen & Svensen, 2017). This species was however only found at one station, and only during summer.

The largest differences between the spring and summer CCA with animal data, were that the summer community was significantly affected by wave exposure, in addition to Δ DIN and slope, and that during spring the station most associated with a steep slope was C5 while for

summer it was A3H (Figure 14 and 15). Many species were not found during both summer and spring, but of those registered on both occasions most was situated similar in the two CCAs (Figure 16 and 17).

4.5.2. Diversity indices and species richness

The site with the highest Shannon diversity was A3 (2.50) and the lowest was at C5 (2.20; Table 8). Station C5 had the highest number of recorded species (43) and C4 the lowest (28). There was, however, no significant difference in the Shannon Diversity Indices and species richness induced by seasonality.

4.5.3. Functional groups

At all stations the coverage of perennial algae was around 75-100% of the algae coverage (Figure 18). The highest proportion of perennials was at C4H and the lowest on C5. There were only small differences between spring and summer at all stations, and for all of them spring had a lower proportion of perennials than summer. The control stations had marginal differences while the aquaculture one had around 15% higher proportion of perennials during summer. The algae functional group composition was not significantly different between spring and summer, thus this variation seems to just be natural variation.

Station A3, A3H, C4, and C4H had a similar cumulative coverage of sessile animals at around 200-250%, while station C5 and C5H had almost twice the amount at both stations (Figure 19). The largest difference between spring and summer was at station C5, where in the data collected in spring a coverage of 618 % was recorded and in summer there was 161% less coverage (C5H). The other two stations had only marginally higher coverage during summer. These differences in sessile functional groups were, however, not significantly induced by seasonality.

Grazers was the dominating mobile animal group and predators the second most dominating at all stations (Figure 20). C5 and C5H had a similar composition while the variation was a bit larger between A3 and A3H, and C4 and C4H. Even though there were some differences between spring and summer, these differences were also not significant, and they were most likely caused by natural variation.

4.6. Limitations and possible improvements

4.6.1. Environmental variables

There were some limitations to my environmental variables. First of all, the maximum resolution of the NORWECOM model was not high enough to predict with the preciseness wanted (Figure 6). For example, station A3 looks like it is surrounded by two small, separated, islands, but in theory these islands were connected by a molo and the Northward current had only one small outlet under a bridge. Since this map was used to create the Δ DIN values, these values might not be as correct and detailed as they seem. Measurements of nutrients effluents in the water masses is complicated and time consuming to conduct, and would have led to more uncertainties (Dalsgaard & Krause-Jensen, 2006; Jansen et al., 2016, 2018). The model gives an indication of predicted current direction and distance of DIN, however, I might have gotten different results with a higher resolution.

As mentioned multiple times, the relative wave exposure, or cartographic wave exposure, calculated might not be a good representation of the true wave exposure. For matters of simplicity this value was calculated only taking the fetch of each station into consideration. This method has been used successfully before, but since I found a significant difference between stations on the west and east side of the archipelago, it seems like it did not work as well when trying to compare stations situated in dissimilar environments (Armitage et al., 2014). Factors like wave diffraction and wind direction was not considered in this calculation, all of which were most likely higher at stations situated closer to open ocean, leading me to believe that the westerly stations in theory had a higher wave exposure than the easterly. Another plausible explanation for the significant difference between sides of the archipelago could be that other factors differentiating from the two sides has influenced the result. For example, recruitment of some species (e.g., *H. elongata* and *A. esculenta*) could be more limited inside the fjord. In later studies it would be better to have more similar stations when comparing the calculated relative wave exposure.

4.6.2. Locating the stations

Research has shown a lower coverage of filamentous species at more wave exposed sites due to damage and detaching by waves (Pihl et al., 1999). All my stations had an intermediate wave exposure, but waves and whiplash might have influenced the abundance of annual

algae. Farm size was one of the factors used to discriminate between farms, and only high production farms were picked due to them having the highest release of nutrients. This automatically excluded farms situated in more sheltered areas with a lower wave exposure, where responses of eutrophication might have been more visible (Fowles et al., 2018; Kraufvelin et al., 2010; Liu et al., 2010; Ménesguen et al., 2010; Oh et al., 2015; Pang et al., 2010; Pedersen & Borum, 1996, 1997; Teichberg et al., 2008; Valiela et al., 1997). The aquaculture net pens examined are however representative for farms with a high production of salmon around Bergen, and this gives us a picture of how, and if, these intertidal communities are affected.

Station A3, C4, and C5 was, as previously mentioned, more sheltered from the open ocean than the other stations, and they were also more prone to human activity as they were situated on islands with human settlements and were reachable by car (Figure 1). In the results there were often a significant difference between stations on the east and west side of the archipelago and by avoiding this difference by only examining station situated in similar environments, the response to nutrient enrichment could have been easier to detect and interpret.

