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Biotic and abiotic drivers of barnacle recruitment along a sub-Arctic intertidal rocky shore

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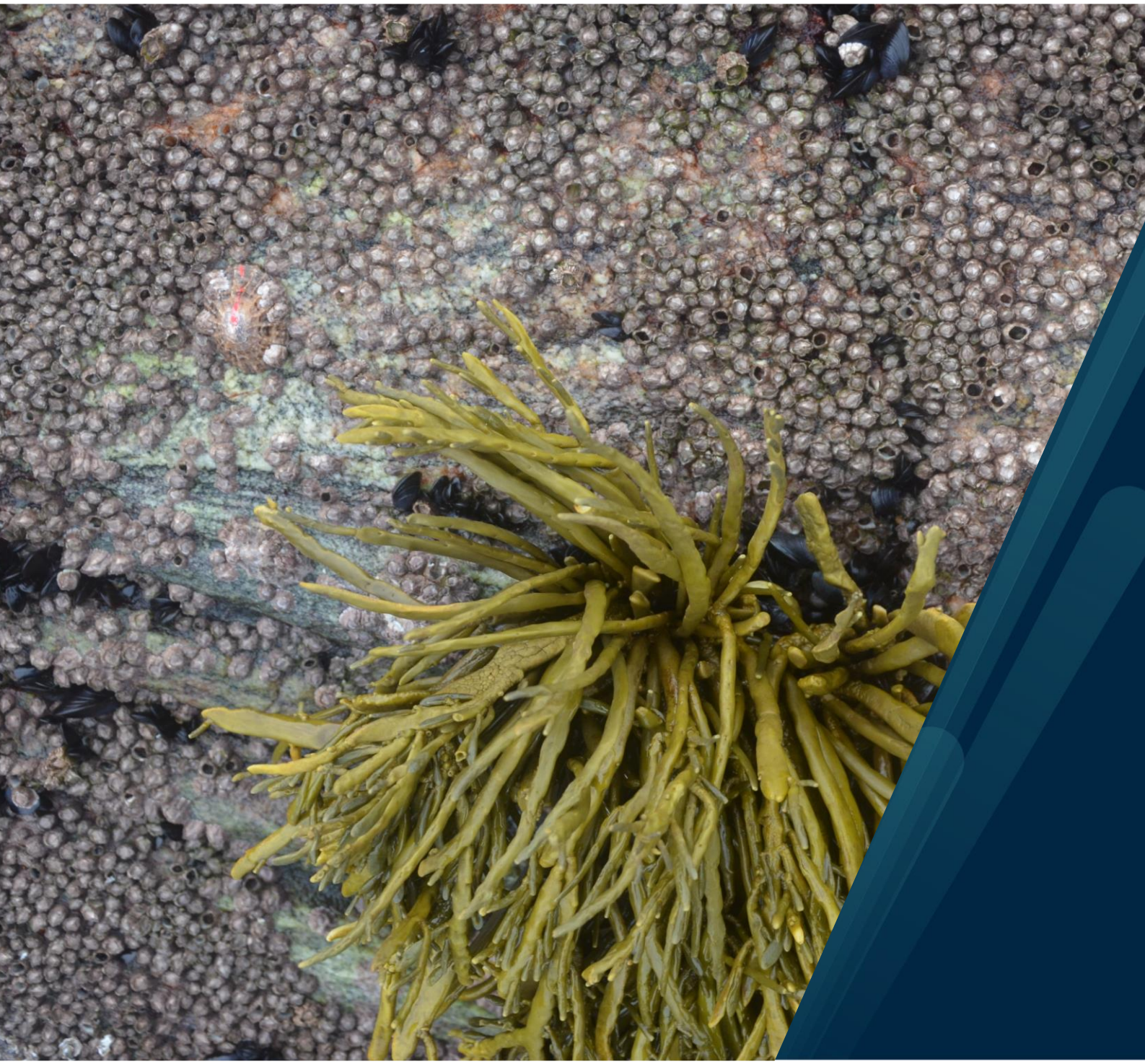

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ABSTRACT

Most marine ecological research in the Arctic has focused on open water ecosystems, while coastal ecosystems are systematically under-studied. However, Arctic near-shore ecosystems are highly stressed environments and play a major role in biogeochemical cycling (e.g., nutrient input from thawing permafrost). Furthermore, the Arctic region has extreme environmental conditions which are expected to be stronger modified by climate change than most other regions on earth. Ecological models state connections between environmental stress and the relative importance of species interaction regulating ecological communities. Many studies testing environmental stress models have been conducted on rocky intertidal shores of the temperate zones, which are commonly inhabited by sessile invertebrates, such as mussels and barnacles, slow moving predators, such as dogwhelks and limpets, and canopy-forming macroalgae. These studies showed, for instance, that barnacle (*Semibalanus balanoides*) settlement and recruitment are negatively affected by seaweed canopy whiplash and limpet bulldozing and also vary over small spatial scale with shore height due to strong desiccation gradients. However, canopies can also benefit both limpets and barnacles, providing a microclimate with reduced desiccation effects. The empirical evidence of those studies from temperate regions, may, however, not be applicable to the Arctic intertidal. This study focusses on the limpet-seaweed-barnacle interactions in the Arctic intertidal zone, as a highly stressful environment for which information on species interactions is extremely limited.

Here, I report on: (1) the effect of shore height on barnacle (*S. balanoides*) settlement success and recruit density in relation to the effect of seaweed (*Ascophyllum nodosum*) canopy presence and (2) the separate and combined effects of the presence of seaweed (*A. nodosum*) canopy and, limpets (*Patella vulgata*), on the density of barnacle cyprids, recruits and adults.

This experimental study was performed along the intertidal coast of Kvaløya island, Tromsø, northern Norway. The samples were collected from the intertidal zone that range about 1.84 m in coastal height. The study is composed of two experiments that were conducted both using a randomized-block design. Both experiments study the effects of biotic and abiotic drivers on barnacle adult, recruit, and settlement density.

The results showed that barnacle cyprids and recruits were highly negatively affected by desiccation, being merely present at high-shore zones. Moreover, seaweed-canopy had a large negative effect on barnacle density while the limpet effect was relatively small. The combined

effects of canopy whiplash and limpet bulldozing suggest an additive effect on barnacle density. These results indicate that the presence of an algal canopy does not enhance limpet performance (e.g., grazing activity) to add extra pressure on barnacle survival. This study shows that the functional role of intertidal organisms such as canopy-forming macroalgae may be expressed differently in high latitudinal intertidal communities than what could be inferred from studies done on temperate zone.

Keywords: Arctic, rocky intertidal; *Semibalanus balanoides;* algal whiplash; bulldozing; desiccation; multiplicative effect, limpets, species interactions, benthic.

1. INTRODUCTION

1.1 Arctic and temperate coastal conditions

Coastal Arctic ecosystems have a critical role in Arctic biogeochemical cycling (Fritz et al., 2017). However, these systems are systematically under-studied since most marine biological experimental research in high latitudes is limited to ship-based research on pelagic ecosystems (Fritz et al., 2017; Thyrring & Peck, 2021). Moreover, the few coastal studies done in Arctic regions are mainly observational studies which lack experimental results (Poore et al., 2012; Thyrring & Peck, 2021). Therefore, manipulative experiments are needed for a better understanding of the biogeochemical processes and interactions taking place in coastal ecosystems. On top of that, the study of these ecosystems is crucial as the Arctic region has one of the strongest variations in climate where rising temperatures have been documented (IPCC, 2022).

The ecology of the Arctic coastal regions is not comparable to temperate zones, where most ecological studies have been performed. Coastal zones in Arctic environments are regulated by a highly seasonal solar radiation controlling primary production and atmospheric conditions such as temperature (Gili & Petraitis, 2009). Moreover, the low water temperatures, usually not higher than 12 °C (Drinkwater & Kristiansen, 2018) and highly variable air temperatures (Freiwald, 1998), ranging from -7 °C to 27 °C (*in situ* temperature recorded with HOBO UA-002-64 Pendant Temp/Light data loggers during the field experiments for this thesis) have strong effects on coastal Arctic ecology.

The intertidal zone is generally characterized as challenging for organisms to live in. Firstly, intertidal zones are high stress environments that are exposed to wave action coming from storms in the open ocean and freshwater run-offs from rivers that can also alter salinity concentrations (Høgslund et al., 2014). Moreover, this ecosystem is exposed to strong changes in air and sea surface temperatures (Høgslund et al., 2014).

The Arctic intertidal zone presents extreme environmental conditions such as ice-scouring, freezing of the intertidal substrate during low tide and large amount of freshwater from snow melting (Høgslund et al., 2014). The impact of climate change on Arctic marine ecosystems also enhances the loss of sea ice, replacement of sea ice by open water and the rise of sea-level (Deb & Bailey, 2023). In consequence, coastal ecosystems can suffer strong changes in the structure and function of the ecosystems, impacts on species phenology and trophic

interactions, increase of invasive species or/and shift in species distribution and abundance (Deb & Bailey, 2023). These abiotic pressures are very low or missing in temperate zones, where most of the intertidal experiment research has been done. Therefore, the Arctic intertidal zone may be one of the most stressful habitats for marine biota.

Moreover, a study showed latitudinal variation in the number of predators in the intertidal zone with low predator diversity in higher latitude communities (60 – 85 ˚N; Thyrring & Peck, 2021). The lower redundancy of predator's ecological functions in Arctic regions can make them very vulnerable to changes in the ecosystem as there are few species that are able to compensate with similar functions (Thyrring & Peck, 2021).

1.2 Intertidal community regulation in the stressful Arctic environment

Ecological theory states connections between environmental stress and the relative importance of species interactions regulating ecological communities. An early study revealed differences in intertidal ecological regulations depending on the levels of environmental stress (Menge, 1976). Under high stress, communities were mainly influenced by intraspecific competition and environmental stressors including wave exposure and desiccation whereas predation and interspecific competition had no notable effect (Menge, 1976). A further study led to a foundational environmental stress model (ESM) based on the assumption that the relative importance of consumer control decreases with increasing physical stress (Menge & Sutherland, 1987). There are many examples of experimental studies showing the effect of physical stress on consumer control. In marine environments, for example, predation rates by gastropods on oyster spat are reduced at high stress levels due to changes in temperature and salinity (Garton & Stickle, 1980).

Contrarily, the Menge and Olson model (1990) predicts that physical stress could increase consumer control. This model suggests a synergistic effect in the relative importance of physical stress on consumer control if the reduction in prey is greater when consumers and physical stress are both present than when they act alone (Silliman & He, 2018). For example, in salt marshes, droughts can decrease plant quality and, therefore, increase susceptivity to snail grazing ultimately limiting the plant population (Silliman & He, 2018). In addition, this contraposition will lower the possibility to extrapolate results from temperate to Arctic regions.

The ESM model was later modified by inclusion of facilitation (Figure 1A) (Bruno et al., 2003). In high stress environments, Bruno et al. (2003) states that abiotic stress will be less strong due to positive interactions (Figure 1A). Facilitation also includes stress amelioration by neighboring species, which is precited to reduce the effect of physical stress (Bruno et al., 2003) (Figure 1B). For example, at high elevations, terrestrial plants coexistence is favored since less interspecific competition takes place (Callaway et al., 2002). Plant species act as competitors at low stress levels but they act as compliances at high stress levels due to stress amelioration (Callaway et al., 2002). Another example in coastal environments showed that intertidal macroalgal canopies enable organisms to survive by providing a temperature stable area preventing external physiological stress by extreme temperature conditions (Bruno et al., 2003). A study done in Nova Scotia, Canada showed that bladder wreck (*Ascophyllum nodosum)* canopies can protect understory organisms from cold air temperatures during winter since understory air temperature below the canopy was circa 1 °C higher than air temperature next to the canopies (Scrosati & Ellrich, 2018). Another example observed in the Gulf of Maine, USA indicated that *A. nodosum* canopies reduced substrate temperature during summer by 5° – 10 °C less under the canopy than in canopy free areas (Bertness et al., 1999).

Both stress amelioration reducing stress conditions and facilitation as positive species interactions, will most likely affect prey and predator differently and in a species-specific manner under different levels of stress. To that end, more experiments are needed to understand the underlying mechanics of the interactions and community regulations (Figure 1).

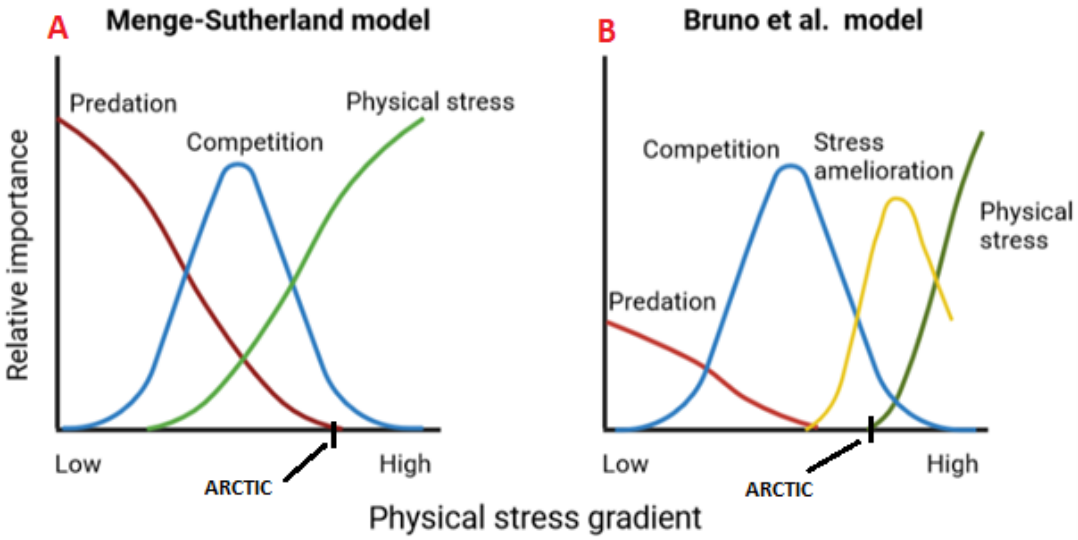

Figure 1. Graphical representation of the ecological models representing environmental stress and the relative importance of species interaction regulating ecological communities. (A) Menge-Shutherland model (1987) (ESM). (B) ESM model of Bruno et al. (2003) including facilitation.

1.3 Barnacle (*Semibalanus balanoides*) ecological functions

In mid and low intertidal zones, seaweed (*A. nodosum)* can act as a stress amelioration organism. During low tides on sheltered shores, *A. nodosum* canopies lie flat on the substrate, limiting understory water loss and temperature variability (Beermann et al., 2013). The north Atlantic rocky intertidal shores are mostly occupied by barnacles of the species *Semibalanus balanoides* (Jenkins et al., 2008; Santini et al., 2019). This species is very sensitive to water loss and, in the upper intertidal zone, they are exposed to extreme conditions limiting their survival (Bertness, 1989). The upper shore limits for *S. balanoides* are determined by physical stress (Wethey, 1984). At high temperatures, the intolerance of heat stress and desiccation restrict *S. balanoides* distribution to shaded environments (Wethey, 1984; Jones et al., 2012). Canopies can regulate *S. balanoides* settlement and recruitment offering a protecting environment reducing the effects of high temperature and desiccation (Hawkins, 1983; Beermann et al., 2013).

Limpets, like *Patella vulgata*, are also highly affected by heat stress and desiccation in the intertidal zone (Moreira et al., 2021). Therefore, *A. nodosum* presence can also benefit them by providing a microclimate with less exposure to extreme temperatures (Davies et al., 2008). Moreover, limpets may be attracted to barnacle-free spaces under canopies to feed on the early life stages of canopy-forming seaweeds (Hawkins, 1983; Davies et al., 2008). Adult limpets also have a strong resistance against canopy whiplash effects as they have solid attachment to resist higher forces in comparison to *S. balanoides* (Delroisse et al., 2023). Limpet attachment to the substrate protects from strong negative environmental forces, mostly from wave action (Delroisse et al., 2023). Therefore, whiplash effect should not influence limpet survival.

Patella vulgata is also known to be a homing species, a crucial ability to move around while feeding and return to the same location to settle (Russell, 1907; Funke, 1968; Hartnoll & Wright, 1977). The presence of homing or non-homing limpet species would have different consequences for barnacle survival. Non-homing limpets are less active, mostly settle and feed in lower intertidal areas (Underwood, 1977). Therefore, non-homing limpets would have lower impact on barnacle survival during their grazing activities. Homing behavior should increase direct (feeding on diatoms and algae propagules) and indirect (bulldozing) effects in and around their homesite and, in consequence, enhance patchiness of species that get directly or indirectly affected by limpets. The pattern that we see around *A. nodosum* is an example of patchiness as the “barnacle carpet” gets locally interrupted.

Both homing and non-homing behaviors depend on habitat, tidal range, and local food availability among other conditions (Nuñez et al., 2014). For example, dominance of the substrate by *S. balanoides* adults could impede limpets' ability to adhere to the substratum and therefore resist the detachment by predators or wave action (Santini et al., 2019) (Figure 2).

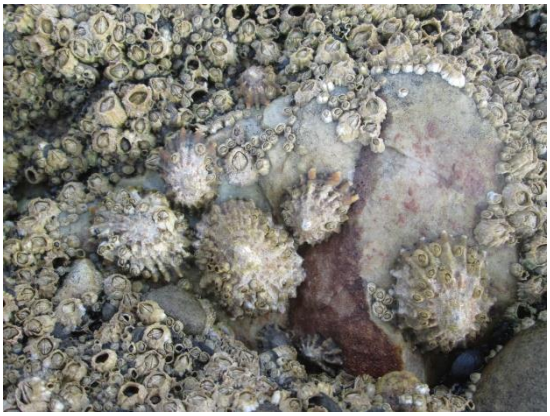

Figure 2. *Patella vulgata* surrounded by *S. balanoides*. Ireland 25 August 2018. Photo credit: Julius Ellrich.

Limpets can also directly limit barnacle settlement and recruitment (Ellrich et al., 2020). During grazing activities, limpets can detach cyprids and bulldoze small barnacles settled on the rocks (Menge et al., 2010; Ellrich et al., 2020). Bulldozing is defined as the removal of barnacles cyprids and recruits by the limpet shell edges while grazing over hard substrates (Dayton, 1971). Limpet bulldozing effects have been widely studied in temperate regions showing strong negative effects on barnacle survival (Dayton, 1971; Paine, 1981; Farrel, 1988; Miller & Carefoot, 1989; Farrel, 1991; Menge et al., 2010). The results of these studies could be applied as a comparative between limpet bulldozing effects in Arctic and temperate regions. A study done by Hawkins et al. (1989) found barnacle shell pieces in limpet (*P. vulgata)* guts implying strong bulldozing effects. Moreover, where canopy-forming algae ameliorate heat stress, limpets are able to move higher on the shore and extend their grazing range more into the barnacle zone and hence expand their bulldozing range (Davies et al., 2008).

Figure 3. Whiplash effect showed as an empty "patch" created by *A. nodosum* in a substrate dominate by barnacles. Kvaløya island, Tromsø. May 2022. Photo credit: Marta Prieto.

Semibalanus balanoides are also highly affected by whiplash. During high tides, *A. nodosum* is swung by water motion hitting the substrate repeatedly (Beermann et al., 2013). This whiplash effect has a negative effect on *S. balanoides* settlement and recruitment detaching settling barnacles from the substrate (Beermann et al., 2013). This effect can be observed in many studies done in temperate intertidal shores like New England, USA and Nova Scotia, Canada (Bertness, 1998; Scrosati,

2021). Both studies showed the substrate fully covered by barnacles recruits while they were mostly absent creating an empty "patch" around the canopy (Bertness, 1998; Scrosati, 2021) (Figure 3). The relative contribution of positive (moist microclimate) and negative (whiplash) effects that canopies have on barnacles may be dependent on size and morphology of the canopy as well as the amount of stress and variation of tidal and climate the barnacles are exposed to (Alam & Noda, 2016). Along northern Norwegian shores, with high physical stress conditions and on wave-exposed shores, where my experiment was set up, canopy whiplash should have stronger effects than the regulation of water loss and temperature amelioration (Beermann et al., 2013).

Moreover, *S. balanoides* larvae settle in microhabitats that are already colonized by adults and on the bases of detached adults (Wethey, 1984; Chabot & Bourget, 1988). A positive relationship adult-recruit barnacles have been recorded (Scrosati & Ellrich, 2017) as larvae are chemically and visually attracted to adults (Gabbott & Larman, 2018; Elbourne & Clare, 2010; Matsumura & Qian, 2014). The presence of adult barnacle suggests higher food supply and an adequate area for growth and reproduction (Rodriguez et al., 1993; Clare, 2011). In consequence, the scarce presence of barnacles below canopies and its conspecific settlement behavior lead to enhanced low abundance of barnacles under canopies and, thus, limpets.

As a result of limpets benefitting stronger from seaweed canopy cover than barnacles in combination with limpet homing behavior, I expect multiplicative effects of canopy and limpets on barnacle abundance. This synergism should be reinforced by the gregarious settlement behavior of barnacles, as few barnacles will attract fewer conspecific larvae, while patches with high barnacle abundance should strongly stimulate settlement of conspecific larvae.

1.4 Knowledge gaps and aims of the study

Multiplicative effects of *P. vulgata* and *A. nodosum* on *S. balanoides* abundance are therefore very likely but have not been examined. More research is needed to better understand the ecology of coastal ecosystems. Moreover, if we want to mitigate the effects of climate change on coastal ecosystems, it would be crucial to focus research on the Arctic as climate change is predicted to have stronger effects on the Arctic than on temperate ecosystems.

The objective of this study is to increase our mechanistic understanding of patterns at high latitude shores using the above-described limpet-seaweed canopy-barnacle system, for which only evidence from temperate shores exists. Therefore, I predict that:

Experiment 1: The relative effect of shore height in barnacle (*S. balanoides*) settlement and recruitment density is higher compared to the seaweed canopy (*A. nodosum)* relative effect (Figure 4).

Experiment 2:

- Barnacle (*S. balanoides*) recruitment success depends on seaweed (*A. nodosum*) canopy presence and limpet bulldozing (Figure 5).
- Seaweed (*A. nodosum)* canopy presence and limpet bulldozing have a multiplicative effect on barnacle (*S. balanoides*) recruitment (Figure 5).

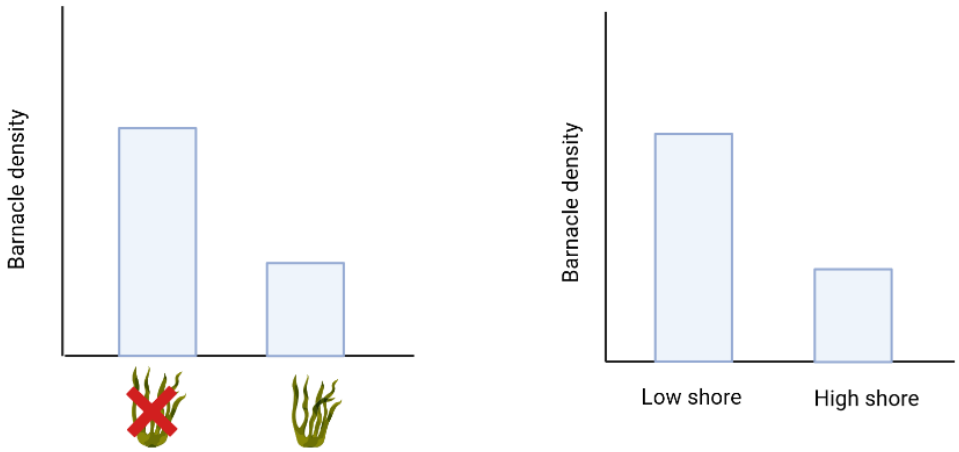

Figure 4. Representation of the hypothesis tested by Experiment 1. On the left, *S. balanoides* density would be higher in *A. nodosum* absence. On the right, barnacle density would be higher low on the shore than higher on the shore.

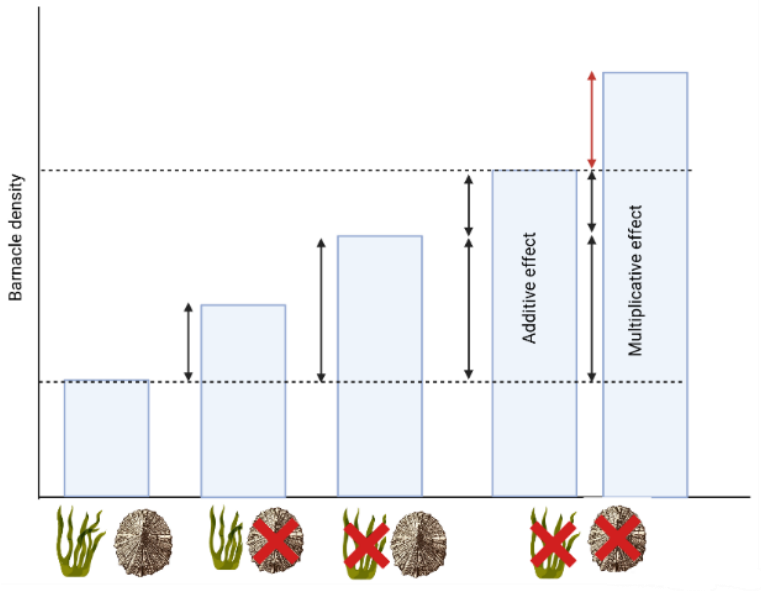

Figure 5. Representation of hypothesis tested by experiment 2. Barnacle density would be negatively affected by presence of *A. nodosum* and *P. vulgata* (additive effect represented with black arrows). Its combination would have a multiplicative effect (red arrow).

2. MATERIAL AND METHODS

2.1 Experimental site

The experiment was performed along the intertidal coastal area of Kvaløya island, Tromsø, northern Norway (69°37'28.6¨N, 18°07'54.1¨E), a wave-exposed rocky shoreline of the Norwegian Sea (north Atlantic) formed by granite and granodiorite bedrocks and boulders (Migała et al., 2016; Oug, 2001).

The samples were collected from the intertidal zone that range about 1.84 m in coastal height (Carpman & Thomas, 2016). Differences in tidal ranges regulate community structures, forcing organisms to adapt to high changes in temperature, salinity, and moisture (Haarpaintner & Davids, 2020). Lower on the shore, we can encounter mainly macroalgae, particularly winged kelp (*Alaria esculenta*), toothed wrack (*Fucus serratus*) and oarweed (*Laminaria digitata)* (Haarpaintner & Davids, 2020). The intertidal area exposed and submerged roughly the same amount of time is dominated by barnacles of the species *Semibalanus balanoides* and molluscs such as common blue mussels (*Mytilus edulis*) and common limpets (*Patella vulgata*). Knotted wrack (*Ascophyllum nodosum)* and wrack siphon weed (*Vertebrata lanosa)* seaweeds are also highly present. In the higher intertidal zone, exposed to the air for most of the time, the main community is based on barnacles of the species *S. balanoides*.

I used three temperatures loggers ("HOBO UA-002-64 Pendant Temp/Light, Onset Computer, Bourne, Massachusetts, USA") to record the temperature from June 2021 to October 2022. The loggers were attached at three different shore heights (same as experimental set ups): low intertidal at 78 cm, mid intertidal at 133 cm, and high intertidal at 218 cm considering the chart datum as low tide. Each height was measured using a scaled stick painted with 25 coloured spaces of 5 cm each. The stick was set at the low tide and with a telescope fixed next to each logger, I spotted the number of spaces, and therefore of cm, from the low tide to the loggers (Figure 6).

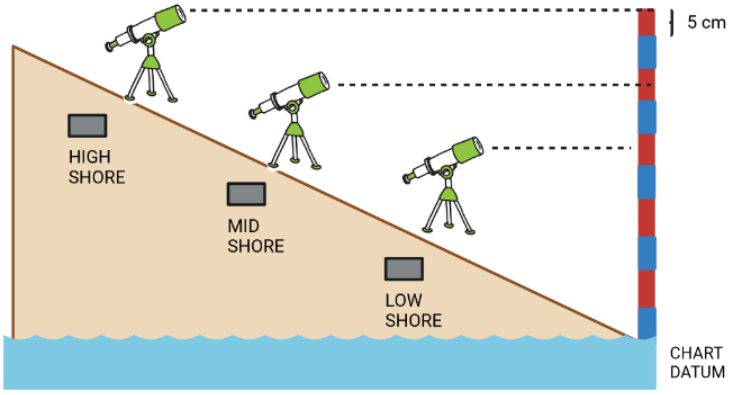

Figure 6. Representation of the measurements done to determine shore heights in the study system. I used a 100 cm scaled stick of 5 cm painted in red and blue.

Temperature during the study ranged from 1 °C to 23 °C, in the low intertidal zone, from -3 °C to 27 °C in the mid intertidal zone, and from -7 °C to 30 °C in the high intertidal zone. The experiments were set up in the mid intertidal zone which had a mean temperature of 10.18 °C. Moreover, differences between seasons were not extreme, having a mean temperature of 11 °C in summer (1st of June to 1st of October 2022) and a mean temperature of 7 °C in winter (2nd of October to 31st of May 2022). As a high latitude area, there is a strong light seasonality with a dark period called "Polar Night" during the winter and a light period when the sun does not set in the summertime (Freiwald, 1998). Considering the low position of the sun at this high latitude, the UV radiations fluence rates do not exceed approximately 107 W m^{-2}, the highest value measured at Andøya in 2017 (Svendby et al., 2018).

Semibalanus balanoides are distributed along the Atlantic and Pacific waters, from temperate to boreo-arctic intertidal shores (Crickenberger & Wethey, 2018). Settlement timing of *S. balanoides* as one of the most abundant intertidal species varies depending on the latitude, adapting to different temperature rages (Lewis, 1986). There is seemingly no information about settlement timing for *S. balanoides* in northern Norway. However, similar latitudes can be used to describe their breeding and settlement times.

In Greenland and Svalbard, *S. balanoides* releases its larvae during winter/spring, coinciding with high food source availability (phytoplankton blooms) (Davenport et al., 2005; Meyer et al., 2017). The nauplii (first larvae stage) develop in the sea between February and April (later in higher latitude areas) and settle as juvenile cyprids in May/June (King et al., 1993; Meyer et al., 2017). During late spring and summer, the development of boreal barnacles (high latitude barnacles) is dependent on the temperature and shore height settlement. Elevated temperatures and decrease of sea exposure submergence on higher shores give rise to desiccation and death (Meyer et al., 2017). *Semibalanus balanoid*es is also considered a fast-growing, poor competitive colonizer that occupies rapidly the intertidal zone just after the colonization by bacteria and diatoms, that are usually a pre-requisite for its settlement (Meyer et al., 2017). Settlement is defined as the planktonic larvae organisms that set up permanently in contact with the substrate (Jenkins et al., 2000) while recruits are considered as the metamorphosed individuals after the settlement season that have reached an arbitrary size (Cole et al., 2011). The transformation from cyprid to recruit takes around one or two days, determined by the species and environmental conditions (Cole et al., 2011; Connell, 1961; Jarrett, 2000). However, its development is dependent on biological and abiotic factors like temperature variations, presence of macroalgae canopy or presence of competitors such as limpets (Ellrich

et al., 2020). *Semibalanus balanoides* recruitment can also be affected by extreme temperatures, food supply and intraspecific interactions (Bertness, 1989; Ellrich et al., 2016).

Patella vulgata achieve sexual maturity around nine months of age. The eggs develop from pelagically, with a lifespan of about two weeks, to sessile organisms settled on the shore (Fretter & Graham, 1976; Fretter & Graham, 1994). Spawning and settlement seasons fluctuate depending on years and localities. Breeding time can start in December in southern areas like Portugal (Bowman & Lewis, 1986) to July/August in its highest limit distribution latitude (Tromsø) (Bowman & Lewis, 1986). During the early months of the year and in higher latitudes year-round, sea and air temperatures are low, which limits limpet growth (Blackmore, 1969; Bowman & Lewis, 1986).

Patella vulgata is the dominant grazer species in mid-intertidal zones of northern Europe and is distributed across the intertidal zone (Jenkins & Hartnoll, 2001). *Patella vulgata* regulates the recruitment of macroalgae (*A. nodosum*) by feeding on its early stages as well as on microalgae, cyanobacteria, and diatoms (Jenkins & Hartnoll, 2001). During grazing activities, *P. vulgata* can destroy *S. balanoides* cyprids and bulldoze small barnacles settled on the rocks (Trueman & Clarke, 1985). Limpets are also known to be a homing species, a crucial ability to forage for the algae they feed on and at the same time have a home site where the shell can adjust the delineation of the rock. Limpets depend on the exactness match to the floor to avoid desiccation (Hartnoll & Wright, 1977).

Ascophyllum nodosum seaweed (Figure 8) is common on the rocky intertidal shores along the north Atlantic. This macroalgae has a short reproduction period of around two weeks during the late spring/early summer (Pereira et al., 2020). The exact time of reproductive maturation of the canopy is dependent on water conditions: strong wave actions can reduce *A. nodosum* recruitment success (Pereira et al., 2020). Northern *A. nodosum* populations appear restricted to a narrow shore-line in the mid intertidal zone (Figure 7) (Viana et al., 2014).

Ascophyllum nodosum has been shown to have impacts on the intertidal community regulating factors such as temperature levels, irradiance, or water loss. By lying on the substrate during low tides, *A. nodosum* shades the habitat below maintaining stable temperatures and preventing other species from desiccation (Watt & Scrosati, 2013). My study presented relatively big seaweed *A. nodosum* canopies of approximately 23 cm length and 400 g of weight (data measure in the laboratory at the start of the experiment set up).

Ascophyllum nodosum can also be a host of a complex group of species, including the ascomycete *Mycophycias ascophylli* and the red algae *Vertebrata lanosa* that can also be a host of other red algae parasites (Garbary et al., 2005).

Figure 8. Individual of *A. nodosum* attached to the substrate. Kvaløya island, Tromsø. November 2022. Photo credit: Marta Prieto.

Figure 7. *Ascophyllum nodosum* population distributed in a narrow area of the intertidal shore. Kvaløya island, Tromsø. November 2022. Photo credit: Marta Prieto.

2.2 Experimental design

This study is composed of two experiments that were both ran using a randomized-block design. Both experiments study the effects of abiotic and biotic drivers on *S. balanoides* adults, recruit and settlement density termed as *S. balanoides* response. Adults of *S. balanoides* were defined as individuals settled before 2022 and grown-up recruits of 2022. (1) The first experiment called "Settlement panel experiment" tests two factors: Effects of height (high and low) and, at low-shore, effects of *A. nodosum* (presence and absence) on S. *balanoides* response. (2) The second experiment, called "Removal experiment", tests for the effect of the presence and absence of *A. nodosum* and/or *P. vulgata* on the S. *balanoides* response.

2.2.1 Settlement panel experiment (Figure 9)

To test separately for the effects of shore height or *A. nodosum* presence on *S. balanoides* response, settlement panels (Figure 9) were fixed in two randomly selected areas (= blocks) in the intertidal zone, at the study site. To assess the effects of shore height, each shore was set with five replicate plots with two treatment levels for shore height (high and low). Each plot included a permanent panel to quantify recruit density and one replicate panel (= experimental unit; EU) to assess short-term barnacle settlements (monthly panels). To assess the effects of

canopy presence, the same blocks were set with five replicate plots with two treatment levels for canopy (presence and absence) at low level of shore height. Each plot also includes a permanent panel and one replicant as monthly panel. Settlement panels experiment has a total of 60 EUs.

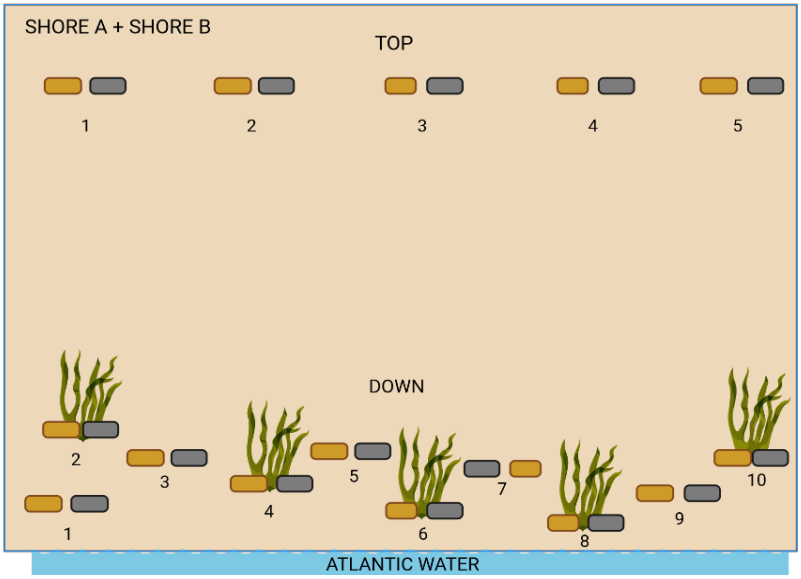

Figure 9. Representation of the Settlement panel experiment where it's analysed the difference between shore height (TOP vs DOWN) and presence/absence of *A. nodosum* (DOWN) on *S. balanoides* density.

2.2.2 Removal experiment (Figure 10)

To study the effect of canopy (*A. nodosum)* and limpets (*P. vulgata*) presence on *S. balanoides* response, four blocks were set up in randomly selected areas. Each block examined the effects of *A. nodosum* presence (fixed factor, two levels: canopy present or removed) and limpet presence (fixed factor, two levels: limpets present or removed) in a fully orthogonal design with three replicates per treatment level (total of 48 EUs).

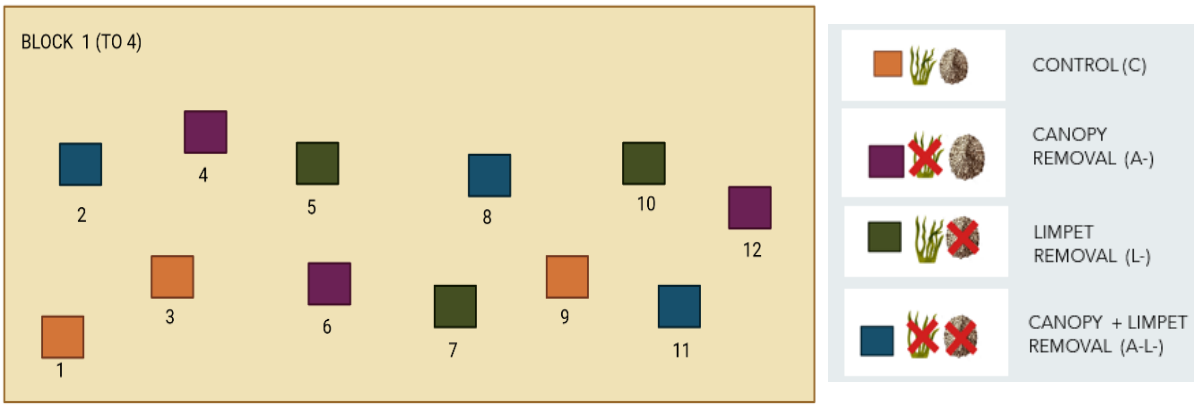

Figure 10. Representation of the Removal experiment where three different treatments (squares coloured) where applied to the four different shores (=blocks) to study *S. balanoides* density.

2.3 Set up

The two field experiments were ran from 21st of March to 28th of October 2022.

2.3.1 Settlement panel experiment

The two shores (= blocks) each covered a circa 10 m, wide stretch of the intertidal zone and were separated from each other by about 20 m. Shore height of the two plot positions (high and low) was measured by defining low tide as chart datum in the same way as for the temperature loggers (see "Experimental site" above). Low shore was defined as 1.1 m above low tide and high shore as 2.5 m above low tide.

Settlement panels were assembled using rectangular plastic panels of around 10 cm × 3.5 cm × 0.5 cm (L × W × H). The panel surfaces were covered by adhesive sandpaper (Permastik self-adhesive anti-skid safety tread; RCR International, Boucherville; Quebec, Canada) of the same sizes. Settlement panels (Figure 11) were attached to the rocks using an electric screwdriver. Monthly panels were replaced approximately every month, while permanent panels were deployed throughout the whole experiment. Both monthly and permanent panels were used to quantify and compare the difference in *S. balanoides* recruitment and settlement success over time.

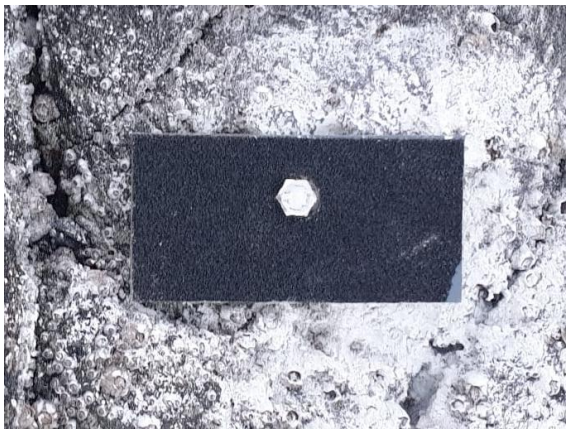

Figure 11. Settlement panel screwed to the shore substrate. Kvaløya island, Tromsø. October 2022. Photo credit: Marta Prieto.

2.3.2 Removal experiment

The experiment consisted of four blocks of approximately 11 m length, positioned at the same shoreline of 1.7 m height from the low tide. Mean block distance to each other was around 21 m. In each block, plots were placed with four different conditions: (1) Removing *A. nodosum*, (2) removing limpets (*P. vulgata*), both using a metal spatula to scratch between the rocks and the individual, (3) removing both species, and (4) as a control with no manipulations. Plots were separated to each other by at least 50 cm. To identify each condition in the field, every plot was marked with a small white plastic panel with the information of the plot (type of treatment, position, block, and treatment repetition number) written on it. Each plot also presented one permanent settlement panel to quantify the number of cyprids and recruits in each treatment.

In some random plots, wax tablets were added to study the movements of *P. vulgata* by analysing the scratch marks left on them. Wax tables were made in the laboratory before the field trips using liquid wax introduced in small round plastic containers of around 1 cm of diameter. In the field, a drill with the similar height and diameter of the tablet was used to create a hole where the tablet was fixed. To prevent its loss by wave exposure, small pieces of straw were placed around the space left between the rock and the tablet (Figure 12).

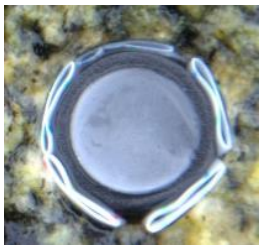

Figure 12. A wax tablet held by straw pieces set on the substrate. Kvaløya island, Tromsø. October 2022. Photo credit: Marta Prieto.

2.4 *Semibalanus balanoides* treatments

Three different effects on *S. balanoides* were studied in the experiments: (1) Shore height effect between low-shore defined as 1.1 m above and high shore defined as 2.5 m from above low tide. (2) Effect of *A. nodosum* canopy presence and (3) effect of *A. nodosum* and/or limpet *P. vulgata* presence on *S. balanoides* response.

Ascophyllum nodosum abundance was measured in the field for every treatment. Each plot was photographed inside a frame (50 cm × 50 cm) at the beginning of the experiment before applying any treatments. All the pictures were analyse using an image analysis software (ImageJ version 2.9.0/1.53t) that calculates the abundance of the macroalgae (as percentage) inside the frame for each plot. Wax tablets collected from the field were also analysed. The first step was using graphite powder to cover a thin layer on its surface. Then, using a stereo microscope (Leica MZ12), pictures of the wax tablets (Figure 13) were taken and analysed using the aforementioned image analysis software to obtain the area of scratches on each wax tablet. Apart from that, to maintain the absence of limpets in the specific treatments, approximately every month since the experiment settlement, all the limpets inside and around the plot were removed by hand using a metal spatula.

Figure 13. Scratches done by *P. vulgata* on a wax tablet while it was placed in the shore. The picture was taken using a stereo microscope (Leica MZ12). UiT Benthos laboratory, January 2023. Photo credit: Marta Prieto.

2.5 *Semibalanus balanoides* response

This study analysed *S. balanoides* recruit, settlement and adult density (*S. balanoides* response) under different biotic and abiotic contiditions over an eight month period. A stereomicroscope was used to determine the number and stage (cryprids or recruits) of the barnacles that were established on the panels (permanent, monthly and on the removal experiment plots). Adult abundance was estimated using picture samples of a 5 cm × 5 cm grid taken in the field. Four samples per plot were taken: two pictures in the area where the canopy was present at the start of the experiment and two outside that area (Figure 14). The mean of both samples was used for the analysis. Pictures were taken every month since the beginning of the experiment. Each picture was analysed by counting the number of individuals inside the grid. The individuals were classified as adults of *S. balanoides*, alive or dead.

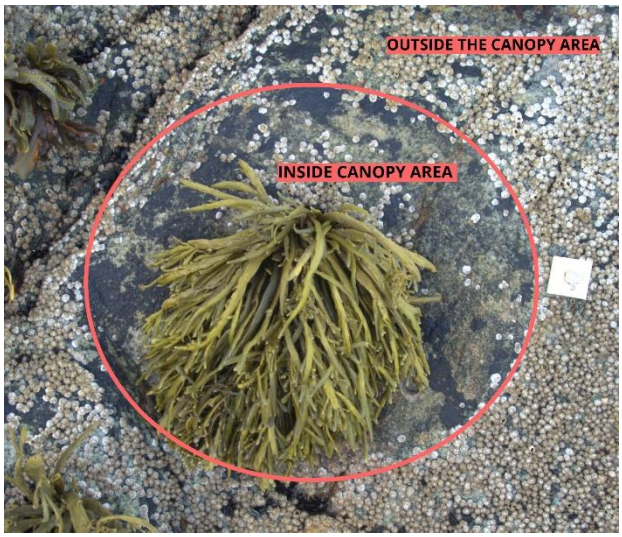

Figure 14. *Ascophyllum nodosum* whiplash effect on *S. balanoides* barnacle density showed by a "canopy area" with few barnacles, vs "outside the canopy area" as a *S. balanoides* carpet. Kvaløya island, Tromsø. October 2022. Photo credit: Marta Prieto.

2.6 Statistical analysis

All data of the study were analysed using RStudio (version 2022.12.0.0353), an open-source integrated development environment (IDE) for R programming. External RStudio packages were also downloaded for specific analysis: the "lubridate" package was used for dates and times transformations, the "readlr" package was used for reading `.csv files´, the "tidyr" package for organizing and changing the shape of the dataset and the "boot" package for plot design and editing. Moreover, the "metafor" package was used to conduct meta-analysis and the "GAP" package for the ANOVA designs. Welch two samples t-test was chosen over Student´s t-test due to the presence of heterogeneous variances (Ruxton, 2006).

2.6.1 Settlement panel experiment

The permanent panel dataset was only analysed for barnacle recruits as no cyprids has settled on them. For the monthly panels, only data from June was available on both recruits and cyprids. A Welch *t*-test was used to analyse the difference between the treatment means.

Moreover, a 2 x 2 mixed factorial ANOVA was used to study the effect of shore height/canopy in the different shores on recruit and cyprids of *S. balanoides.*

2.6.2 Removal experiment

The four different treatment effects on barnacle settlement density were explored using a 2 x 2 mixed factorial ANOVA. