



Department of Arctic and Marine Biology

Drivers of an unexpected unimodal vertical pattern in size distribution of intertidal blue mussels (*Mytilus spp.*)

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Abstract

Blue mussels (*Mytilus spp.*) are important ecosystem bioengineers and provide numerous of ecosystem services. They are found worldwide, but face a global population decline for unclear reasons in many regions. A pilot study in the subarctic rocky intertidal shore in Northern Norway revealed an unexpected unimodal pattern in the body size of blue mussels along a vertical transect from low to high shore. Here, the size of blue mussels increased with shore height, contradicting ecological theories and other studies where mussel size decreased with shore height. It is well-established that size is a known trait proximately enhancing survival and reproduction, thereby influencing population dynamics. This study aims to validate and elucidate the processes behind the unusual size pattern through five field experiments conducted from February to August 2023. (1) First, two open-coast and two inner-fjord sites were selected, replicating the pilot study transects, where mussel size and density were recorded. (2) Recruitment distribution across the different intertidal zones was examined. (3) A mussel-transplantation experiment between high and low intertidal zones was conducted to quantify blue mussel growth. (4) To explore density-dependent effects on mussel growth, a mussel-patch manipulation experiment was performed to test whether reduced density enhanced their growth. Finally, (5) an assessment of the coverage of potential predators, competitors, and facilitators was conducted along the transects. Results showed that the unexpected pattern is limited to open-coast sites, and absent at the inner-fjord sites, suggesting local variation in mussel size patterns across intertidal transects. Growth conditions were most favorable in the low intertidal zone (effect size = 0.81), while recruit density was not statistically different across the intertidal zones. Dogwhelks (*Nucella lapillus*) emerged as the primary contributor to mussel mortality ($\approx 70\%$) in the low intertidal, in addition to exhibiting a feeding preference for larger mussels ($>16.5\text{mm}$). The mussel-patch manipulation did not provide enough data to determine the effect of intra-specific competition; however, mussel-patch survival was limited to the patches with associated *Corallina*-turf (*Corallina officinalis*). This, along with other facilitations, like canopy-forming brown algae (*Ascophyllum nodosum*) suggests that biological interactions may be of high importance to blue mussel populations in the subarctic coast of Northern Norway. In conclusion, this study suggests that abiotic stressors limit mussel size in the top intertidal zone, while biotic interactions, such as facilitation, enhance survival and growth at the high intertidal zone. In the lower intertidal zones, the size structure of blue mussels is influenced by predation from dogwhelks, and the potential effects of density-dependency. This study highlights the necessity for more localized experiments to comprehend the impact of species interactions on the declining blue mussel populations and their size structure in subarctic intertidal zones.

Key words: subarctic - Intertidal - *Mytilus spp.* - Size pattern - Facilitation - Dogwhelks - Environmental stress - *Corallina* turf - Field experiment

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Markus and myself during fieldwork under the northern lights, February 2023

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1 Introduction

In the intertidal zone at the open-coast of Northern Norway, a pilot study revealed that the size of blue mussel (*Mytilus spp.*) size increases with shore height elevation (Figure 1a). Established ecological theories state that mussel size is expected to decrease with increasing shore height, as a result, the smallest mussels are predicted to inhabit the most stressful upper areas of the intertidal. This is supported by several studies, (Barbosa et al., 2021; Connor & Robles, 2015; Leeb, 1995; McQuaid et al., 2000; Suchanek, 1978) and the general pattern is presented in Figure 1b. The results from the pilot study thus show an unexpected vertical size pattern in the distribution of mussel body size along a gradient of environmental stress, which, to the extent of my understanding, is contradictory to all previous studies. The currently accepted theories are primarily grounded in studies conducted in temperate regions, suggesting that potential variations in size patterns may exist in subarctic ecosystems. Despite blue mussels being a well-studied species both for their economic and ecological importance, drivers of population dynamics of blue mussels along the Northern Norwegian coast remain undocumented. Building upon the pilot study findings, this thesis aims to delve deeper into the complex dynamics of potential drivers of blue mussel size patterns across the intertidal zone of Northern Norway.

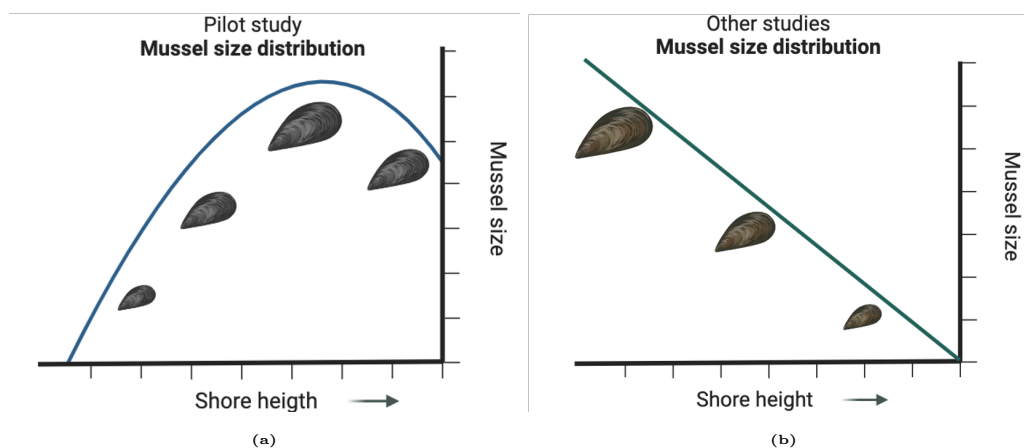


Figure 1: Size pattern observations made from the pilot study from the rocky intertidal zone of Northern Norway (a) (M.Molis pilot study) and a general size pattern from other studies in temperate regions (b) (Barbosa et al., 2021; Connor & Robles, 2015; Leeb, 1995; McQuaid et al., 2000; Suchanek, 1978). Created in biorender.

1.1 Blue mussels

Blue mussels (*Mytilus spp.*) are molluscs distributed across both the Northern and Southern hemispheres and are predominant in temperate and subarctic regions, however, their range extends northward to Svalbard (Berge et al., 2005). They are a keystone species in many intertidal ecosystems, providing many ecosystem services and acting as an ecosystem engineer, increasing biodiversity by providing refuge for smaller invertebrates (Gosling, 2003; Jones et al., 1994). They possess a high tolerance for extreme environmental conditions, such as wide fluctuations in tem-

perature, salinity, and desiccation, enabling them to thrive across a broad global and tidal range (Berge et al., 2005; Gosling, 2003; Westerbom et al., 2002; Widdows, 1976). As filter feeders, mussels play an important role by fixing organic pollutants and toxic substances, as well as counteract eutrophication from human activities (Gren et al., 2009; Potrykus et al., 2003; Smaal et al., 2001). This makes them an important organism in biomonitoring, and why mussels are one of the most studied benthic marine organisms. Blue mussels are commonly harvested and commercially farmed for food sources worldwide (Smaal et al., 2019). Despite being well studied both for aquaculture purposes and as a tool in biomonitoring, there are many unanswered questions about the drivers of these mussel populations, especially in the intertidal zone in subarctic regions like Northern Norway.

Blue mussel populations are declining on a global scale, including the Norwegian coast (Andersen et al., 2017; Baden et al., 2021; Janssen et al., 2016). Several factors such as, increased temperature, ocean acidification, predation, and eutrophication have been proposed as potential causes for this decline, but none has been definitively verified. Most likely, multiple factors with complex interactions and regional differences are at play (Strohmeier et al., 2022). This underscores the need for a comprehensive understanding of ecological interactions and the drivers affecting blue mussel ecology

1.2 Ecological importance of body size

Size represents one of the most fundamental characteristics of organisms and is linked to many aspects of life history and ecology (Peters & Peters, 1986). Larger individuals are better equipped to withstand a variety of external stressors, both physical and biological. Larger individuals often have, for instance, high reproductive rates due to larger gonad size (Glaudas et al., 2020; Peters & Peters, 1986; Werner & Gilliam, 1984). Additionally, larger individuals exhibit greater resistance to diseases and lower susceptibility to parasites (Moore & Wilson, 2002; Seluanov et al., 2018; Werner & Gilliam, 1984). Predators may avoid attacking individuals of a certain size if handling them is too energy-demanding, a phenomenon commonly observed in intertidal organism and fish (Dayton, 1971; Jackson, 1961; Pyke et al., 1977; Smallegange & Van Der Meer, 2003). In competitive environments, larger individuals often prevail when competing for resources (Johnsson et al., 1999). Thus, attaining a larger size is beneficial in many ways for both survival and reproduction, however not all individuals can reach maximum growth. Indeed, growth is a costly process, and it diminishes when survival is at stake (Hulbert & Else, 2000). For example, when plants are exposed to drought, they activate a signaling process that reduces water loss and optimizes root systems for water uptake, prioritizing essential functions over growth (Chaves et al., 2003). This allocation trade-off reflects the need to prioritize essential functions and survival, rather than growth, in the presence of biotic or abiotic stressors in the environment.

1.3 Environmental stress and the intertidal zone

Environmental stress includes any environmental factor that triggers changes in either individual organisms or entire ecosystems (Freedman, 1991). Population dynamics and species traits are therefore often studied along a stress elevation gradient. A stress elevation gradient, representing a gradual increase in environmental stressors, offers valuable insights into how organisms respond to varying stress levels. When ascending a mountain, there is a decline in air and soil temperatures and an increase in harsh weather conditions. Thus, increasing altitude corresponds to increasing physical stress and consequently decreasing vegetation size and density (Sundqvist et al., 2013; Whittaker, 1956). In the same way, a similar stress elevation gradient is represented in the intertidal zone. Ecological theories suggest that environmental stress has significant influence on species interactions, with impacts at both the individual and community level (Menge, 1976). This conceptual framework gave rise to the development of the Environmental Stress Model (ESM), as illustrated in Figure 2a (Menge & Sutherland, 1987).

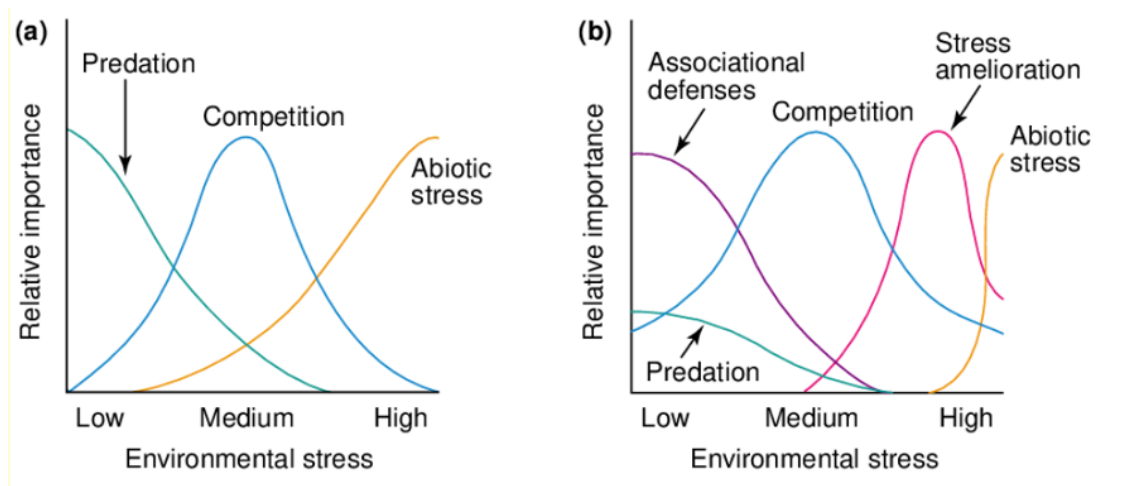


Figure 2: The Menge-Sutherland (1987) model for environmental stress without facilitation (a), and the modified model (b) including facilitation by (Bruno et al., 2003).

According to the ESM, predation pressure is relatively strong, in an environment with low abiotic stress. As a result, prey survival relies on their ability to avoid predation. This can be achieved by attaining a size large enough to act as a protective refuge (Dayton, 1971; Jackson, 1961). In the low intertidal zone, this means that the majority of the survivors are the largest mussels. This explains the mussel pattern found in previous studies, with low environmental stress in the low intertidal zone and more predation pressure (Barbosa et al., 2021; Connor & Robles, 2015; Leeb, 1995; McQuaid et al., 2000; Suchanek, 1978). In environments with medium stress levels, competition dominates. These environments are equivalent to the mid-intertidal zone, where competition for limited resources, like space and food occurs both inter- and intra-specific. Blue mussels are dominating benthic settlers in the intertidal zone, which often results in intra-specific competition (Bertness, 1989; Menge, 1976; Paine, 1974). They have high recruitment in the low and mid

intertidal, based on preferred settlement substratum (*Corallina sp.* and filamentous algae) and submergence time (McQuaid & Lindsay, 2005). This results in high-density patches of mussels, with density dependent effects, which are limiting for growth and food availability (Bertness & Grosholz, 1985; Cubillo et al., 2012). Body size is therefore predicted to decrease from low to mid intertidal zone as competition and environmental stress increase. In environments with high environmental stress, abiotic stress is the dominating force that reduces the individuals' performance. In the high intertidal zone, abiotic stress is linked with air exposure. Longer air exposure causes more temperature and salinity fluctuations, as well as higher levels of desiccation (Seed, 1969; Suchanek, 1978). Also, as the time of submergence decreases, filter feeders have less opportunity to feed (Coulthard, 1929). Consequently, the progressive reduction in resource availability as stress levels increase leads to a reduction in body size.

In 2003, Bruno et al. proposed that positive interactions among species had a significant influence on communities and could potentially help explain population dynamics in stressful environments. Positive species interactions, such as stress amelioration and facilitation, mitigate abiotic stress and increase the chances of survival. The original ESM model was therefore modified (Figure 2b). In the intertidal zone, brown canopy-forming algae typically reduce temperature variations and desiccation, thus making conditions less stressful for underlying organisms, and enhancing growth (Bertness et al., 1999; Menge, 1978; Tam & Scrosati, 2014). The model also suggests that associational defense can reduce predation pressure in less stressful conditions, by making prey less available for predators, either by hindering or hiding. For instance, several crustose algae can grow as an epibiont on gastropods' shells, allowing them to cover their host's surface completely, which may, in turn, protect their hosts from predation (Thornber, 2007). These stress-relieving processes might result in larger individuals, as survival is enhanced. However, as these processes increase the survival of prey, they will also enhance competition. This might result in reduced body size. Predicting outcomes on population dynamics can therefore be challenging, as they vary depending on the species-specific interactions and geographic location.

1.4 Subarctic intertidal ecology

The pilot study (Figure 1a) revealed a mussel size pattern that contradicts with studies from the temperate zone. This study was conducted in the subarctic, a region which serves as an intermediary between the extensively studied temperate zones and more extreme environments in the Arctic. This prompts inquiry into whether observed differences stem from latitude or local environmental conditions. To assess the generality of the pilot study's pattern, I extend the analysis to include other open-coast sites and a distinctly different sheltered inner-fjord site. This comprehensive approach aims to discern whether the observed pattern is locally specific or influenced by latitudinal factors. If the pattern is exclusive to open-coast sites, further investigation is necessary to determine whether mussel growth is limited in the low intertidal zone compared to the high intertidal zone, where the largest mussels are found.

The intertidal zone in the subarctic is understudied, and many ecological interactions remain poorly understood in this region. Some of the main ecological drivers mentioned in the ESM (Figure 2) may have a different impact on community regulations in the subarctic. For instance, in the Arctic and subarctic intertidal communities, predators are often considered of minor importance due to their low abundance, while environmental factors dominate (Blicher et al., 2013; Thyrring & Peck, 2021). However, a recent study on the west coast of Norway has suggested that dogwhelks (*Nucella lapillus*) could potentially play a vital role in the Scandinavian blue mussel population (Meister et al., 2023). This can also be linked to the optimal foraging theory (Pyke et al., 1977) where only small blue mussels survive at shore height where dogwhelk abundance is high, as the dogwhelks prefer mussels with a body size of 20 - 25 mm (Crothers, 1985; Hughes & Dunkin, 1984). If the mussels are smaller, the energy requirement is not fulfilled and with mussels >40mm the cost of prey handling is too high (Crothers, 1985). This highlights the necessity for local-scale experimental studies to unravel the intricate processes and interactions within the intertidal zone.

Species interactions have different effects on intertidal community structure and are difficult to predict. A general observational transect was therefore performed to record the abundance of some species from different functional groups along the shore height. This was done to map out some potential interactions that can drive mussel size along the intertidal stress gradient, directly or indirectly. For instance, if canopy-forming algae could help ameliorate environmental stress and potentially enhance blue mussel's growth at shore heights where these brown-algae are abundant. Intraspecific competition is also an important controlling mechanism on mussel populations. Here I assess mussel abundance, recruitment and abundance of potential other benefactors besides canopy-forming algae could affect the size at different shore height. From visual observations on the low intertidal zone, the small mussels here were aggregated in patches and often associated with red encrusting algae (hereafter: REA). I therefore hypothesize that these aggregations could have a density-dependent effect, limiting growth in the mussel patches (Bertness & Grosholz, 1985). In addition, these mussel-aggregations, with associated REA seem to be the only area where limpets

could not attach, opening the possibility that limpets compete with mussel recruits for space, as they do for barnacle cyprids (Menge et al., 2010; Steffani & Branch, 2005). This is prompting that these REA patches act as associational defenses for mussel recruits (Bussell et al., 2007). This can enhance survivorship and therefore extend the period for mussels to growth.

1.5 Aim and hypothesis

The overarching objective of this study is to validate the initial observation of a unimodal size pattern of blue mussels in the intertidal zone. By investigating two additional sites with similar environmental conditions to enhance test power, this study aims to gain insights into the generality of the findings from the pilot study (**H1.1**). In addition, I broaden the perspective of the study by including two distinctly different sites (**H1.2**). The second part of this study (**H2 - H5**) includes experiments on processes that can serve as possible explanations for the observed pattern in the vertical distribution of mussel sizes.

This study will be a supplementation to Institute of Marine Research's mussel-monitoring assessment, where their goal is to identify potential threats to the mussel-populations along the Norwegian coast and follow the temporal and spatial patterns (Strohmeier et al., 2022).

To achieve this goal, I tested the following hypotheses:

H_{1.1}: Shell length of open-coast blue mussels will increase from low to high intertidal zone.

H_{1.2}: The vertical size pattern of blue mussels that inhabit the inner-fjord sites differs from the vertical size pattern of blue mussels near the open coast sites.

H₂: Mussel growth is greater in the low intertidal zone compared to the high intertidal zone.

H₃: Recruitment of blue mussels will be higher in the low- and mid-intertidal zone, compared to higher on the shore.

H₄: When reducing the density of aggregated blue mussels in the low intertidal zone, increased mussel growth will occur.

H_{5.1}: A negative correlation between the cover of limpets (competitor), dogwhelks (predators), and REA with blue mussel cover along the shore height on the open-coast sites will occur.

H_{5.2}: A positive correlation between the cover of canopy-forming brown algae (stress ameliorator) with blue mussel cover along the shore height on the open-coast sites will occur.

2 Material and Methods

2.1 Study site

Four study sites with contrasting features were selected, two sites exposed to open-coast conditions and two within sheltered fjords (Figure 3). The open-coast sites, Hillesøya (N 69°38'48, E 17°59'34) and Brensholmen (N 69°37'14, E 18°4'53) exhibit fully marine conditions, with wave exposure and rocky substrates. The two inner-fjord sites, Nordfjorden (N 69°38'12, E 18°23'38) and Sørfjorden (N 69°35'20, E 18°16'48), are wave-protected and have a soft-bottom substrate. The fjord sites are subject to freshwater run-off from nearby rivers, resulting in lower salinities.

The hard bottom communities have high biodiversity. On the open-coast sites, a large variety of brown seaweeds is observed, with *Fucus ser-ratus*, *Pelevetia canaliculata*, and *Ascophyllum nodosum* dominating in the upper intertidal zones. *Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima* dominate the sub-littoral, and red encrusting algae like *Coral-lina officinalis*, *Lithothamnion glaciale*, *Clath-romorphum compactum* dominate the low in-tertidal zone. Blue mussels are the most abun-dant invertebrate, forming continuous belts in the high intertidal zone and smaller patches in the low intertidal zone. Other invertebrate species such as gastropoda (*Littorina littorea*, *L. obtusata*, *Patella vulgata*) and barnacles (*Semibalanus balanoides*) were also observed. Additional species inhabiting these study sites

include green crabs (*Carcinus maenas*) and dogwhelks (*Nucella lapillus*), these are observed in crevices or more sheltered areas. At the soft-bottom sites, brown algae *Ascophyllum nodosum* associates and other invertebrates were observed in addition to the highly dominate blue mussel species. Generally, three distinct species of coexisting and interbreeding blue mussels are observed throughout Europe: *Mytilus edulis*, *M. trossulus*, and *M. galloprovincialis* (Brooks & Farnen, 2013). Visual identification is not possible, therefore, *Mytilus spp.* are often collectively referred to as blue mussels, and I do so also in this study.

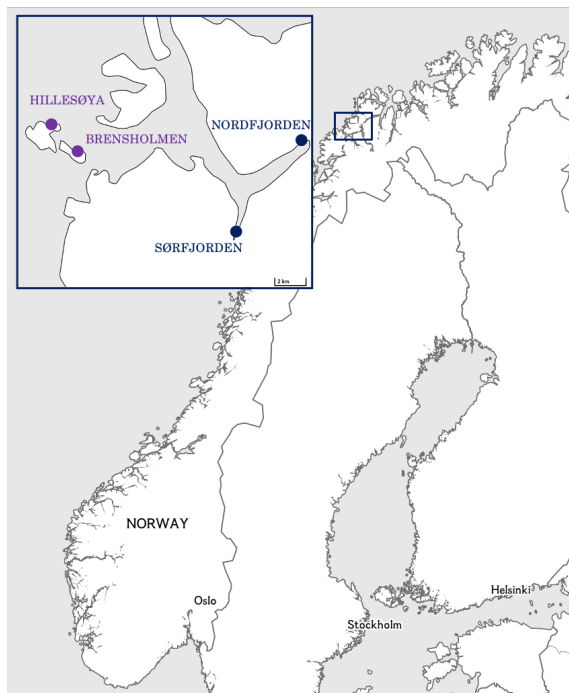


Figure 3: Map over study site: Hillesøya, Brensholmen, Sørfjorden and Nordfjorden (GoogleMaps, 2023).

2.2 Study design and set-up

This study is divided into two parts, an observational part (i) and an experimental part (ii). In the observational part (i), the vertical size distribution of the blue mussels at all four sites was documented and the impact of shore height on blue mussel recruitment at the Hillesøya study site was investigated (Sections 2.3.1 and 2.3.2). In addition, a species cover transect was performed to investigate the correlation between the cover percentage of predators (dogwhelks), competitors (limpets), facilitative species (canopy-forming algae and REA) on the shore height (2.3.3) The experimental section (ii) investigates different potential-drivers of the mussel size and population structure. The first experiment, a growth-transplantation experiment, tested growth condition in the low-, and high intertidal zone (2.4.1) at the Brensholmen and Hillesøya test sites. The second experiment aimed to determine whether mussel aggregation, leading to density-dependent effects, could potentially limit mussel growth on Hillesøya (2.4.2). All experimental designs were 1-factorial, testing the effect of the intertidal zone on mussel size, recruitment, and growth. On each site, the intertidal zone was divided into four zones at the start of the fieldwork: Top, High, Mid, and Low. Figure 4 illustrates the zonations in this study, and the observed blue mussel size based on the pilot study.

The height of each zone varied from each site. The lowest position was established from the lowest water level at low-tide up to the highest point where blue mussels were present. This was measured by setting up a measuring pole at the waterline at low-tide and a laser pointer on the highest point of the blue mussel belt. The water-level at low-tide was added to the measurements to get the actual shore height, and then divided by four, creating the four intertidal zones. Results from shore height and zone distance measurements are presented in Table 1

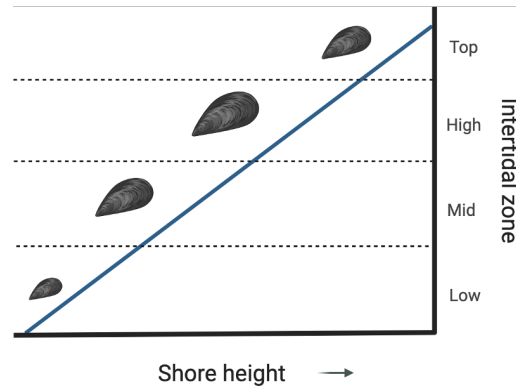


Figure 4: Each study site was divided into four intertidal zones: Top, High, Mid and Low. Here the zonation is illustrated including mussel size pattern from pilot study. Created in BioRender.

Table 1: Overview over the shore-height in (cm) and distance in (m) of each zone from the study sites. The measurements collected are added on to the established tide height of the day to provide the correct height.

	Brensholmen		Hillesøya		Nordfjorden		Sørfjorden	
	Height	Distance	Height	Distance	Height	Distance	Height	Distance
Top	155 - 195	1	150 - 192	1	98 - 114	3	54 - 65	18
High	115 - 155	1.5	117 - 150	0.5	82 - 98	3	42 - 54	16
Mid	75 - 115	1.5	90 - 117	2.5	66 - 82	2	31 - 42	3
Low	35-75	0.5	62 - 90	0.5	50 - 66	1	20 - 31	2

2.3 Observational studies

2.3.1 Vertical size distribution

To confirm the pattern observed in the pilot study, an investigation with a broader sample range was conducted. In addition, a comparison of the pattern observed in the open-coast (Hillesøya and Brensholmen), waves exposed sites, with the pattern in a wave protected, and less saline, inner-fjord environment (Nordfjorden and Sørfjorden) was performed.

Frames were allocated randomly in each of the described zones (Figure 4), with a minimum distance of 1.5m between each sample. The blue mussels contained within the frames were collected (Figure 5). The samples had with a minimum distance of 1.5 m apart. For the open-coast sites, an 8×8 cm frame was used, and six samples were collected in each zone (N=24). A 16×16 cm frame was used for the inner-fjord sites and here, 10 samples were collected in each zone (N=40). A larger frame due to variations in mussel size and density between the sites. The mussel samples were removed by a scraper, placed into a zip bag and stored at -20°C freezer. Density was determined by the number of individual mussels per sample area (cm²).

Epibionts on the mussel shells were removed to avoid incorrect measurements. Maximum length of each mussel (N=8652) was measured using vernier calipers [maximum anterior–posterior dimension according to (Seed, 1968)] to the nearest 0.1 mm. Samples were dried in a drying oven at 60 °C until constant weight (min. 48 h - up to 96 h). Biological material takes up water from the cold air when taken out of the oven, so the samples were weighted twice, and in opposite order the second time. From this, a mean of biomass was calculated using the constant dry weight (g) divided by sample area (cm²). During the sampling in Nordfjorden, there was high prevalence of snowmelt, making the water level higher than expected and some of the low zone could not be sampled as it was submerged.



Figure 5: Blue mussel samples from size distribution experiment. (a) is from Hillesøyas low zone and (b) is from Brensholmens high zone, illustrating the 8 x 8 cm square sample, while (c) show the 16 x 16 cm square sample from the mid zone in Sørfjorden.

2.3.2 Recruitment distribution

In order to examine whether blue mussel larvae settle preferentially at a particular shore height, I conducted a recruitment experiment. The objective was to determine whether the distribution of recruits across different shore heights may account for the observed variations in blue mussel size in the intertidal zones.

The recruitment of blue mussels in Tromsø (68°N) was expected to be later than in Southern Norway (60°N) (Bøhle, 1971), however earlier than in Finnmark (71°N) (Frantzen, 2007), giving us some uncertainty of when the settlement peak would occur. To ensure an adequate number of recruits, the collection of recruits was conducted from the beginning of May until start July. To measure the density of *Mytilus spp.* recruits, plastic pot scourers, hereafter called collectors (Figure 6a), were used to collect blue mussel recruits (Porri et al., 2006; von der Meden et al., 2015). Four collectors were mounted on the shore using screws and brake disc, with a minimum distance of 1 m between. This was done in each of the intertidal zones (Figure 4) plus an additional four collectors above the top zone to ensure good coverage over the shore height (Super-top, Top, High, Mid, and Low). The deployed collectors were replaced with new clean ones approximately fortnightly to monitor the temporal recruitment and the spatial variability between the zones. Due to a delayed delivery of equipment, the period between start-June till mid-June only had half of the collectors deployed compared to the other sampling rounds.

In the lab, the collectors were rinsed in fresh water using sieves with mesh sizes of 300, 500 and 1000 μm , to remove larger meso- and meroplankton (Platz, 2018; Porri et al., 2006). The residual of the 300 μm was examined under a stereo microscope to identify and count *Mytilus spp.* larvae (Figure 6b and c). The collectors were dried for 24 hours in a drying oven to obtain the weight for abundance measurements.

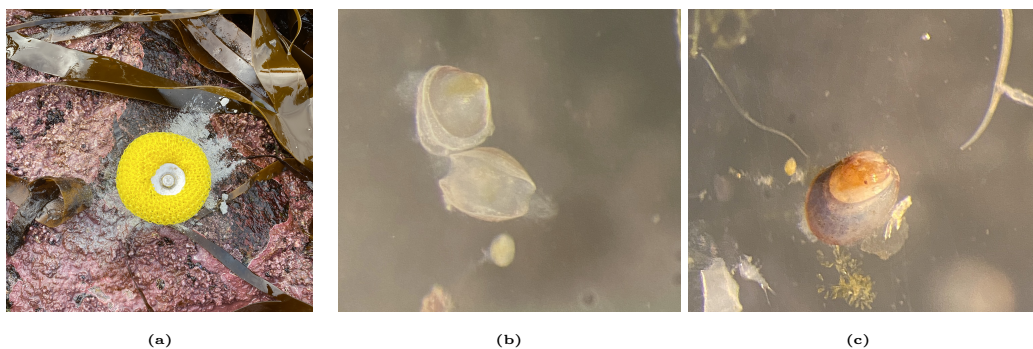


Figure 6: (a) Larvae collector placed on the rocky shore on May 3rd before collection. (b) and (c) are mussel recruits identified in the lab from early June sample.

2.3.3 Species cover transect

A general observation on the experimental sites gave rise to these transects. To investigate the possible effect of predation, interspecific competition, and facilitation on blue mussel abundance along the shore height.

Seven transects from low to top intertidal zone, with >1 m between transect lines, were conducted on June 19th on Hillesøya and on August 30th on Brensholmen. A 0.5 x 0.5 m square was placed with approximately 10 cm in-between the squares following the shore height on Hillesøya, and Brensholmen (Figure 7). Percent coverage of limpets (*Patella vulgata*), canopy-forming brown algae (*Fucus sp.* and *Ascophyllum nodosum*), dogwhelks (*Nucella lapillus*), blue mussels and REA were recorded per frame.



Figure 7: Photo of 0.5 x 0.5 m square placed on the shore height from low to top intertidal zone. Coverage of dogwhelks, limpets, brown algae, REA, and blue mussels were recorded from each frame.

2.4 Experimental studies

2.4.1 Growth-transplantation experiment

A mussel transplantation experiment was performed on Hillesøya and Brensholmen to assess the potential variability in growth conditions between low and high intertidal zone as described in Figure 4. The experiment included four treatments where blue mussels were transplanted from: (1) high to low zone (HL); (2) from low to high zone (LH), and mussels replanted from (3) low to low (LL); and from (4) high to high (HH).

Each treatment had a minimum of 6 samples, and each of the samples containing 4 blue mussels. Sampled mussels were placed in a cage and installed randomly on the corresponding shore height (N=219). The cages were constructed with plastic mesh fence (mesh size 50 x 50 mm, unbranded) around a PVS net (10×18 cm, with mesh size of 10 mm) and cable ties, attached with screws, brake discs and an ID-tag for the treatment (Figure 8). Two medium-sized mussels (16.5-20 mm) and two small-sized mussels (13-16.5 mm) were placed in each net. The mussels were tagged with unique numbers glued (Cyanoacrylate glue) on the shells. The specific size classes were used because length increments of larger specimens were expected to be too small to clearly demonstrate the growth effects. Length, height, and width of the mussels were measured using vernier calipers, as previously described.

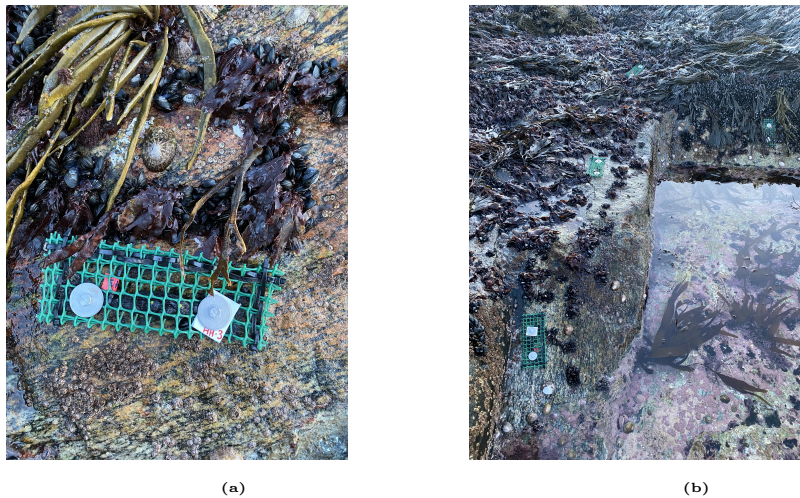


Figure 8: Experimental set up in the high intertidal zone. (a) Replanted single cage (HH) and (b) is several transplanted cages (LH) on the Hillesøya shore

Challenging weather conditions during experimentation resulted in inconsistencies in the timing of transplantations. At the Hillesøya site, the transplantation took place on 8 March and for Brensholmen, on 20 March. However, this is not expected to have any significant effect on growth rates due to low levels of photosynthetic activity, making the water column low in available food around Tromsø during this time of year (Degerlund & Eilertsen, 2010). After 19 weeks for Brensholmen and 21 weeks for Hillesøya, the cages were retrieved and the measuring was done prior to the ex-

periment was repeated, to calculate the size increment. Measurements were performed according to equation 1, where $L1$ is the shell length at the start of the experiment and $L2$ is the shell length at the experiment's end.

$$\text{Size Increment (\%)} = \frac{(L2 - L1)}{L1} \times 100 \quad (1)$$

Upon retrieving the cages, it was observed that out of the initially deployed 219 blue mussels, 77 were found to be deceased. Among these, 48 exhibited a drilled hole in the shell, indicative of predation by dogwhelks.

2.4.2 Patch experiment

In order to examine whether the density of mussels in patches could explain the smaller mussel size observed in the lower intertidal zone, I conducted this experiment. The investigation involved manipulating the mussel density within these patches to explore its potential relationship. Hillesøya was selected as the study location for this experiment due to the high abundance of REA patches compared to the other study sites. Additionally, the blue mussels at Hillesøya were also observed to have the biggest size difference between low and high zones in experiment 2.3.1. The patches were located in the mid to low intertidal zone, and were linked to a variety of other species including *Corallina sp.*, *Palmaria palmata* and, more sporadically, *Fucus sp.* They are often attached around or in between the mussel patches like *Corallina officinalis* (Figure 9), or underneath as a substrate *Clathromorphum compactum*.

Two treatments were applied to 10 patches. Treatment consisted of removing 80% of the blue mussels on the patch with no specific pattern using forceps on 10 patches. The remaining 10 patches were unmanipulated as a control. The patches were randomly chosen, but with a preference based on accessible location. Treatments were assigned by randomly picking a pre-labelled tag from a bucket, which was then screwed to the rock for plot identification. After removal, three remaining individual mussels ($N=60$) per patch were marked with bright yellow or pink color (Magic marker) for easy recognized throughout the experiment. Mussels of approximately the same size were chosen for easy comparison. At the start of the experiment, a Dremel drilling tool was then used to make a

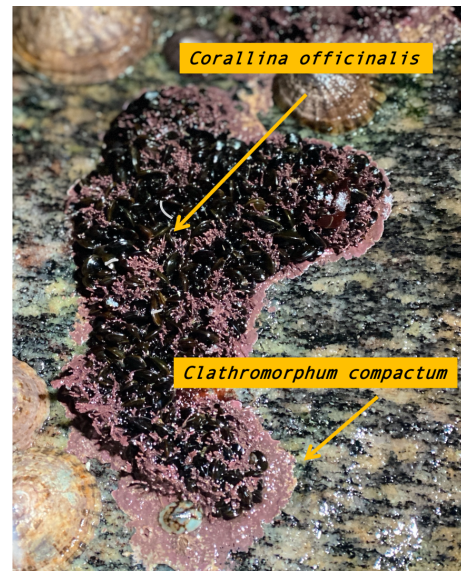


Figure 9: Blue mussel patch in the low intertidal zone at Hillesøya. The branching calcareous algae in between the mussels are the *Corallina officinalis*, while the smooth, crust-like appearance around the edges of the patch are *Clathromorphum compactum*.

cut a notch in the posterior edge of the shells and initiate the start of the experiment (Figure 11b). The removed mussels were counted in the lab for abundance measurement. Seven out of twenty (35 %) samples had (*Corallina officinalis*) associated with the patch, while six of twenty (30 %) had *Clathromorphum compactum*. The remaining six patches (30 %) had no REA present.

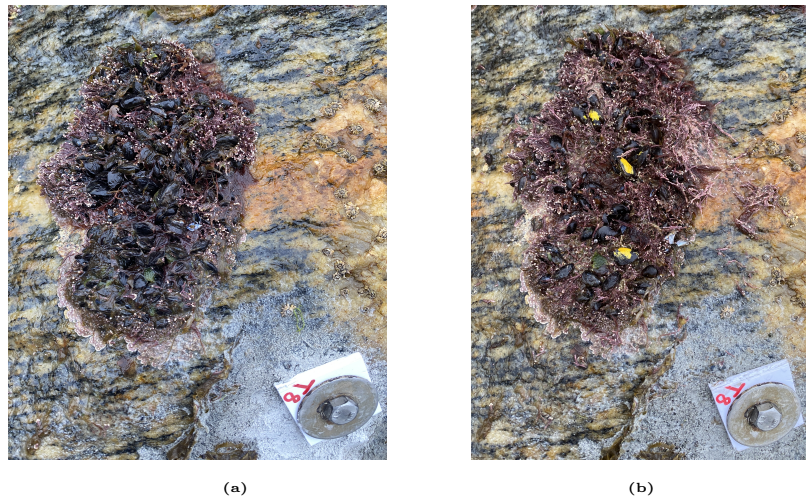


Figure 10: Patch experiment set up on Hillesøya. Mussel patch with associated *Corallina* before treatment (a) and after treatment (b) with marked individuals in yellow.

By counting the mussels left on the patch and the mussels removed, the total abundance of mussels within the patches and the percentage of removal were determined. It was observed that during the initial removal, only around 60-70% of the mussels were taken out on most patches. This information allowed for the calculation of the number of additional mussels that needed to be removed the following day. After 16 weeks, the marked mussels were collected and transported back to the lab for growth measurement. This was executed by using the cut made by the Dremel as a start point and measuring the additional shell growth from this point (Figure 11). Over the course of the experiment, 28 out of the 30 mussels from the treatment patches were lost, while in the control patches, 21 out of the 30 mussels were lost.

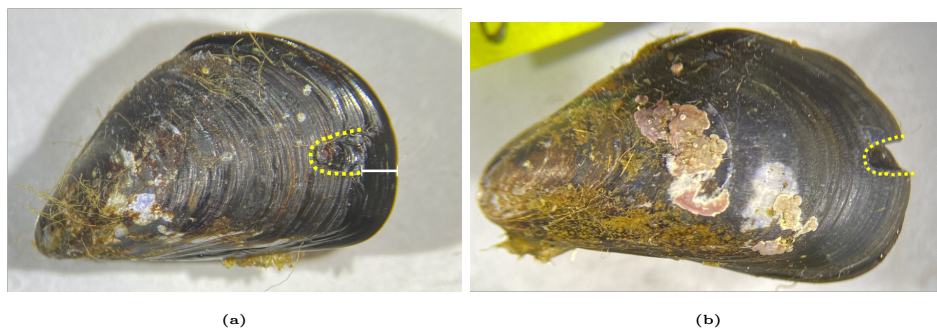


Figure 11: Measuring method after treatment. Dremel cut is marked with a yellow dotted line, and growth area measured is marked with a white line for figure (a). Figure (b) shows a mussel with no growth, but rather a repair of the cut.

2.5 Statistical analysis

All statistical analyses were performed using R-studio version 4.2.3 (2023-03-15) (R Core Team, 2023). All assumptions were tested prior to running ANOVA tests. One-way ANOVA was run on most of the data, except when assumptions were not met or when testing categorical variables. If significant difference, a post hoc test (Tukey test for ANOVA and Dunn-test for Kruskal-Wallis) was performed. To test for variance homogeneity, a Levene's test was run. For normal distribution a Shapiro-Wilks test was performed, and if the normal distribution assumptions were not met, the non-parametric Kruskal-Wallis test was performed for groups >2, and a Mann-Whitney U test (Wilcox) when comparing only two groups. The Pearson's Chi-Squared test was performed when testing two categorical variables (dogwhelk-data). For smaller sample sizes, and when the assumptions for the Chi-Squared Test were not met, Fisher's Exact test was used to determine if there was a non-random association between patch-disappearance and REA. When investigating the correlation between shore height and specie cover, the Pearson coefficient, was used to measure the strength of the association between two continuous variables. The strength of correlation coefficient translates into descriptors with the following terms 0.0 - 0.1 as negligible, 0.1 - 0.39 as weak, 0.4 - 0.69 as moderate, 0.7 - 0.89 as strong and 0.9-1.0 very strong (Schober et al., 2018). A significance level of $p < 0.05$ was used in all tests. A polynomial regression was performed on the size distribution data for the two open-coast sites. While a linear regression was performed on the two inner-fjord sites.

RStudio packages were used for different analysis: The "ggplot2" package was used for all plots (Wickham, 2016). For creating and customizing "ggplot2"- based publication ready plots, the "ggpubr" package was used (Kassambara, 2023). The "tidyverse" package helps to transform and better present data (Wickham et al., 2019) and the "boot" package was used to bootstrap the data (Canty & Ripley, 2016). Moreover, the "metafor" package was used to run random-effect models and create forest plots (Viechtbauer, 2010).

The effect size was also calculated using the logarithm response ratio (LRR) eq.2 and often presented in forest plot. The magnitude of a treatments was determined by the following (Durlak, 2009): < 0.2 small effect, > 0.5 medium effect and > 0.8 as a strong effect. Boxplots were done using bootstrapping the means (n=1000 iterations) of the dataset.

$$\text{LRR} = \log \frac{\text{mean treatment}}{\text{mean control}} \quad (2)$$

3 Results

3.1 Vertical size distribution

$H_{1.1}$: Shell length of open-coast blue mussels will increase from low to high intertidal zone.

Shore height had a significant effect on mussel length on Hillesøya (one-way ANOVA, $F=21.96$, $df_{(3,20)}$, $p < 0.0001$, Figure 12A) and on Brensholmen (one-way ANOVA, $F=15.66$, $df_{(3,20)}$, $p < 0.0001$, Figure 12B). At both sites, the length of low-zone blue mussels was significantly less than of conspecifics from the three zones higher on the shore, with no significant difference among the latter (Figure 12). The effect size between mean length of mussels in the high zone and the mean length of mussels in the low zone was 0.45 on Hillesøya and 0.34 on Brensholmen (Figure 15). The mean shell length for mussels located in the low intertidal was 11 mm (± 2.4 SE), 15.6 mm (± 1.2 SE) in the mid intertidal, 17.3 mm (± 1.6 SE) in the high intertidal and 15.7 mm (± 0.8 SE) in the top intertidal zone on Hillesøya. While on Brensholmen, mean shell length was 10 mm (± 1.4 SE) in the low intertidal, 12.6 mm (± 1 SE) in the mid intertidal zone, 14 mm (± 0.7 SE) in the high intertidal zone and 13.5 mm (± 0.4 SE) in the top intertidal zone.

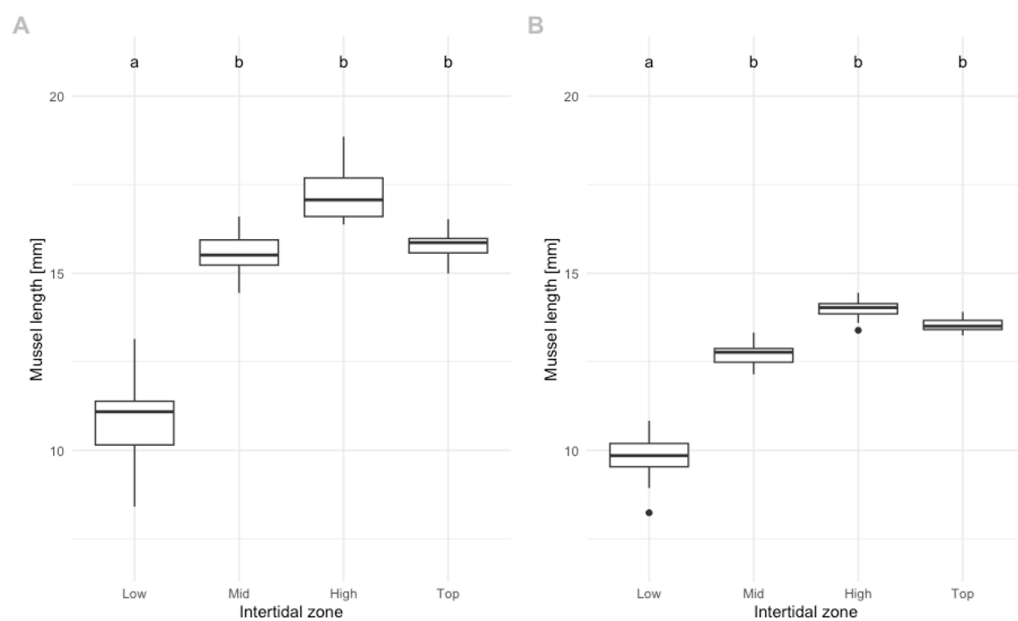


Figure 12: Mussel length [mm] at the four intertidal zones at Hillesøya (A) and Brensholmen (B) ($n=6$). Boxes represent the interquartile range (IQR) of the bootstrapped means ($n=1000$). The mean is marked with a thickened line. Whiskers extend to the minimum and maximum values within 1.5 times IQR. Black points indicate outliers. Treatments sharing a minor letter are non-significantly different from each other ($p > 0.05$).

Using polynomial regression, a significant relationship between shore height (cm) and mussel length (mm) was detected at Brensholmen (F -statistic = 381.4, $p=0.036$, Figure 13A) and Hillesøya (F -statistic = 201.8, $p=0.049$, Figure 13B). A unimodal relationship explains, $> 99\%$ of the observed variation in mussel size with shore height for both sites.

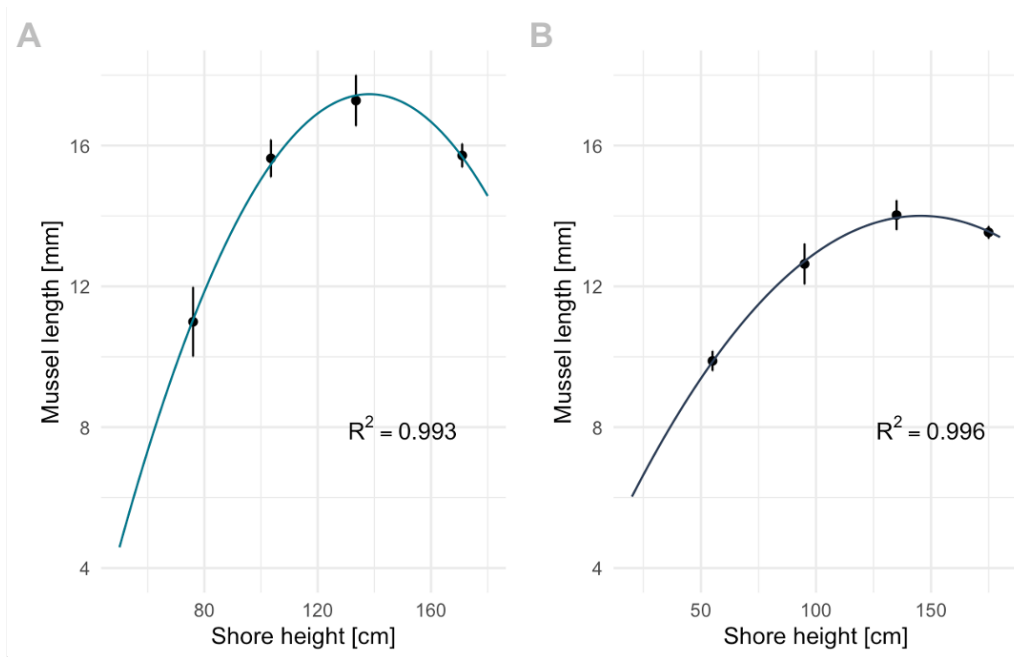


Figure 13: Second-degree polynomial regression of the relationship between the mussel length [mm] and the shore height [cm] for Hillesøya (A) and Brensholmen (B). The model equation for Brensholmen was $(y = 12.51 + 2.76 x - 1.62 x^2)$ and for Hillesøya was $(y = 14.90 + 3.30 x - 3.33 x^2)$. Black points represent the mean mussel size of all samples ($n=6$). Error bars represent standard error. Note that neither the y- or x-axis start at zero and that the scale of the x-axis differs between plots (A) and (B).

H_{1.2}: The vertical size pattern of blue mussels that inhabit the inner-fjord sites differs from the vertical size pattern of blue mussels near the open coast sites.

Performing a linear regression, a significant negative relationship between shore height (cm) and mussel length (mm) was detected at Sør fjorden (F-statistic = 228, $p = 0.0043$, Figure 14A) and Nordfjorden (F-statistic = 20.3, $p = 0.044$, Figure 14B), explaining 99 and 91%, respectively, of the variation in mussel length with shore height.

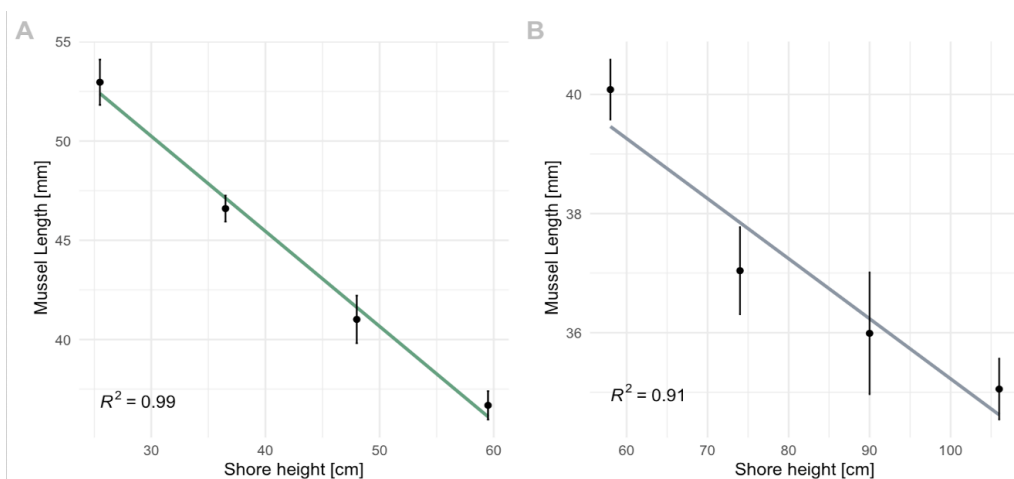


Figure 14: Linear relationship between mussel length [mm] and shore height [cm] for Sør fjorden (A) and Nordfjorden (B). Model equation for Sør fjorden $(y = 64.6 - 0.5 x)$ and Nordfjorden $(y = 45.3 - 0.1 x)$. Black points represent the mean mussel size ($n=10$). Error bars represent standard error.

A higher position in the intertidal zone had a small to medium positive effect on mussel length for Brensholmen (LRR= 0.34 [95% CI: -0.14, 0.82]) and Hillesøya (LRR= 0.45 [9% CI: 0.01, 0.90]). The opposite effect occurred in the fjord sites with a small negative effect on Nordfjorden (LRR= -0.11 [95% CI: -0.22, 0.01]) and Sørkjorden (LRR= -0.26 [95% CI: -0.37, -0.14]). The forest plot in Figure 15 shows a comparison of these effect sizes (LRR) with other similar studies.

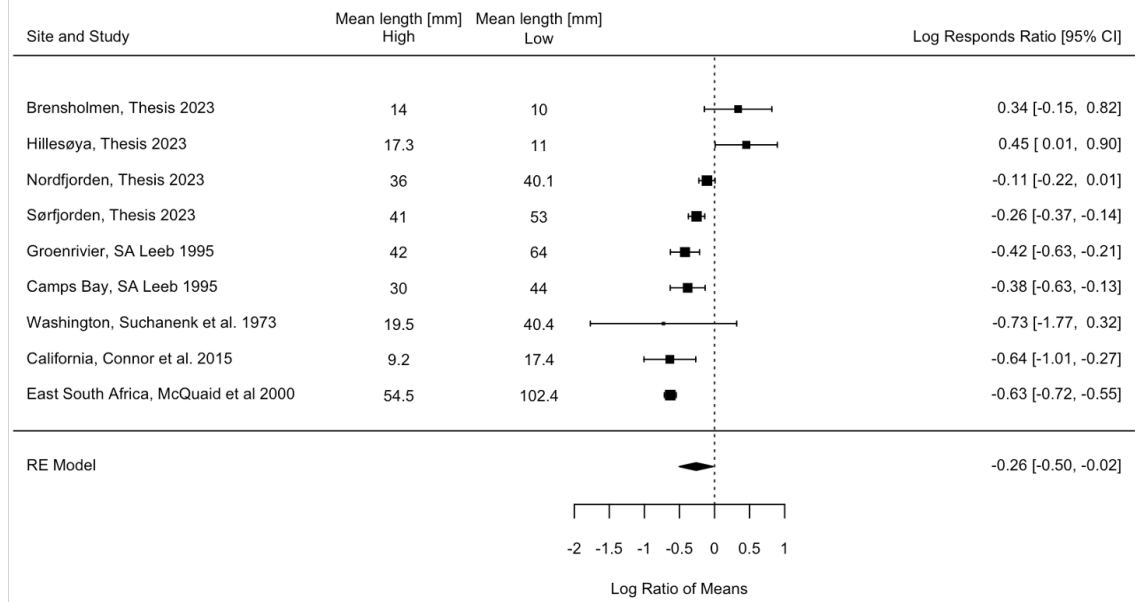


Figure 15: Effect of shore height (high vs. low) on mussel size [mm] from different studies. For each study, the estimated mean effect size is plotted as a box and the 95% CI is displayed as the whiskers. The size of the boxes is proportional to the weight of the study to the pooled effect size estimate (indicated by the diamond in the line RE model). Log ratio of means and CI are presented in the right column (LRR [95%]). The vertical dotted line represents $\text{Log}[\text{RoM}] = 0$ i.e., no difference in the length of mussels positioned in the high and low zone.

3.2 Recruitment distribution

H_3 : Recruitment of blue mussels will be higher in the low- and mid-intertidal zone, compared to higher on the shore.

Blue mussels did not recruit in collectors deployed above the shore height where adult blue mussels occur (i.e. super-top zone, Figure 16). Super-top were therefore excluded from the statistical test. The density of blue mussel recruits was not significantly affected by shore height in the remaining four zones (Kruskal-Wallis test, $\chi^2 = 4.04$, $df = 3$, $p = 0.258$). The mean recruit density observed in the low and high zone was 0.911 and 0.804 mussel recruits per gram collector, respectively. Although this was approximately twice the recruit density observed in the high zone (Figure 16), this difference was not statistically significant.

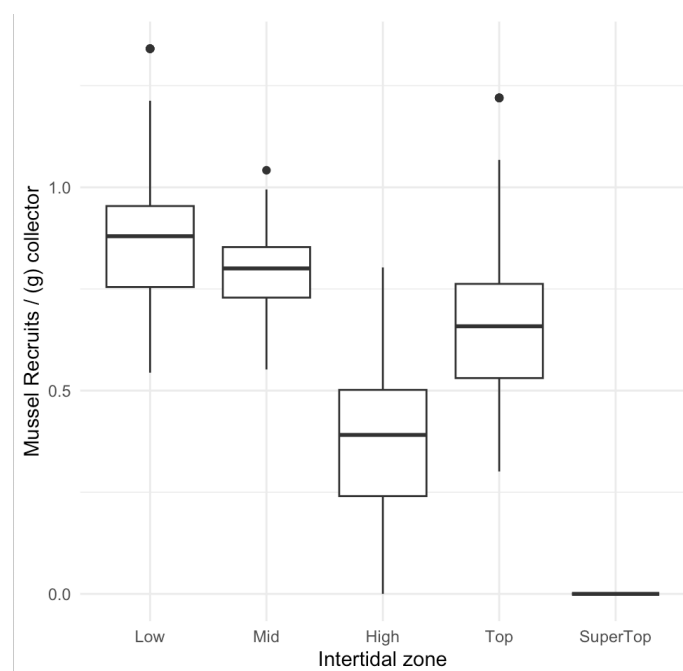


Figure 16: Abundance of mussel recruits per gram of recruit-collector (dry weight), at five intertidal zones on Hillesøya. No recruits were found at the highest intertidal zone i.e., “SuperTop”, hence it is excluded from the statistical analysis. Symbols and their interpretation as described in Figure 12.

3.3 Growth-transplantation experiment

H_2 : Mussel growth is greater in the low intertidal zone compared to the high intertidal zone.

Shore height had a significant effect on relative length increment of mussels on Hillesøya (Kruskal-Wallis test, $p = < 0.0001$, $df = 3$, $\chi^2 = 23.157$, Figure 17A), but not at Brensholmen (one-way ANOVA, $F = 1.61$, $df_{(3,60)}$, $p = 0.196$, Figure 17B). On Hillesøya, the relative length increment of mussels placed in the low zone was, on average, 20.7 % (LL) and 25.4 % (HL). This was approx. double the increment for the mussels placed in the high zone 10.8 % (HH) and 12.8% (LH). On Brensholmen mean mussel length increment for the low zone was 15.5% (LL) and 15.2 % (HL), the high zone 13.2 % (HH) and 8.3 % (LH). There was no significant difference between the treatments (transplantation) and the corresponding control (replantation).

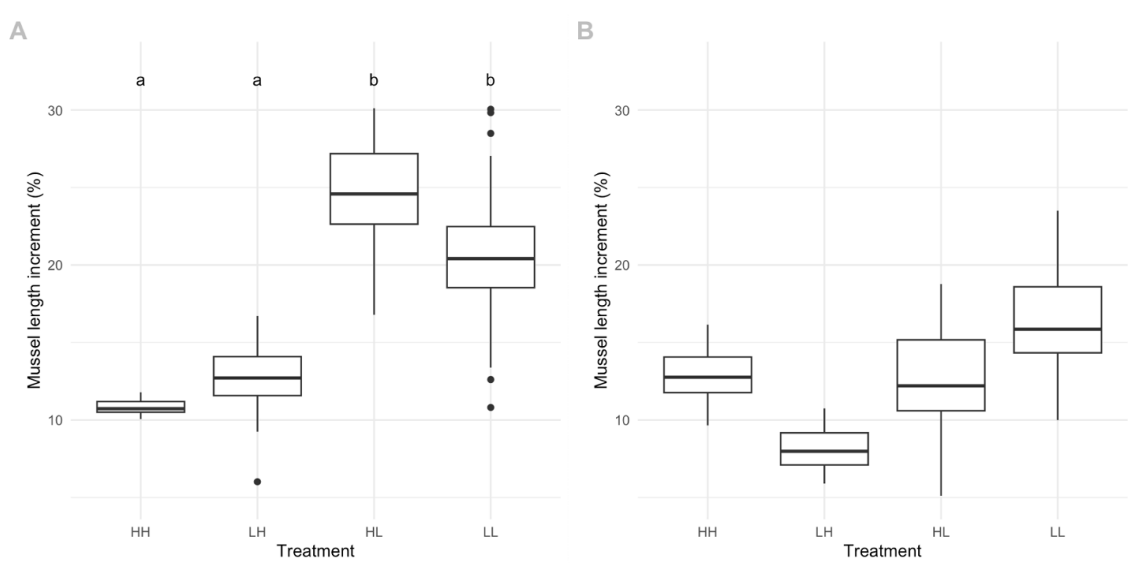


Figure 17: Boxplot illustrating the mussel length increment (%) for the different treatments for Hillesøya (A) and Brensholmen (B). Transplantation from low shore to high shore (LH), and high shore to low shore (HL). While replantation from low shore back to low shore (LL), and high shore back to high shore (HH). Boxplot elements as described in Figure 12.

A lower position on the shore had strong positive effect on mussel growth on Hillesøya (LRR= 0.81 [95% CI: 0.21, 1.41] Figure 18) and a small positive effect on Brensholmen (LRR= 0.14 [95% CI: -0.67, 0.95] Figure 18). Mussels placed on the high intertidal zone, had a medium negative growth effect on both Hillesøya (LRR= -0.53 [95% CI: -1.06, -0.00]Figure 18) and Brensholmen (LRR= -0.60 [95% CI: -1.16, -0.03], Figure 18).

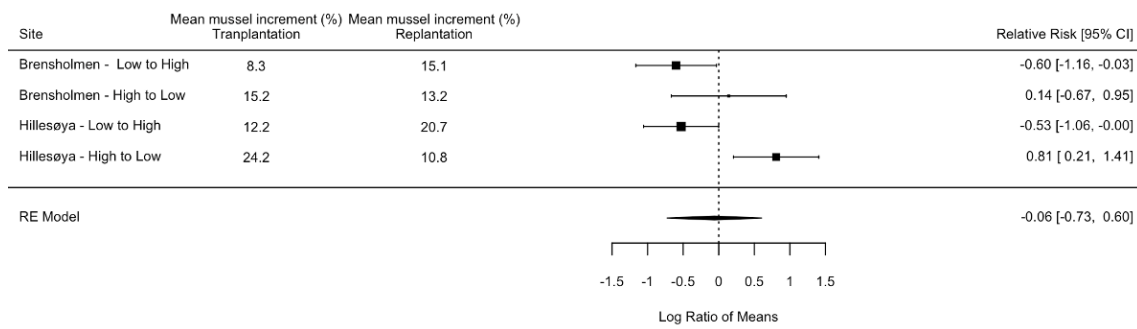


Figure 18: Effect of shore height on mussel growth from Brensholmen and Hillesøya. Tranplantation is the treatment (LH and HL), and replantation is the control (HH and LL). Symbols and their explanation as described in Figure15

3.4 Dogwhelks predation in the low intertidal zone

During the transplantation experiment, the number of casualties of mussels positioned low on the shore was significantly higher than of those positioned high on the shore at Brensholmen ($p = < 0.001$, $df = 1$, $\chi^2 = 19.7$, $N = 106$, Figure 19) and on Hillesøya ($p = < 0.001$, $df = 1$, $\chi^2 = 19.2$, $N = 110$, Figure 19). In the lower zone, the majority of the mussels had died due to predation from dogwhelks at Brensholmen ($p = < 0.001$, $df = 2$, $\chi^2 = 27.1$, $N = 35$, Figure 19) and on Hillesøya ($p = < 0.001$, $df = 2$, $\chi^2 = 19.4$, $N = 28$, Figure 19). The mortality rate in the low intertidal zone was 4.3 (Brensholmen) and 5.6 (Hillesøya) times higher than in the high intertidal zone.

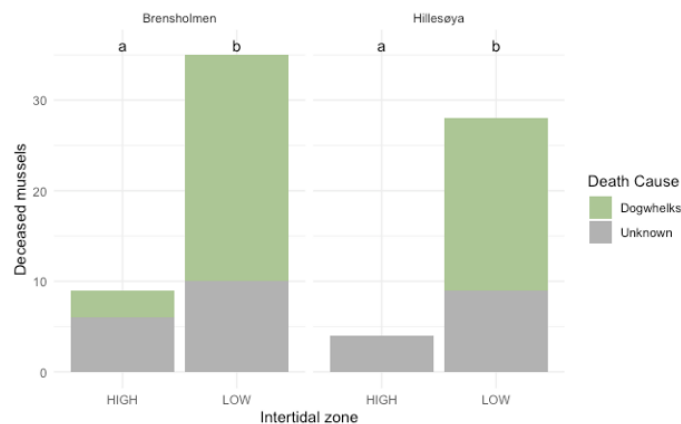


Figure 19: Number of dead mussels from the low and high intertidal zone at Brensholmen and on Hillesøya at the end of the transplantation experiment. The different colors represent if the cause of death was dogwhelks (drilled hole in the shell) or unknown. Treatments sharing common letters are non-significantly different from each other ($p > .05$)

On Hillesøya, dogwhelks consumed significantly more of medium than small blue mussels ($p = 0.03$, $df = 1$, $\chi^2 = 4.6$, $N = 33$, Figure 20) with a medium effect size (0.59). At Brensholmen, dogwhelks did not significantly prefer medium over small blue mussels ($p = 0.35$, $df=1$, $\chi^2 = 0.8$, $N = 44$, Figure 20), despite a slightly higher mortality rate of the medium-sized mussels with a small effect size (0.28).

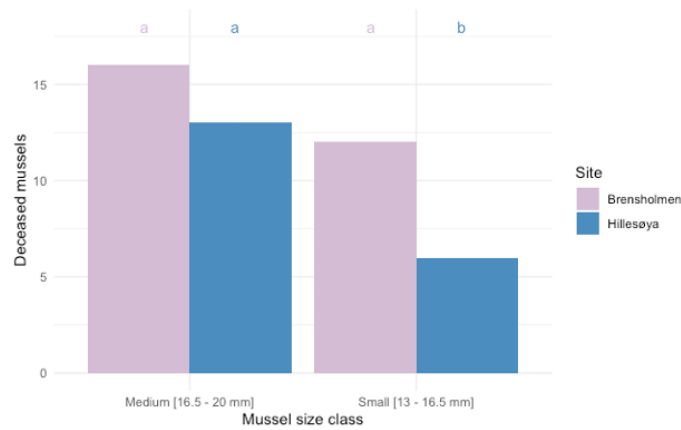


Figure 20: Mortality caused by dogwhelks related to size class on open-coast. The different colors represent the study site. Treatments sharing common letters and color are non-significantly different from each other ($p > .05$)

3.5 Patch experiment

H_4 : When reducing the density of aggregated blue mussels in the low intertidal zone, increased mussel growth will occur.

The density of blue mussels across different intertidal zones showed significant differences on Hillesøya (Kruskal-Wallis test, $p = < 0.01$, $df = 3$, $\chi^2 = 11.08$, Figure 21A), but not at Brensholmen (one-way ANOVA, $F = 1.29$, $df_{(3,20)}$, $p = 0.305$, Figure 21B). On Hillesøya, blue mussel density was significantly higher in the low intertidal compared to the other three zones, with no significant difference among the latter. The effect size from low to high was small (0.27) for Brensholmen and medium (0.63) for Hillesøya.

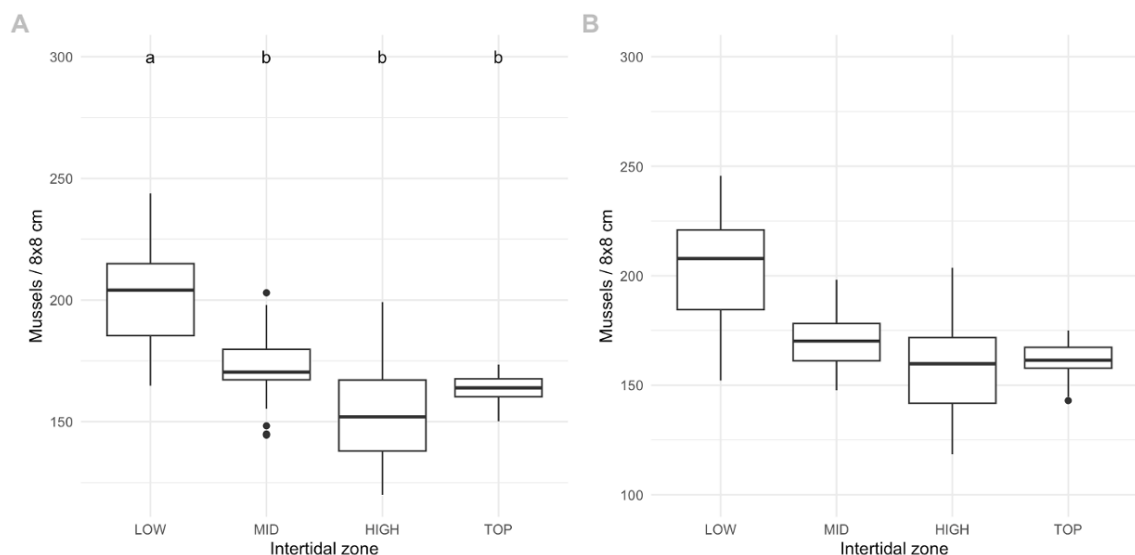


Figure 21: Boxplot illustrating the mean mussel density per 8 x 8 cm frame ($n=6$) from the different intertidal zones for Hillesøya (A) and Brensholmen (B). Boxplot elements as described in Figure 12

Six of the ten treated mussel patches had lost all blue mussel individuals by the end of the experiment. All of the four remaining treated patches had *Corallina officinalis* associated with the patch, while the 6 lost patches had been associated with *Clathrostromes sp.* or were lacking REA (Figure 22). There is a significant relationship between the loss of mussel patches and substratum type (Fisher's Exact Test, $p < 0.0001$). From the remaining treatment patches, only 2 of 30 initially marked mussels were present at the end of the experiment and had a relative increment of 13.4 % and 13.7 %. Statistical analysis was therefore impossible on increment data. All the control patches were recovered, but only 9 of 30 initially marked mussels survived. Of the recovered control mussels, just two had increased in length. Seven mussels managed to repair the cut, but did not increase in size. The mean relative increment from the 9 survivors was 2.14% (range: 0.0 - 13.1%), and the two who had visible increment, had a mean of 9.65% (Appendix - Table 2)

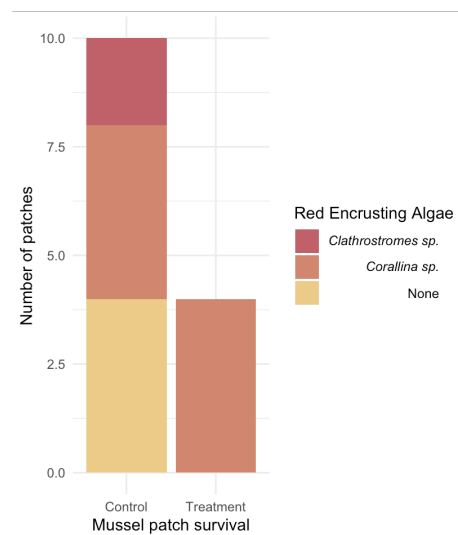


Figure 22: Number of mussel patches associated with the different REA whether they remained on the shore or disappeared after treatment

3.6 Antagonists and benefactors of blue mussels along the shore height

H_{5.1}: A negative correlation between the cover of limpets (competitor), dogwhelks (predators), and REA with blue mussel cover along the shore height on the open-coast sites will occur.

H_{5.2}: A positive correlation between the cover of canopy-forming brown algae (stress amelioration) with blue mussel cover along the shore height on the open-coast sites will occur.

On Hillesøya, blue mussel cover correlated positively with brown algae cover (0.89) yet negatively with dogwhelks (-0.48), REA (-0.77) and limpet cover (-0.82) (Appendix - Table 5, Figure 23A). Similar trends were observed at Brensholmen, where blue mussel cover correlated positively with brown algal cover (0.92) and negatively with cover of REA (-0.62), limpets (-0.67) and dogwhelks (-0.68) (Appendix - Table 6, Figure 23B).

At both sites, blue mussels abundance principally decreased from high to low shore. The same applies to brown algae. At both sites, the abundance of blue mussels and brown algae peaks at shore heights slightly below their uppermost occurrence. In contrast to REA, which at the lowest level had up to 100% coverage (Hillesøya), decreasing with increased shore height. Dogwhelks were not found above mid intertidal zone for either site, and had the highest abundance lowest on the shore, particularly at Brensholmen. Limpet coverage had a slow increase from low to mid-shore and decreased from mid-shore and above at Hillesøya. On Brensholmen the highest limpet cover

was lowest on the shore and decreased with shore height. The largest difference is the maximum cover percentage on brown algae. On Hillesøya, the mean brown algae cover is 70%, while the cover on Brensholmen is 30%. There is also a higher percentage of limpets (30%) and dogwhelks (15%) on the lowest intertidal on Brensholmen, compared to Hillesøya limpets (8%) and dogwhelks (5%)

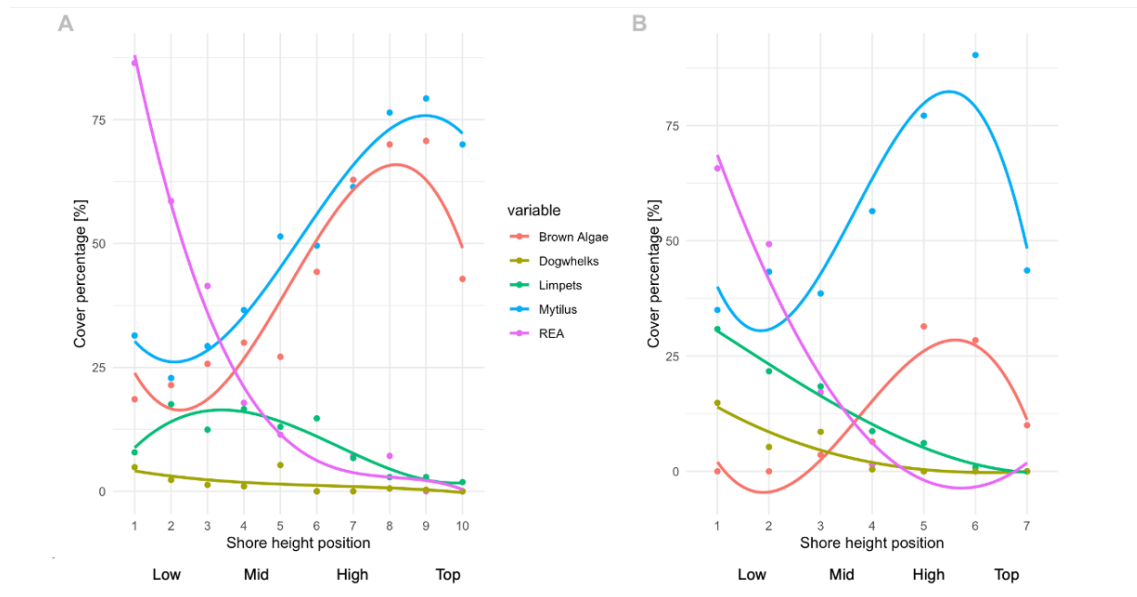


Figure 23: Cover percentage (%) of brown algae, blue mussels, dogwhelks, limpets, and REA along the shore height for Hillesøya (A) and Brensholmen (B). Each point represents the cover (%) mean (n=7) from each shore height

4 Discussion

The main findings are presented here in the order they are discussed below:

- There is a unimodal size pattern for blue mussels with an increase in mussel size from low to high and a decrease from high to top, as observed in the pilot study (**H1.1**)
- The unimodal size pattern is limited to the open-coast sites, and not to the inner-fjord sites. The fjord sites show a linear relationship, with size decreasing with increasing shore height (**H1.2**)
- Environmental conditions favor growth in the low shore on Hillesøya (**H2**)
- Dogwhelks are the primary contributors to blue mussel mortality in the low intertidal zone.
- Dogwhelks exhibit a preference for larger blue mussels (>16.5 mm) over smaller ones (<16.5 mm).
- *Corallina* plays a crucial role in patch aggregation, and mussel patches tend to have a higher survival rate when they are associated with *Corallina* turfs compared to those without such association.
- There is no significant difference in recruitment distribution between intertidal zones (**H3**)

4.1 Blue mussel size pattern

In this study, the size pattern of blue mussels within the intertidal zone was investigated at two coastal sites and two inner-fjord sites. The results obtained from quantifying blue mussel size from low to top intertidal zone at the inner part of Kattfjorden (Sørfjorden and Nordfjorden), show a monotonically decrease in mussel size with an increase in shore height. This pattern is well documented in other studies and supported by stress gradient theories (Bertness & Grosholz, 1985; Suchanek, 1978). The key abiotic stressors thought to contribute to this pattern include temperature and salinity fluctuations, desiccation, and other physical processes, incurring additional metabolic costs (Harger, 1970; Kennedy, 1976; Suchanek, 1978; Westerbomb & Jattu, 2006; Westerbomb et al., 2002). Consequently, less energy is available for growth (Maar et al., 2015). Moreover, an important biotic factor is the accessible food supply and feeding duration for mussels, this is directly influencing growth. The overall size pattern observed in Nordfjorden and Sørfjorden is supported by the majority of other studies done on mussel size along the intertidal zone. Comparing the magnitude of the shore height effect from the inner-fjord sites of my study, with that of other studies, they all show the same negative effect (Figure 15). A larger magnitude of effect is presented by the other studies (Connor & Robles, 2015; Leeb, 1995; McQuaid et al., 2000; Suchanek, 1978). with medium to large effect sizes, while the inner-fjord sites in this study

show a small negative effect. This means that generally, blue mussels in Northern Norway are not a unique in size-pattern, as the inner-fjord possesses a similar trend to what studies from the temperate region does. However, the results from the open-coast study sites contradict those from the inner-fjord study sites (Figure 13 and 14). Here, the size distribution of the coastal blue mussels confirms the findings from the pilot study.

The results show an increase in mussel size from low to high intertidal zone, followed by a small decrease in mussel size from high to top intertidal zone. In addition to the difference in the size pattern between the mussels from inner-fjord sites and open-coast sites, there is also a big difference in mussel size. The mean size of the mussels in the inner-fjord low intertidal zone was more than three times larger than the mean size of the mussels in the open-coast high intertidal zone.

Firstly, This difference could possibly be attributed to age. Previous studies in the Arctic and northwest Atlantic have investigated the age and size dynamics of mussel populations. In these areas, mussels exposed to hard physical stressors, such as wave exposure and ice-scouring, tend to have a younger population with a smaller size typically <3 years old and <15mm shell size (Blicher et al., 2013; Tam & Scrosati, 2014). Older mussels are typically larger and thus more resistant to other kind of stressors like predation, and disease (Blicher et al., 2013).

Secondly, the predator-prey interaction can be freshwater-modulated (Brooks & Farnen, 2013). In a freshwater-influenced fjord, blue mussels can withstand the low salinity (Westerbom et al., 2002), while predators like dogwhelks will reduce feeding with a decrease in salinity (Stickle et al., 1985). This indicates that fjord mussels are not exposed to the same predation pressure as open-coast mussels are. If this is true, there is a possibility that the fjord mussels have reached older age because of the lack of predators, and therefore reached a size refuge.

The third aspect, is the difference in wave stress. Smaller sized mussels are more resistant to the physical force of wave action, as there is less drag from the mussels body (Hunt & Scheibling, 2001; O'Connor, 2010). On very wave-exposed sites, only the mussels with small and compact body sizes can withstand this force. Indeed, in the north-west Atlantic older and larger blue mussels (6-8 years and >45mm) were found in sheltered sites, while exposed sites had younger and smaller mussels (2 years and <10mm)(Tam & Scrosati, 2014).

Our results also align with the findings from Tam and Scrosati (2014), where mussels in low-salinity habitats have a good supply of suspended organic matter, and are able to reach large size, maintain low densities and avoid intense intraspecific competition (Guiñez, 2005; Tam & Scrosati, 2014). Furthermore, high nutrient concentration due to fluvial inputs in the fjord may lead to more favorable growth conditions for blue mussels due to higher phytoplankton abundances (Mann, 2009). Similar size and density patterns occur in mussel populations from similar habitats on the northeast Atlantic coast, emphasizing that mussel age, size, and predation is linked to environmental stress and that the rocky shore Arctic and subarctic mussels are thus typically younger and smaller (Blicher et al., 2013; O'Connor, 2010). Although time limitations did not allow age determination in this study, this would be an interesting aspect for further studies to

determine the age structure across the intertidal zones.

Despite the unexpected increase in size from low to high intertidal zone for the open-coast mussels, there is also a decrease from high to top intertidal zone, that aligns more with what one expect according to previous size pattern studies. This decrease in mussel size from the high to top intertidal zone on the open-coast confirms the effect of physical stress on mussel size at the top intertidal zone. As the EMS model indicates, on the highest position on the shore, abiotic factors will have the relative strongest effect on the community structure and individual survival (Menge & Sutherland, 1987). Furthermore, this indicated that there must be other mechanisms than abiotic stress that affect the size lower on the shore.

This also gives rise to the suggestion that stress is mitigated at the position with larger mussel. Under high environmental stress, the ESM predicts that stress amelioration may substantially reduce abiotic stress. For example, shade provided by canopy-forming algae can reduce heat stress and consequential desiccation of understory organisms such as *Mytilus spp.* (Menge, 1978). Several other studies have emphasized the importance of facilitation from macro algae beds as refugees from predators and wave stress for mussel population structure (Blicher et al., 2013; Menge, 1978; Tam & Scrosati, 2014). Our cover transect data shows a positive correlation between blue mussel cover and brown algae cover, particularly in the high intertidal zone. The cover percentage of brown algae increases noticeably from the mid to high intertidal zone, correlating with the rise in environmental stress and the increase in mussel size on the open-coast sites. The facilitation mechanism from the canopy-forming algae may lower the stress on the mussels, causing more favorable conditions and therefore enhancing growth for mussels on the high intertidal zone. Moreover, the brown algae cover on Hillesøya was more than twice that of Brensholmen, indicating that the stress amelioration is higher on Hillesøya. The distribution characteristics of *Ascophyllum nodosum* indicate a preference for more wave-protected sites (Tam & Scrosati, 2014; Vadas et al., 1990). Brensholmen is more wave-exposed than Hillesøya, as visual observations' suggest during rough, windy, and wavy field days. Which may be linked to the more pronounced effect on size difference and mussel growth on Hillesøya. We do not have evidence to say that this can explain the larger mussel size present high in the intertidal zone, nor that the difference between the two sites are something other than natural variances. However, a thorough field experiment testing the effect of mussel growth with and without the cover of brown algae, on the different sites should be of interest for further studies.

4.2 Growth-transplantation experiment

The largest mussels were consistently found in the high intertidal zone at both open-coast sites, suggesting that the higher intertidal zone had the most optimal growth conditions. However, the results from the transplantation experiment on Hillesøya showed that the mussels placed from the high to the low intertidal zone had twice the relative size increment compared to conspecifics remaining in the high intertidal zone or being transplanted from the low to the high intertidal. When transplanting mussels from the high intertidal zone to the low intertidal zone, our results demonstrated a strong positive effect on mussel size increment, particularly at the Hillesøya study site. When transplanting the mussels from the low intertidal zone to the high, they show a medium negative effect on mussel increment for both Hillesøya and Brensholmen. These results provide evidence that the environment lower in the intertidal zone has better growth conditions for mussels. Since there were no difference in replant and transplant, it indicates that the original intertidal zone of the mussels is not relevant and that the growth is primarily influenced by the shore position. Mussels are sessile filter feeders and depend on water flow to feed (Coulthard, 1929). As tidal emergence occurs, the mussels positioned higher on the shore will have less access to food. The effect of shore height on mussel growth on Hillesøya was, in accordance with previous studies, suggesting a reduction in mussel growth with decreasing submergence time (Bertness & Grosholz, 1985; Buschbaum & Saier, 2000; Seed, 1968; Suchanek, 1978). Lower on the shore, the feeding time increases as the immersion time is prolonged. According to the growth-transplantation experiment, suggesting that mussel size is reduced at lower shore height, rather than enhanced at high intertidal zone. Thus, unconventional growth conditions cannot explain the size pattern on the open-coast sites.

4.3 Dogwhelk predation

Mussels in the low intertidal zone from the growth-transplantation experiment had high mortality rates. Dogwhelks are known to be more abundant and have a higher feeding activity on the mid to low shore compared to the high shore (Tyler-Walters, 2007), and our findings show that predation from dogwhelks was responsible for 68% of mussel deaths at Hillesøya and 71% at Brensholmen in the low intertidal zone. Like other species in the intertidal, dogwhelks are prone to the same environmental stress gradient but are less adapted to wave exposure and air exposure compared to blue mussels (Burrows & Hughes, 1989; Menge, 1976). This difference in sensitivity towards environmental stress is typical for mobile predators with sessile prey, where the predator responds to environmental stressors via emigration rather than by evolving tolerance of environmental stress (Menge, 1978). Indeed, results from our transect to assess species coverage revealed that the presence of dogwhelks decreases with increasing shore height, and they are altogether absent above the mid-intertidal zone. This confirms the ESM prediction that with an increase in environmental stress, there is a decrease in predation pressure (Bertness & Callaway, 1994; Bruno et al., 2003).

Morphological characteristics in the deceased mussels at Hillesøya showed that the majority of deceased mussels were of the largest size class (16.5 – 20 mm shell size), and only two small mussels (< 15 mm shell size) had holes drilled by dogwhelks. A similar trend occurred on Brensholmen, but without a statistically significant effect. Seemingly the dogwhelks prefer the mussel with a size >16.5mm, and this supports the findings of other studies on dogwhelks' foraging (Hughes & Dunkin, 1984). Based on the principles of optimal foraging theory, predators aim to maximize their food intake while minimizing costs, potentially resulting in accelerated growth (Schoener, 1971; Stephens & Krebs, 1986). Dogwhelks foraging behavior has been studied by Hughes et al. 1984 where the preferred mussel size for the predator was 20 – 25 mm. Dogwhelks feed on mussels by drilling a hole through mussel shells with their toothed radula and consuming their flesh (Carriker et al., 1981). This process can take from hours to several days (Miller, 2013; Morgan, 1972) and is a energy costly process, especially in a stressful environment (Garton & Stickle, 1980; Stickle et al., 1985). Several studies (Crothers, 1985; Quinn et al., 2012) have suggested that if the mussel was bigger, the cost of drilling through the shell was too high, if the mussel was smaller, the profit was not sufficient. Predators like dogwhelks exhibit lower drilling levels and survival when exposed to salinity and temperature fluctuations compared to constant levels (Garton & Stickle, 1980; Zachary & Haven, 1973). Indicating that they are more commonly situated in less stressful environments, such as the lower regions of the intertidal zone. Mussels in these environments will therefore experience a greater pressure from predation here, and this might limit their survivorship and possibilities of growing larger.

The impact of dogwhelk predation on blue mussel communities in western Norway was recently assessed in study by Meister et al. 2023, which showed a notable decline in the blue mussel population within a few weeks. Indicating the effect of dogwhelk predation. A number of studies have investigated the growth of blue mussels on the natural rocky shore compared to that on floating structures. They all show that mussels on the floating attachment resulted in a size increase twice that of the mussels on natural rocky shores. Not only are they sheltered from harsh environmental conditions like wave exposure, temperature fluctuation, and air exposure, but these structures provide refuge from crawling predators (Meister et al., 2023; Suchanek, 1978; Wallace, 1980).

With coastal low-shore mussels averaging 10 - 11 mm, and dogwhelks favoring those >16mm the rarity of large mussels on the lower intertidal zone may be due to heightened dogwhelk predation. This preference could explain the unusual size pattern of blue mussels on the coastal sites. Furthermore, a study conducted on barnacle size distribution in Nova Scotia revealed that the largest barnacles, were more prevalent in high shore zones, while the smallest were primarily found in low shore areas. This study proposed that biotic interactions, such as predation and competition, played a more significant role than previously hypothesized abiotic factors on the Canadian coast (MacPherson & Scrosati, 2008). This prompts us to contemplate our own study system and the potential for a similar scenario in the case of blue mussels in Northern Norway.

4.4 Cost and benefits of *Corallina* turfs

Intraspecific competition is an additional explanation to the abundance of small mussels in the low intertidal zone. The preferential consumption of larger, more profitable prey by predatory dogwhelks will increase the density of smaller blue mussels low on the shore. The density of blue mussels was highest in the low intertidal zone on both open-coast sites. This observation aligns with our hypothesis of a density-dependent effect on available space in the low intertidal zone. Higher mussel density results in stronger intraspecific competition, particularly for space and food resources (Bertness & Grosholz, 1985; Bertolini et al., 2020; Gascoigne et al., 2005). Consequently, a density-dependent effect resulting in limited mussel growth.

From the patch experiment, all but two marked mussels of manipulated patches were lost, presumably due to wave dislodgement. Both mussels, however, grew faster than conspecifics competing in control patches. In addition, most of the blue mussels from the control patches did not increase in size but rather just healed the cut, which may indicate high levels of intraspecific competition in control patches. However, due to the low number of mussel survivors from the treatment patches, I cannot draw any statistical inferences whether mussel density is a controlling mechanism of growth on *Hillesøya*. Indirect evidence of density-dependent growth rates in blue mussels comes, however, from the growth-transplantation experiment. As the growth conditions were favorable low on the shore. It should also be noticed that the growth-transplantation experiment does not reflect natural densities of coastal low-shore mussels, implying that intraspecific competition for food may, at least in part, explain the observed small mussel sizes. According to the results of the growth-transplantation experiment, mussels demonstrate growth potential; however, the conditions observed in the patch experiment may suggest that they do not presently favor the attainment of larger sizes.

Despite applying an untried and experimental method as a treatment to these patches, it is less likely that there is a strong influence of the artifacts on the results. Given the similarities in cut depth and patch positioning, these factors should not significantly affect the growth rate of blue mussels from control and treated patches. Moreover, mussels from the same size class were intentionally selected, and although their position in the patch varied, the selected mussels were often the most visible and at near the outer edge of the patches. This could have caused a sampling bias, as the selected mussels were less “packed” in their attachment to the patch and were likely the first to get dislodged. Furthermore, the manipulation that was applied might have been too extensive, as the removal of 80% of blue mussels from a patch resulted in dislodgement of the entire patch in 6 out of 10 cases. However, the limited increase in size among the mussels suggests that the availability of space for growth might be a controlling factor influencing mussel size for the control patches (Bertness & Grosholz, 1985).

The patch experiment, however, gave rise to more interesting questions regarding the aggregation of the mussel patches. Manipulation of the patch structure during experimentation resulted in the loss of many of the entire mussel-patches, potentially indicating the importance of aggregation for mussel survival. Mussels self-organize into aggregated patches to reduce the chance of dislodgement from wave exposure, increase reproductive success, ameliorate environmental conditions, and reduce the risk of predation (Bertness & Grosholz, 1985; Nicastrò et al., 2012). The loss of aggregation density due to the sampling procedures used in this study may have resulted in a co-loss of the benefits of aggregation, suggesting that aggregation is more critical for the mussels than the cost of growth reduction (Eschweiler & Christensen, 2011). This experiment therefore, hints to the importance of *Corallina* patches to protection of blue mussels against wave dislodgement, since only *Corallina*-associated mussel patches “survived” the manipulation treatment.

Another aspect of this turf-mussel interaction, is the possibility that smaller mussels are more inaccessible for predators than the larger ones, hence small mussels will have a higher survival rate in a dense patch. As established, mussels of larger size are preferentially preyed on compared to smaller mussels (Section 4.3), and in addition, mussels living in the center of aggregation patches are more difficult for predators to catch than individuals living at the patch edge or in solitude (Svane & Ompi, 1993). Hence, large mussels along the edge of a patch are the most likely to be preyed upon (Okamura, 1986). Mussels in the *Corallina* turf are positioned with the anterior end, the thinnest part of the shell, attached to the substratum (Eggermont et al., 2020). This weak point on the mussel shells is the preferred drilling point for dogwhelks (Hughes & Dunkin, 1984). When small mussels are positioned inside these turfs, their weakest point is unreachable to dogwhelks (as illustrated in Figure 9 - Patch experiment). This aggregation strategy can therefore enhance survival for densely packed low-shore coastal mussels (Visual observation).

Corallina turfs often have a high abundance of small invertebrates and bivalve species within the structure, including blue mussels, indicating that there is more than one benefit associated with these turfs (Buršić et al., 2021; Bussell et al., 2007; Liuzzi & Gappa, 2008). This beneficial relationship, is also supported by Dommasnes in (1968), which investigated the meiofauna in *Corallina* turfs on different water depths and noted that *Modiolus modiolus* in the 1-12 mm size range, reinforced the structure of the turf. This suggests that mussel recruits settle in these substrata and stay as juveniles and maintain their position there until they grow to 12 mm, which coincides with the size classes observed in the low intertidal zone in this study. Therefore, hypothesizing that *Corallina* turf might provide shelter for juvenile mussels, where predation and wave dislodgement might act upon the bigger mussels that cannot gain the same shelter from these turfs.

The result from the species cover transects shows a steep decline in REA from low to mid intertidal zone and a complete absence above the mid-zone. This aligns with the density of small mussels being highest in the low intertidal and gradually decreasing, in addition to the consumer pressure following the same gradual decrease. This pattern also aligns with the ESM, incorporating the

possibility of *Corallina* turf acting as an associational defense. In environments with low stress, but high predation pressure, facilitation like these defenses are of high importance to prey communities (Bertness & Callaway, 1994).

In addition to serving as a shelter from dogwhelks, the turf-structures may also provide shelter from bulldozing by limpets. Bulldozing is defined as the unintended removal of juvenile benthic cyprids or juvenile blue mussel recruits by the edges of limpet shells while grazing (Dayton, 1971). This antagonistic interaction has been extensively studied between limpets and barnacle cyprids (Dayton, 1971; Menge et al., 2010), although, it has received less attention concerning mussel recruits (Stefani & Branch, 2005) the same mechanisms might apply on our study site. Limpets are recognized for their homing behavior, which involves moving around while feeding and subsequently returning to the same spot for settlement (Hartnoll & Wright, 1977). This behavior resembles patrolling, and it is limited to hard rocky substrates, causing limpets to "clear" areas on the rocky shore, making it harder for benthic larvae to settle. Bazterrica et al. in (2007) found a negative correlation between the limpet density and *Corallina* cover, because the *Corallina* hairy-like surface is not conducive to limpet attachment. Therefore, one might consider *Corallina* turfs as protection for mussel recruits, and organisms living within these are sheltered towards the bulldozing behavior. By creating these preferable attachment substratum for mussels, they might allow survivorship, but also increase intraspecific competition.

Results from the transects on species coverage indicate that limpets are abundant in the low, but also in the mid intertidal zone (Figure 23). According to the EMS model, competition is of high importance where environmental stress is medium, in our study system this translates well to the mid-intertidal zone. Here, competition for space and food will have more influence on mussel population structure than positions with lower and higher environmental stress (Bruno et al., 2003). Competition for space inter-specifically shapes the physical structure of the mussel patches (Bertness & Callaway, 1994). Based on visual observations during sampling, the mussel coverage in these areas consists of spatial patches before transitioning into more continuous belts higher in the intertidal. For further studies, a suggestion would be to investigate whether limpets' bulldozing mechanism can play a role in structuring the blue mussel population in the mid intertidal zone, by experimentally test the bulldozing on mussel recruits. Additionally, test whether removal of limpets will cause less patchy distribution in the mid and low intertidal zone.

In conclusion, the observed relationship between *Corallina*-turfs and mussel size underscores the pivotal role of these associational defenses and how they can promote high-densities. This can result in high intraspecific competition, that may limit mussel size. Furthermore, the benefits gained from the *Corallina* by juvenile mussels promotes a preference for them as a settlement substratum in the low intertidal zone.

4.5 Mussel recruitment

Mussel recruitment is controlled by tidal height, suggesting that there should be higher recruitment in the low and mid intertidal zone (McQuaid & Lindsay, 2005; Porri et al., 2007). Lower on the shore is also correlated with the high density of mussels from our study and the higher abundance of REA from the species cover transect. Substratum choice is known to be an important factor in mussel recruitment (Paine, 1974; Petraitis, 1990). *Corallina* turfs increase recruitment success for blue mussels, as water-soluble extracts of these coralline algae induce settlement for many species of marine invertebrates (Hadfield & Paul, 2001; Morse & Morse, 1984). The mussel recruits will gain shelter from predators (Shepherd & Turner, 1985) and protect against wave dislodgement (Dommasnes, 1968). This is supported by findings by McQuaid and Lindsay 2005, which proposed that *Corallina* turfs seem to be a good option for mussel recruits to settle. Paine in 1974 established that mussels do have certain preferences in settlement sites, and Petraitis in 1990 that substratum is the main limiting factor for mussel recruits. Later McQuaid proposed that the dominant substratum for mussel recruitment was the foliose coralline alga *Corallina sp.*, followed by adult mussels, and then rhodophyte *Gelidium pristoides* (McQuaid & Lindsay, 2005). Additionally, several other studies have also highlighted filamentous algae as an important settlement surface for *Mytilus* larvae (Hunt & Scheibling, 1997; Morello & Yund, 2016). These findings, alongside this study and previously discussed results, support that the *Corallina* turfs are a preferred substratum for the recruits to settle on, and would explain why the majority of blue mussels in the low intertidal zone are found on *Corallina* patches.

The recruitment experiment did not show any significant difference in the number of recruits from the different shore heights, unlike other studies have suggested (McQuaid & Lindsay, 2005; Porri et al., 2007). However, it is notable that the average number of mussel recruits in the low- and mid-intertidal zones was double that of the high intertidal zone, even though this difference did not reach statistical significance in the results. As a low number of larvae was observed, there is a possibility that the settlement peak was not covered, which could also explain the low levels of recruits. As there have been limited studies on spawning and recruitment in Northern Norway (Frantzen, 2007; Wallace, 1983), it is not determined when the exact settlement peak occurs. Several studies have pointed out that spawning *M. edulis* in cold-water areas coincides with temperature increase (Thompson, 1984; Thorarinsdóttir & Gunnarsson, 2003). This annual variation making it challenging with a short time window. During the experimental period, there were very low average sea temperatures in May (6.5 °C) and the first half of June (7.5 °C) which might explain a delay in peak mussel spawning. Mussel spawning is usually initiated when sea temperatures rise above 9.5 °C (Chipperfield, 1953) making it possible that the peak was not covered during our collection period, that ended in the beginning of July. However, there were more mussels in the July-collectors, and these results do not indicate an unexpected recruitment pattern that could explain this unexpected size pattern.

4.6 Environmental stress model applied

In Figure 24 I have applied the modified ESM (Bruno et al., 2003) to the open-coast sites, and what the results from all experiments, similar studies, and visual observations during sampling indicate. Environmental stress in this model can easily be replaced with shore height. I suggest that in the low intertidal zone, predation pressure by dogwhelks is high for mussels, unless they are able to use *Corallina* turfs as associational defenses to avoid predators. Dogwhelks will prefer larger mussels (20-25 mm) and only the smallest mussels will remain sheltered in the *Corallina* turf. In the mid-intertidal zone, I suggest that both intraspecific competition and interspecific competition are of high significance, as predation is lower when environmental stress is increasing. In this case, space is the limiting resource, where both limpets and other mussels are competitors. This will decrease the available resources and resulting in smaller sized mussels. Higher in the intertidal zone, stress amelioration is of importance, and canopy-forming brown algae mitigate abiotic stress for blue mussels and enhance growth, resulting in larger blue mussels. The top intertidal zone is dominated by abiotic stressors, here: desiccation-, temperature-, and salinity stress will reduce the mussel size.

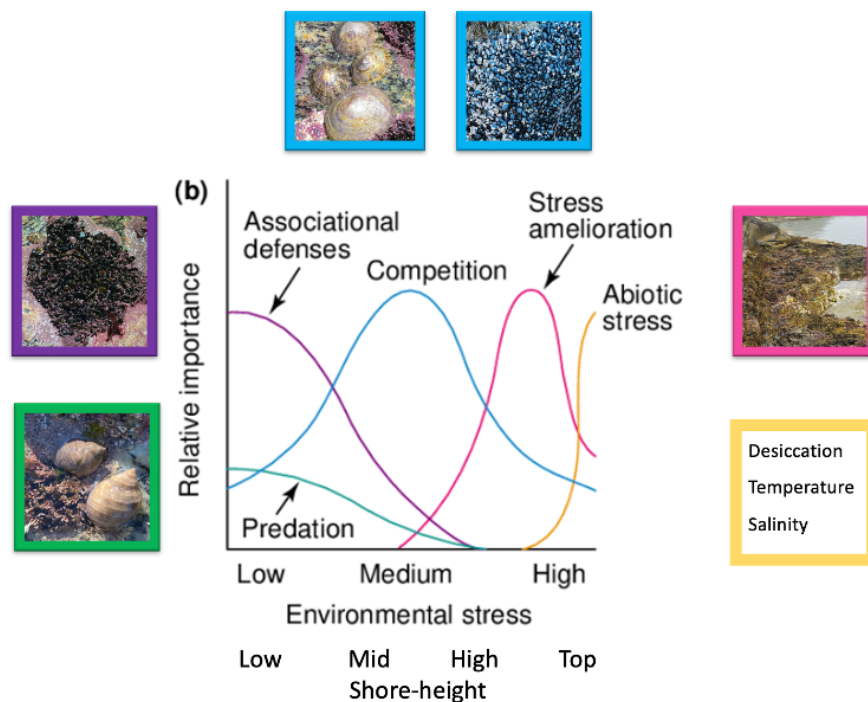


Figure 24: Environmental stress model by Bruno et al. (2003) with species interaction on the open-coast sites. The x-axis with environmental stress levels from low to high can easily be replaced with shore height. The y-axis shows the relative importance of the ecological process. The green frame and line indicate predation from dogwhelks, the purple line associational defenses from REA, blue line competition intra- and interspecific, pink is the importance of stress amelioration from brown algae and yellow the most dominating abiotic stressors: desiccation; temperature; and salinity.

5 Conclusion

Through an investigation into the unexpected vertical size pattern of blue mussels in the Northern Norwegian intertidal zone, my thesis has demonstrated that this unimodal pattern occurs at open-coast sites, but not in the nearby inner-fjord sites. Additionally, the results underscore the likelihood of biotic interactions being more significant in subarctic regions than previously assumed. Harsh physical conditions, such as desiccation, salinity, and temperature variations, influence mussel size in the top intertidal zone. The stress-ameliorating effect from canopy-forming brown algae in the high intertidal zone, might reduce stress and increases mussel size. In the mid and low intertidal zones, it is probable that biological processes affect the population structure and individual survival, with both inter- and intraspecific competition for space. Predation by dogwhelks can lead to a decline in the low intertidal zone among larger mussels (>16.5 mm). While smaller juvenile mussels are suspected to benefit from the shelter provided by *Corallina* turfs, this is also indirectly increasing the intraspecific competition, making the majority of mussels in the low intertidal zone smaller and most likely juveniles. These processes are illustrated in Figure 25.

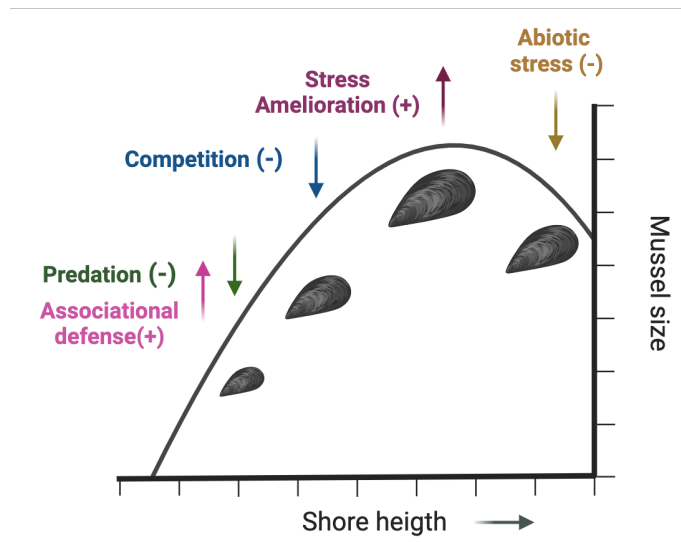


Figure 25: Interactions affecting mussel size along the shore height gradient on the open-coast sites of Northern Norway. Created in biorender.

Determining the exact drivers and outcomes of these interactions remains a challenge, and it is crucial to emphasize the need for further research to fully substantiate these theories. As the population of blue mussels is experiencing a global decline, it is important to emphasize the significance of conducting field experiments to map out potential threats. Such assessments serve as valuable tools for understanding the factors contributing to the population decline before it reaches a critical stage. The intertidal zone acts as an “early warning habitat” for the impacts of climate change. The direct exposure of the intertidal zone to air and water temperature changes makes it a valuable environment for investigating the biological effects of such changes (Hawkins et al., 2008; Sagarin et al., 1999). Moreover, given the scarcity of subarctic intertidal research and

the anticipated significant impacts of climate change on these areas (Solomon, 2007), conducting more comprehensive studies is essential to gain a deeper understanding of the ecological interactions among intertidal species in this highly underexplored environment like the subarctic coast of Northern Norway.

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6 Appendix

Table 2: Mussels from Patch-experiment that had visible increment

Id	Treatment / Control	Associated REA	Size increment (mm)	Relative increment (%)
22	T	Corallina	1.78	13.4
28	T	Corallina	2.22	13.7
41	C	None	1.05	6.2
44	C	None	2.71	13.1

Table 3: All assumptions and statistical tests run

Data	Normality / N=	Homogeneity or test	Test performed	F or χ^2	MS	Df	P-value	Posthoc
Brensholmen Mussel length ~ Intertidal Zone	0.3902	0.2482	ANOVA -1	21.96	20.52, 0.934	3, 20	1.54e-06 ***	Tukey
Hillesøya Mussel length ~Intertidal Zone	0.7745	0.1703	ANOVA -1	15.66	42.26, 2.72	3, 20	2.27e-05 ***	Tukey
Hillesøya Growth ~Intertidal Zone	6.298e-08	0.7048	Kruskal Wallis	$\chi^2 = 23.157$		3	3.746e-05	Dunn
Brensholmen Growth ~Intertidal Zone	0.09032	0.2788	ANOVA-1	1.61	1.025, 0.6364	3, 60	0.196	
Brensholmen Cause of death ~Size class	N= 44	Pearson	Chi-squared	$\chi^2 = 0.838$		1	0.3471	
Hillesøya Cause of death ~Size class	N= 33	Pearson	Chi-squared	$\chi^2 = 4.664$		1	0.0308	
Brensholmen Survival ~Zone	N= 106	Pearson	Chi-squared	$\chi^2 = 19.751$		1	8.823e-06	
Hillesøya Survival ~Zone	N= 110	Pearson	Chi-squared	$\chi^2 = 19.228$		1	1.16e-05	
Brensholmen Cause of death ~Low	N = 35	Pearson	Chi-squared	$\chi^2 = 27.143$		2	1.276e-06	
Brensholmen Cause of death ~Low	N = 28	Pearson	Chi-squared	$\chi^2 = 19.35$		2	6.261e-05	
Hillesøya Recruitment ~Intertidal zone	6.579e-07	0.8073	Kruskal Wallis	$\chi^2 = 23.157$		3	0.2577	
Patch survival ~ Substratum	N= 30		Fisher's				2.312e - 08	
Brensholmen Density ~ Intertidal zone	0.4342	0.0744	ANOVA-1	1.29	2738, 2122	3,20	0.305	
Hillesøya Density ~Intertidal zone	0.04188	0.003442	Kruskal-Wallis	$\chi^2 = 11.0801$		3	0.00809	Wilcoxon

Table 4: Regression equations

Site	Data	Model	Equation	R2	F-statistic	p-value
Brensholmen	Mussel length ~Shore height	Polynom	$y = 12.51846 + 2.75991 * x - 1.62198 * x^2$	0.9987	381.4	0.03618
Hillesøya	Mussel length ~Shore height	Polynom	$y = 14.9054 + 3.3062 * x - 3.3352 * x^2$	0.9975	201.8	0.04972
Nordfjorden	Mussel length ~Shore height	Linear	$y = 64.60786 - 0.47889 * x$	0.9913	228	0.0043578
Sørfjorden	Mussel length ~Shore height	Linear	$y = 45.30882 - 0.10081 * x$	0.9103	20.3	0.04589

Table 5: Hillesøya species cover correlation In this table, each row and column represent a species, and the values in the cells represent the correlation coefficients between the species cover. The diagonal cells represent the correlation of each species with itself, which is always 1.

	Mytilus	REA	Patella	Nucella	Brown Algae
Shore height	0.941	-0.870	-0.716	-0.642	0.821
Mytilus	1.000	-0.770	-0.817	-0.475	0.888
REA	-0.770	1.000	0.326	0.626	-0.626
Patella	-0.817	0.326	1.000	0.299	-0.760
Nucella	-0.475	0.626	0.299	1.000	-0.634
Brown Algae	0.888	-0.626	-0.760	-0.634	1.000

Table 6: Brensholmen species cover correlation. In this table, each row and column represent a species, and the values in the cells represent the correlation coefficients between the species cover. The diagonal cells represent the correlation of each species with itself, which is always 1.

	Blue mussels	REA	Limpets	Dogwhelks	Brown Algae
Shore height	0.5683	-0.882	-0.977	-0.849	0.672
Blue mussels	1.000	-0.622	-0.673	-0.676	0.925
REA	-0.622	1.000	0.932	0.871	-0.672
Limpets	-0.673	0.932	1.000	0.930	-0.711
Dogwhelks	-0.676	0.871	0.930	1.000	-0.654
Brown Algae	0.925	-0.672	-0.711	-0.654	1.000

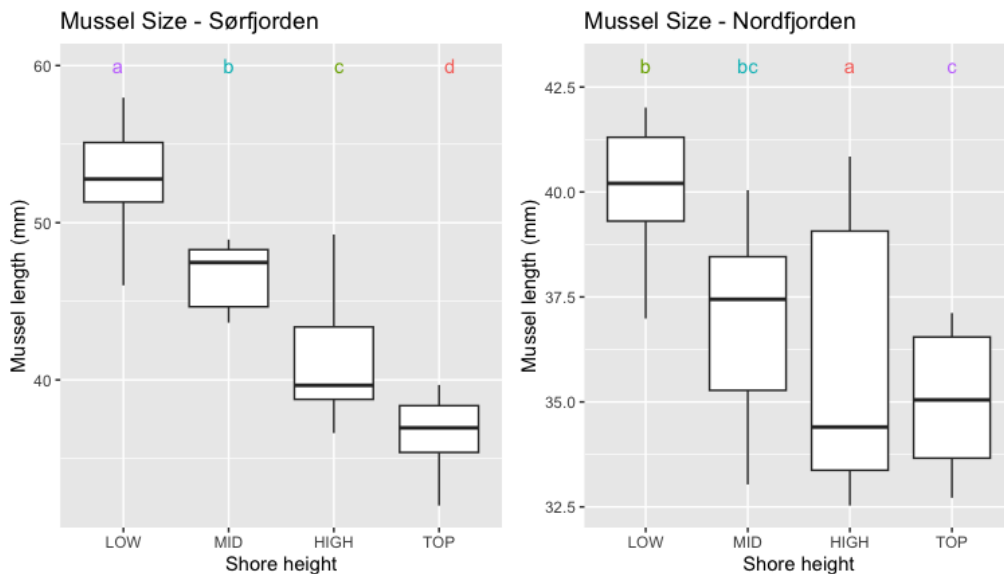


Figure 26: Mussel length [mm] from the four intertidal zones at Sør fjorden and Nordfjorden (n=10). Boxes represent the interquartile range (IQR) of the median. The median is marked with the thickened line. Whiskers extend to the minimum and maximum values within 1.5 times IQR. Treatments sharing a minor letter are non-significantly different from each other ($p > 0.05$).

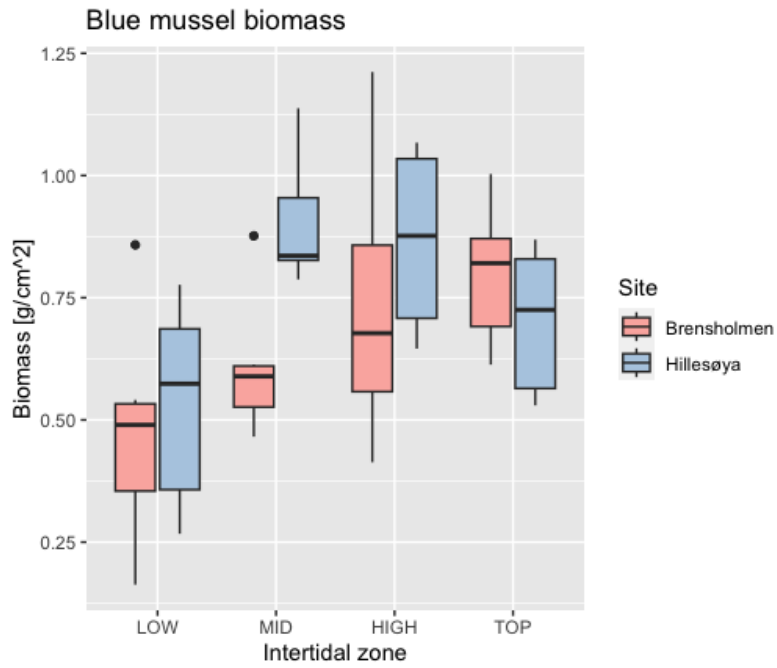


Figure 27: Biomass (g) per cm² from the two open coast sites Brensholmen and Hillesøya. Boxplot parameters as described in Figure 26

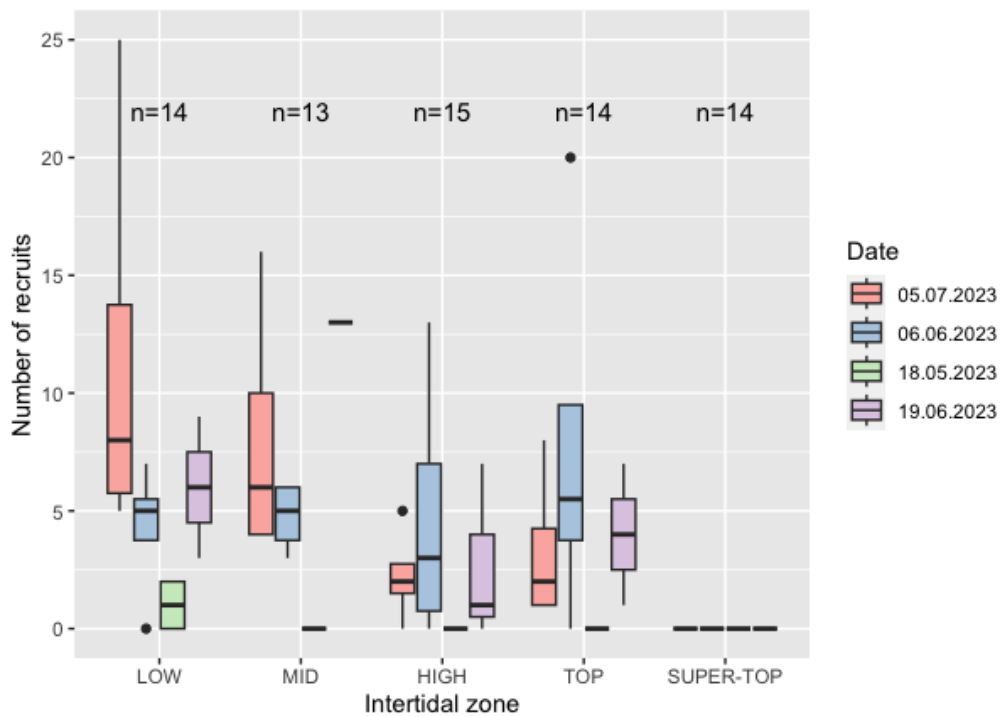


Figure 28: Recruitment of blue mussels in each of the intertidal zones over the experimental period. Boxplot parameters as described in Figure 26

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