Another factor that should have been considered before locating the stations, was the current direction. The nutrient effluents has been shown to extend much longer in the current direction, and that areas counter-current might not be influenced at all (Sanderson et al., 2008). To accomplish this the NORWECOM model would have had to be run multiple times which was not possible. This could, if conducted, have made the stations more predictable. By using the Δ DIN calculated though, my results are reliable either way, but I might have gotten a clearer result if the aquaculture stations were in the main effluent current and thus more heavily impacted by the aquaculture.

4.6.3. Field procedure

With the sampling method used, it was difficult to register all mobile animals inside the plot since many quadrants were dominated with algae providing the animals with hiding spots. As the mobile fauna is mobile it is also difficult to know the pressure these species have on the environment by using this sampling method. In addition, the suspension feeders, especially hydroids and bryozoans, were hard to register as they often grew on all sides of the algae, and

sampling should have been conducted more thoroughly. Both the mobile grazers and the suspension feeding organisms have previously shown to respond to nutrient enrichment, and these organisms should therefore have had a higher focus (Cabral-Oliveira et al., 2013; Christie et al., 2009; Díaz et al., 2012; Haugland et al., 2021; Kraufvelin, Salovius, et al., 2006; Lotze & Worm, 2000; Lubchenco, 1978; Menge et al., 1997; Worm & Lotze, 2006). By using a destructive sampling method, where all biomass from the quadrants were removed and thoroughly examined in the laboratory, I could have gotten more precise results, but this is very time consuming, and I would not have been able to resample a station in many years.

To examine if the response to nutrient enrichment was visible in some season but not all, I also revisited three stations. To get a proper overview all stations should have been revisited, but due to limited time and resources this was not possible and thus only a snapshot of how the stations change between spring and summer was retrieved.

5. Conclusion

The aim of this study was to examine if Norwegian aquaculture salmonid farms have an impact on the nearby intertidal rocky shore community. The intertidal animal community was found to be influenced by the change in nitrogen concentration (Δ DIN), relative wave exposure, and which side of the archipelago the station was situated on, while the algae community was only driven by wave exposure and side of the archipelago. Biodiversity, species richness, or functional group composition were not significantly driven by Δ DIN. The animal communities in both spring and summer were significantly altered by Δ DIN, but seasonality did not have an influence on the biodiversity, species richness, or functional group composition at each station.

The animal composition was found to be influenced by the aquaculture farms, and my hypothesis, that nearby aquaculture farms does have an impact on the intertidal community, has been strengthened. The algae community, however, showed no signs of impact from aquaculture. A plausible explanation for the change in animal and not algae communities, is that the grazing animals are working as a counter-active force to the nutrient enhancement by feeding on opportunistic algae (Hillebrand, 2003). The similar result in summer data strengthens the results of my main investigation further. Previously there has been multiple investigations in Norway finding no sign of effects driven by aquaculture on the intertidal zone, but since the differences I found were not very conspicuous their methods might not have been thorough enough to detect it (Bye-Ingebrigtsen et al., 2019; Husa, Steen, et al., 2014).

Further research should focus on the animal community and try to figure out if, and how, the changes induced by nutrients originating from aquaculture might affect the intertidal community. The result of this study has given more knowledge on environmental effects of salmon farming and should be taken into consideration by the Norwegian authority when handling cases regarding upscaling the industry in the future.

6. References

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Appendix A

Full species list of algae and animals sampled in field, alphabetically sorted into algae and animals. In addition, showing functional group of all taxa.

Species/taxa	Functional group	Reference
Algae:		
<i>Acrosiphonia arcta</i> (Dillwyn) Gain, 1912	annual	(Blomqvist et al., 2014)
<i>Alaria esculenta</i> (Linnaeus) Greville, 1830	perennial	(Garbary, 1976; Tyler-Walters, 2008a)
<i>Asperococcus fistulosus</i> (Hudson) W. J. Hooker, 1833	annual	(Sowerby et al., 1846)
<i>Bangia fuscopurpurea</i> (Dillwyn) Lyngbye, 1819	annual	(Richardson & Dixon, 1968)
<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin, 1947	annual	(Garbary & Tam, 1989)
<i>Bonnemaisonia hamifera</i> Hariot, 1891	annual	(Blomqvist et al., 2014; Garbary, 1976)
<i>Ceramium</i> spp. Roth, 1797	variable	(Blomqvist et al., 2014)
<i>Chaetomorpha ligustica</i> (Kützing) Kützing, 1849	annual	(Blomqvist et al., 2014; Garbary, 1976)
<i>Chordaria flagelliformis</i> (O. F. Müller) C. Agardh, 1817	annual	(Blomqvist et al., 2014)
<i>Cladophora rupestris</i> (Linnaeus) Kützing, 1843	perennial	(Blomqvist et al., 2014)
<i>Cladophora</i> spp. Kützing, 1843	variable	(Blomqvist et al., 2014)
<i>Corallina officinalis</i> Linnaeus, 1758	perennial	(Blomqvist et al., 2014; Garbary, 1976)
Crustose corallines	perennial	(Bôas & Figueiredo, 2004; Jackson, 2003)
Cyanobacteria	annual	(Hihara et al., 2001)
<i>Delesseria sanguinea</i> (Hudson) J. V. Lamouroux, 1813	perennial	(Blomqvist et al., 2014; Garbary, 1976)
<i>Dictyota dichotoma</i> (Hudson) J. V. Lamouroux, 1809	annual	(Norwegian Seaweeds, n.d.-a)
<i>Dumontia contorta</i> (S. G. Gmelin) Ruprecht, 1850	perennial	(Blomqvist et al., 2014)
<i>Ectocarpus</i> spp. Lyngbye, 1819	annual	(Blomqvist et al., 2014)
<i>Elachista fucicola</i> (Vellay) Areschoug, 1842	annual	(Blomqvist et al., 2014)
<i>Euthora cristata</i> (C. Agardh) J. Agardh, 1847	unknown	(Garbary, 1976)
<i>Fucus serratus</i> Linnaeus, 1753	perennial	(Blomqvist et al., 2014; Garbary, 1976)
<i>Fucus spiralis</i> Linnaeus, 1753	perennial	(Haavisto, 2016)
<i>Fucus vesiculosus</i> Linnaeus, 1753	perennial	(Blomqvist et al., 2014)

<i>Gaillona cf. gallica</i> (Nägeli) Athanasiadis, 2016	unknown	No reference found
<i>Gaillona seposita</i> (Gunnerus) Athanasiadis, 2016	unknown	No reference found
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini, 1841	perennial	(Yoneshigue-Valentin & Valentin, 1992)
<i>Himantalia elongata</i> (Linnaeus) S. F. Gray, 1821	perennial	(Stengel et al., 1999)
<i>Isthmoplea sphaerophora</i> (Carmichael) Gobi, 1878	annual	Kjersti Sjøtun (personal comment)
<i>Laminaria</i> spp. J. V. Lamouroux, 1813	perennial	(Blomqvist et al., 2014)
<i>Leathesia marina</i> (Lyngbye) Decaisne, 1842	annual	(Blomqvist et al., 2014)
<i>Leptosiphonia brodiei</i> (Dillwyn) A. M. Savoie & G. W. Saunders, 2019	annual	No reference found
<i>Leptosiphonia fibrillosa</i> (Agardh) A. M. Savoie & G. W. Saunders, 2019	annual	No reference found
<i>Lomentaria clavellosa</i> (Lightfoot ex Turner) Gaillon, 1828	annual	(Blomqvist et al., 2014; Garbary, 1976)
<i>Mastocarpus stellatus</i> (Stackhouse) Guiry, 1984 / <i>Chondrus crispus</i> Stackhouse, 1797	perennial	(Blomqvist et al., 2014; Garbary, 1976; Norwegian Seaweeds, n.d.-b)
<i>Membranoptera alata</i> (Hudson) Stackhouse, 1809	unknown	(Blomqvist et al., 2014; Garbary, 1976)
<i>Monostroma grevillei</i> (Thuret) Wittrock, 1866	annual	(Blomqvist et al., 2014)
<i>Neopyropia leucosticta</i> (Thuret) L. – E. Yang & J. Brodie, 2020	annual	(Blue Ecosystem, n.d.)
<i>Osmundea</i> spp. Stackhouse, 1809	perennial	(Blomqvist et al., 2014)
<i>Palmaria palmata</i> (Linnaeus) F. Weber & D. Mohr, 1805	perennial	(Blomqvist et al., 2014; Garbary, 1976)
<i>Pelvetia canaliculata</i> (Linnaeus) Decaisne & Thuret, 1845	perennial	(Strömngren, 1986)
<i>Petalonia fascia</i> (O. F. Müller) Kuntze, 1898	annual	(Blomqvist et al., 2014)
<i>Planosiphon zosterifolius</i> (Reinke) McDevit & G. W. Saunders, 2017	annual	(Blomqvist et al., 2014)
<i>Polysiphonia stricta</i> (Mertens ex Dillwyn) Greville, 1824	perennial	(Blomqvist et al., 2014; Garbary, 1976)
<i>Porphyra</i> spp. C. Agardh, 1824	annual	(Blomqvist et al., 2014)
<i>Protomonostroma</i> sp. K. L. Vinogradova, 1969	annual	(Seaweed of Canada, n.d.)

<i>Pylaiella littoralis</i> (Linnaeus) Kjellman, 1872	annual	(Blomqvist et al., 2014)
<i>Rhodomela confervoides</i> (Hudson) P. C. Silva, 1952	perennial	(Blomqvist et al., 2014)
<i>Scytosiphon lomentaria</i> (Lyngbye) Link, 1833	annual	(Blomqvist et al., 2014)
<i>Sphacelaria</i> sp. Lyngbye, 1818	perennial	(Blomqvist et al., 2014)
<i>Spongomorpha aeruginosa</i> (Linnaeus) Hoek, 1963	annual	(Blomqvist et al., 2014)
<i>Spongonema tomentosum</i> (Hudson) Kützing, 1849	annual	(Blomqvist et al., 2014)
<i>Ulva</i> cf. <i>prolifera</i> O. F. Müller, 1778	annual	(Blomqvist et al., 2014)
<i>Ulva compressa</i> Forsskål, 1775	annual	(Blomqvist et al., 2014)
<i>Ulva fenestrata</i> Postels & Ruprecht, 1840	annual	(Blomqvist et al., 2014)
<i>Ulva intestinalis</i> Linnaeus, 1753	annual	(Blomqvist et al., 2014)
<i>Ulva linza</i> Linnaeus, 1753	annual	(Blomqvist et al., 2014)
<i>Urospora</i> spp. Areschoug, 1866 / <i>Ulothrix</i> spp. Kützing, 1833	annual	(Blomqvist et al., 2014)
Animals:		
<i>Actinia equina</i> Linnaeus, 1758	suspension feeder	(Chintiroglou & Koukouras, 1992)
<i>Actiniaria</i> indet. Hertwig, 1882	suspension feeder	(Chintiroglou & Koukouras, 1992)
<i>Alcyonidium hirsutum</i> Fleming, 1828	suspension feeder	(Winston et al., 1977)
<i>Asterias rubens</i> Linnaeus, 1758	predator	(Budd, 2008)
<i>Balanus balanus</i> Linnaeus, 1758	suspension feeder	(Hosie, 2008)
<i>Calliostoma zizyphinum</i> Linnaeus, 1758	predator	(Ballerstedt, 2008)
<i>Carcinus maenas</i> Linnaeus, 1758	omnivore	(Neal & Pizzolla, 2008)
<i>Celleporella hyaline</i> Linnaeus, 1767	suspension feeder	(Winston et al., 1977)
<i>Cottidae</i> indet. Bonaparte, 1831	predator	(Landry et al., 2018)
<i>Doris pseudoargus</i> Rapp, 1827	predator	(Ager, 2008)
<i>Dynamena pumila</i> Linnaeus, 1758	suspension feeder	(Rossi et al., 2000)
<i>Electra pilosa</i> Linnaeus, 1767	suspension feeder	(Tyler-Walters, 2005)
<i>Flustrellidra hispida</i> Fabricius, 1780	suspension feeder	(Winston et al., 1977)
<i>Gammarus</i> sp. Fabricius, 1775	omnivore	(Kelly et al., 2002)
<i>Gonothyrea loveni</i> Allman, 1859	suspension feeder	(Rossi et al., 2000)

<i>Grantia compressa</i> Fabricius, 1780	suspension feeder	(Jørgensen, 1952)
<i>Halichondria (Halichondria) panicea</i> Pallas, 1766	suspension feeder	(Thomassen & Riisgard, 1995)
<i>Hiatella arctica</i> Linnaeus, 1767	suspension feeder	(Ali, 1970)
<i>Idotea</i> sp. Fabricius, 1798	grazer	(Korez et al., 2019)
<i>Littorina</i> spp. Férussac, 1822	grazer	(Imrie et al., 1990; Watson & Norton, 1987)
<i>Membranipora membranacea</i> Linnaeus, 1767	suspension feeder	(Winston et al., 1977)
<i>Metridium senile</i> Linnaeus, 1761	suspension feeder	(Anthony, 1997)
<i>Mytilus edulis</i> Linnaeus, 1758	suspension feeder	(Tyler-Walters, 2008b)
<i>Nucella lapillus</i> Linnaeus, 1758	predator	(Turner & Todd, 1991)
<i>Pagurus</i> sp. J. C. Fabricius, 1775	omnivore	(Gerlach et al., 1976)
<i>Patella vulgata</i> Linnaeus, 1758	grazer	(Hill, 2008)
<i>Semibalanus balanoides</i> Linnaeus, 1767	suspension feeder	(White, 2008)
<i>Spirorbis (Spirorbis) spirorbis</i> Linnaeus, 1758	suspension feeder	(Ni et al., 2018)
<i>Spirobranchus triqueter</i> Linnaeus, 1758	predator	(Riley & Ballerstedt, 2005)
<i>Steromphala cineraria</i> Linnaeus, 1758	grazer	(Turner & Todd, 1991)
<i>Tritia reticulata</i> Linnaeus, 1758	scavenger	(Pizzolla, 2005)

Appendix B

Raw data sheet sorted by stations with ID (last character indicates quadrant number, while the rest is the station name), which intertidal zone situated in, the height over chart datum, the slope, and species data for each quadrant sampled. All sessile organisms are registered in percentage coverage and mobile species in abundance, while the “+” indicates less than one percentage coverage. Full species names can be found in appendix A. A1-3 indicates aquaculture station 1-3 and C1-5 indicates control station 1-5. The H in the station name indicates that the station was sampled in summer.

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
A11	Upper	85	9														
A12	Upper	131	6				16										
A13	Upper	86	26							1			4		+		
A14	Middle	83	11	1	5					+			2		4	15	
A15	Middle	72	30	+						+			3		+	4	
A16	Middle	86	24														
A17	Lower	22	15		2								2			50	
A18	Lower	41	13										8		3	50	
A19	Lower	34	36							1			2		+	3	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
A11																	
A12																	
A13									+		+						
A14	1	+							1						1		
A15			+				1		11			1					
A16									6								
A17							1								92		
A18					+		50								13		
A19												1			4		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
A11																	
A12																	
A13				+	+												+
A14					1								+				2
A15						+							+				1
A16													2				
A17			9					1									
A18			5					+					+				
A19			18	+													

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actiniaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
A11																		
A12									3	10								
A13			3															
A14										3								
A15			5		1					5								
A16			+						1									
A17																	+	
A18			4									1						
A19										+					1			

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
A11											5						13	98
A12											1						1	50
A13										1					26		25	70
A14										3	6		9		1		31	83
A15											2				1		13	40
A16														+			22	96
A17			2										15					+
A18			1										4					3
A19			3										8		1		14	18

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
A11				
A12				
A13				
A14				
A15				
A16				
A17				
A18				
A19				

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
A21	Upper	112	16														
A22	Upper	107	13														
A23	Upper	113	17														
A24	Middle	65	24							+							
A25	Middle	77	23														
A26	Middle	82	20					+									
A27	Lower	43	16		+											52	2
A28	Lower	54	17	+						+						60	4
A29	Lower	36	21		+				+							25	30

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
A21												+					
A22									+			4					
A23									+			25					
A24					1				42			+					+
A25					1				40			+					
A26					2				16			3					
A27			+				2					1	47				
A28			+	+	4		19					3	29				
A29			1		4		25						65		1		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
A21													2				
A22													+				
A23																	
A24										+			1				+
A25					+					+			+				
A26													2				
A27			6							+	+		+	+			
A28			6		+					+	+		+				
A29			7	+									+				

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
A21																		
A22																		
A23																		
A24		+	7				+		+	+								
A25			3							+								
A26			1															
A27		+	+		+													
A28			1															
A29																		

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
A21											11						2	81
A22														+			7	90
A23											1			+			5	93
A24										7	11			+			17	75
A25										15	9				1		20	88
A26					++						7						8	80
A27			2	+						2	2		1				5	16
A28				+				1		4	6		1				10	16
A29			4	1						7	1		2				13	15

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
A21				
A22				
A23				
A24				
A25				
A26				
A27				
A28				
A29				

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fusco-purpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
A31	Upper	113	19														
A32	Upper	125	16														
A33	Upper	140	13				37										
A34	Middle	98	18														
A35	Middle	78	15											4		38	
A36	Middle	84	10													1	
A37	Lower	42	17	11									20	+		45	
A38	Lower	54	18										15	+		60	
A39	Lower	49	26	1									55	+		70	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
A31								5				+					
A32								+				+					
A33												+					
A34									67			10					
A35					+				67			3					
A36					4				79								
A37							48		4			+					
A38					1		84										
A39							75							+			

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
A31																	
A32									5								
A33									+				3				
A34																	
A35		+	+	+											1		
A36																	
A37		+		+								+			26		
A38				+	+					+					8		
A39			+												15		

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
A31																		
A32																		
A33									4									
A34																		
A35																		
A36																		
A37																		
A38												1						
A39																		

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
A31											12						2	50
A32											8						7	45
A33																		2
A34		+		+	1	1					21						19	40
A35		+			2	1				2	17						20	10
A36		+		+	1	1				1	50				4		24	2
A37		6		+							5				1			+
A38		14		4				5		1	7				8		6	+
A39		10		4				1		2	10						11	+

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
A31				
A32				
A33				
A34				
A35				
A36				
A37	2			
A38	2			
A39	1			

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C11	Upper	121	14				2										
C12	Upper	104	17				5										
C13	Upper	124	18				4										
C14	Middle	47	28	21						1					7		
C15	Middle	55	25	10	+					+					16		
C16	Middle	32	83														
C17	Lower	14	30	12	5					22			5			60	
C18	Lower	24	22		+					+			10			65	
C19	Lower	33	6							3			1		31	20	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C11																	
C12																	
C13																	
C14									4								
C15			1						18	+							+
C16					2				56	+							
C17			+												21		14
C18					10		90								12		
C19					3		94								2		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
C11													4				
C12													+				
C13													2				
C14					10	6							1				4
C15			3		4	5						+					1
C16					+												
C17			26	2													
C18			22	+	+	+		+					+				
C19			5	1		4											

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C11									3									
C12									24									
C13									35									
C14																		
C15			2			+				+								
C16									1									
C17						+												
C18						+			+			2						
C19			+		+	+				3								

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C11																	2	50
C12																	7	80
C13																	12	40
C14										2					1			40
C15		1			1						1				5		3	50
C16					3					1	14				6		15	90
C17			+	2			4						+					2
C18		5	1	4					2	2	1							1
C19		6	+	+						2	4						4	+

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C11				
C12				
C13				
C14				
C15				
C16				
C17	1			
C18	1			
C19	+			

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C21	Upper	126	18				+										
C22	Upper	88	25														
C23	Upper	99	17				+										
C24	Middle	57	19	+	19					27					+		
C25	Middle	84	16														
C26	Middle	83	12							1			+				
C27	Lower	16	44		3					11			+		9	60	
C28	Lower	35	24	+						+			2		30	22	
C29	Lower	28	16										2		2	80	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C21																	
C22									+								
C23																	
C24			2														+
C25					+				20								
C26					8				40								1
C27					2		12								38		
C28					2		18								12		
C29					3		60								16		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifo-lius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoi-des</i>	<i>S. lomentaria</i>
C21																	
C22													1				+
C23																	
C24																	
C25													+				
C26																	
C27			21		+	+		1		+							
C28	+		15		+	2				+							
C29			32	+													

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actiniaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. zizyphinum</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C21																		
C22																		
C23																		
C24										+								
C25			1															
C26			7															
C27			1															
C28			2							1		+						
C29			0							2		+						

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C21											2							55
C22					2						4			+	29		7	85
C23					15						27				5		2	80
C24										4					3		14	25
C25					12										24		7	75
C26					++					3	7				162		21	65
C27		3	2					5					1		38			+
C28		3	2					1		1	1				3		5	3
C29		4	7	+				19							27			

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C21				
C22				
C23				
C24				
C25				
C26				
C27				
C28				
C29				

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C31	Upper	98	32														
C32	Upper	149	22				6										
C33	Upper	105	34														
C34	Middle	57	14	2	+					+			+		9		
C35	Middle	63	11	2	+					1					8	2	
C36	Middle	87	15														
C37	Lower	45	18	+	1					+				+	32	10	
C38	Lower	24	24	+	26					+					4	15	
C39	Lower	61	8												55	+	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C31					1				3								
C32												+					
C33					+				1								
C34			2		+				11			+	7			+	+
C35			2		+				6			+	1				
C36					2				66			30					
C37			+						2				62		+	+	1
C38													45		6		2
C39									+			1	70			+	

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
C31													5				
C32													+				
C33													9				
C34					+	+				1							2
C35					+	+											+
C36					+					+							
C37					+	+				+							
C38			32	+						+							
C39																	

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C31			2							+								
C32																		
C33			+							+								
C34			3			+				1								
C35			+						+									
C36		+	20							5								
C37		+	+							2	+	+	1				2	
C38										+		1						
C39								+	1	+								

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C31					5						3		+		18		7	80
C32																		15
C33										1	6				2		11	50
C34		+								5	2				1		10	75
C35											2				5		18	90
C36										6	3				2		24	6
C37			3					+							7		6	18
C38			4					15									1	+
C39			+		++				2	1					5		3	21

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C31				
C32				
C33				
C34				
C35				
C36				
C37				
C38				
C39				

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C41	Upper	141	9														
C42	Upper	130	10														
C43	Upper	127	16														
C44	Middle	113	11														
C45	Middle	91	5													+	
C46	Middle	96	0														
C47	Lower	47	10										1	+	3	85	
C48	Lower	48	11										1		1	92	
C49	Lower	49	3										10	+	3	90	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C41																	
C42												+					
C43									+			+					
C44									51								
C45					3				99			12					
C46					6				50			50					
C47							88		4								
C48							100					+					
C49					8		62								+		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
C41																	
C42																	
C43																	
C44																	
C45															2		
C46															3		
C47			1				6										
C48			7														
C49			19	+													

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C41									1									
C42									1									
C43																		
C44																		
C45																		
C46																		
C47																		
C48												+						
C49												2			2			

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C41											4						10	25
C42											6						3	30
C43											18						4	85
C44					1						70						20	7
C45		+		+	1					1	53				1		13	4
C46					1						51				2		12	30
C47		1	1								62						8	
C48		2	5					6		1	52				1			
C49		+	7	2				3			34							

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C41				
C42				
C43				
C44				1
C45	+			
C46				
C47	10			
C48	13			1
C49	7			2

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopur-purea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C51	Upper	118	30														
C52	Upper	102	33														
C53	Upper	108	23														
C54	Middle	65	31										1	+			
C55	Middle	63	27							+			7	2		6	
C56	Middle	90	17														
C57	Lower	17	21						+	1				2	+	7	
C58	Lower	48	26										3	+		+	
C59	Lower	24	39						1	+			1	1	4	9	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C51								14				+					
C52								+				+					
C53								15				+					
C54					5				48								
C55					3				50			3					
C56					2				41			+					
C57						+	40					25				+	
C58							56										
C59				+			10					8				+	

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifo-lius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonost-roma</i> sp.	<i>P. littoralis</i>	<i>R. confervoi-des</i>	<i>S. lomentaria</i>
C51																	
C52																	
C53																	
C54			+										+		4		
C55			7												24		
C56															1		
C57		+	72	+		+						1	+		25	1	
C58		+		+		+									8	+	1
C59			16				1	+		+					36		

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphinum</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C51																		
C52																		
C53									+									
C54																		
C55																		
C56									1									
C57	+							1										
C58												+						
C59	+					1		+										

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C51											10							65
C52											5							75
C53											14							65
C54		1		1							16		+		8		15	92
C55											6						8	95
C56		2		+	2						4						8	93
C57		1		9				1			1				2			7
C58		4		2				1			6				5		7	60
C59				2				+				4			1		7	25

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C51				
C52				
C53				
C54	1			
C55				2
C56	+			
C57	3			
C58				
C59	4			

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
A3H1	Upper	118	21														
A3H2	Upper	129	16														
A3H3	Upper	118	15														
A3H4	Middle	78	17										2	4		3	
A3H5	Middle	78	15							+			+	+		1	
A3H6	Middle	96	17											+		+	
A3H7	Lower	49	10							+			26	+		92	
A3H8	Lower	47	21							+			45	+		95	
A3H9	Lower	53	16										1	5	+	50	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
A3H1									+			10					
A3H2												6					
A3H3								9	1			15					
A3H4							13		70			5					
A3H5					+				97			10					
A3H6									79								
A3H7							95		3						+		
A3H8							86		13			+					
A3H9					5		54		18			+					

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifo-lius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
A3H1																	
A3H2									1								
A3H3																	
A3H4				+													
A3H5					+												
A3H6																	
A3H7			+	+													+
A3H8			3	1								2					
A3H9		+	3														

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. ziphyphium</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
A3H1																		
A3H2																		
A3H3																		
A3H4					3	+				+								
A3H5					1			+										
A3H6					1	+												
A3H7			1		+							+	1			3		
A3H8				1	+	+							2					
A3H9				+														

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
A3H1											2						8	80
A3H2											8							7
A3H3											4						2	18
A3H4		1		8							32				7		28	2
A3H5		5		8							4				43		29	4
A3H6		+		1							24				2		69	3
A3H7		2	+	6				1			10				2	1	11	2
A3H8		4		6							8	5					6	+
A3H9		5		+							6	+			1		11	

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
A3H1				
A3H2				
A3H3				
A3H4	9			
A3H5	+			
A3H6				
A3H7	14			
A3H8	9			
A3H9	4			

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
C4H1	Upper	115	15														
C4H2	Upper	119	7														
C4H3	Upper	98	10														
C4H4	Middle	98	19												+		
C4H5	Middle	64	11											1		17	
C4H6	Middle	84	4														
C4H7	Lower	41	25										+		3	36	
C4H8	Lower	31	6						+				+		16	14	
C4H9	Lower	45	5										80	4	1	97	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
C4H1																	
C4H2																	
C4H3																	
C4H4					+				76			+					
C4H5									68								
C4H6					2				87								
C4H7							100										
C4H8					10		100								1		
C4H9							90										

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
C4H1																	
C4H2																	
C4H3																	
C4H4																	
C4H5							+										
C4H6																	
C4H7			6														
C4H8			2	+													
C4H9							+										

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. zizyphinum</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
C4H1																		
C4H2																		
C4H3																		
C4H4																		
C4H5																		
C4H6																		
C4H7												1	1	+				
C4H8												+		2				
C4H9													8			1		1

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
C4H1											9						3	70
C4H2											14						3	24
C4H3											40				2		1	70
C4H4		+		+							124				11		25	4
C4H5				+							57				1		10	2
C4H6		+		+							86				1		20	+
C4H7		2	4	2							28	7			4	9	2	
C4H8			7	2				3			32	+						
C4H9	1		+	+				1			79					24	2	

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
C4H1				
C4H2				
C4H3				
C4H4				
C4H5	1			
C4H6				
C4H7	14			
C4H8	20			1
C4H9	5	+	20	

ID	Zone	Height_mean	Slope	<i>A. arcta</i>	<i>A. esculenta</i>	<i>A. fistulosus</i>	<i>B. fuscopurpurea</i>	<i>B. minima</i>	<i>B. hamifera</i>	<i>Ceramium</i> spp.	<i>C. ligustica</i>	<i>C. flagelliformis</i>	<i>C. rupestris</i>	<i>Cladophora</i> spp.	<i>C. officinalis</i>	Crustose corallines	Cyanobacteria
CSH1	Upper	121	17														4
CSH2	Upper	124	12														50
CSH3	Upper	114	12														20
CSH4	Middle	76	12			+					1		9	4		7	
CSH5	Middle	89	21										5	+		2	
CSH6	Middle	61	15							+			+	9			
CSH7	Lower	46	8			1				+		+	1	2		15	
CSH8	Lower	35	17						+				26	+		+	
CSH9	Lower	25	14										5			11	

ID	<i>D. sanguinea</i>	<i>D. dichotoma</i>	<i>D. contorta</i>	<i>Ectocarpus</i> sp.	<i>E. fucicola</i>	<i>E. cristata</i>	<i>F. serratus</i>	<i>F. spiralis</i>	<i>F. vesiculosus</i>	<i>G. cf. gallica</i>	<i>G. seposita</i>	<i>H. rubra</i>	<i>H. elongata</i>	<i>I. sphaerophora</i>	<i>Laminaria</i> spp.	<i>L. marina</i>	<i>L. brodiei</i>
CSH1												2					
CSH2												3					
CSH3								2				2					
CSH4									66			4					
CSH5					+			1	65			7					
CSH6									43								
CSH7					2		43		10			+					
CSH8							96					2					
CSH9							100								2		

ID	<i>L. fibrillosa</i>	<i>L. clavellosa</i>	<i>M. stellatus/C. crispus</i>	<i>M. alata</i>	<i>M. grevillei</i>	<i>N. leucosticta</i>	<i>Osmundea</i> spp.	<i>P. palmata</i>	<i>P. canaliculata</i>	<i>P. fascia</i>	<i>P. zosterifolius</i>	<i>P. stricta</i>	<i>Porphyra</i> spp.	<i>Protomonostroma</i> sp.	<i>P. littoralis</i>	<i>R. confervoides</i>	<i>S. lomentaria</i>
CSH1													+				
CSH2																	
CSH3																	
CSH4			+														
CSH5																	
CSH6																	
CSH7			8									+				+	
CSH8			14													+	
CSH9			2														

ID	<i>Sphacelaria</i> indet	<i>S. aeruginosa</i>	<i>S. tomentosum</i>	<i>U. cf. prolifera</i>	<i>U. compressa</i>	<i>U. fenestrata</i>	<i>U. intestinalis</i>	<i>U. linza</i>	<i>Urospora/Ulothrix</i>	<i>A. equina</i>	<i>Actinaria</i> indet	<i>A. hirsutum</i>	<i>A. rubens</i>	<i>B. balanus</i>	<i>C. zizyphinum</i>	<i>C. maenas</i>	<i>C. hyalina</i>	<i>Cottidae</i> indet.
CSH1																		
CSH2																		
CSH3																		
CSH4					+													
CSH5					+	+										1		
CSH6					3													
CSH7			1		15								3					
CSH8					+								7					
CSH9												+	3					

ID	<i>D. pseudoargus</i>	<i>D. pumila</i>	<i>E. pilosa</i>	<i>F. hispida</i>	<i>Gammarus</i> sp.	<i>G. loveni</i>	<i>G. compressa</i>	<i>H. panicea</i>	<i>H. arctica</i>	<i>Idotea</i> sp.	<i>Littorina</i> spp.	<i>M. membranacea</i>	<i>M. senile</i>	<i>M. edulis</i>	<i>N. lapillus</i>	<i>Pagurus</i> sp.	<i>P. vulgata</i>	<i>S. balanoides</i>
CSH1											1							2
CSH2											5							5
CSH3																	1	37
CSH4				1							32				1		9	90
CSH5				+							18				2		19	80
CSH6											10				2		12	80
CSH7		+	+	2				1			1				2		7	45
CSH8		4	3	10				5			10					1		6
CSH9		2	12	1				2			7		+					45

ID	<i>S. spirorbis</i>	<i>S. triqueter</i>	<i>S. cineraria</i>	<i>T. reticulata</i>
CSH1				
CSH2				
CSH3				
CSH4				
CSH5				
CSH6				
CSH7	1			
CSH8	7			
CSH9	11			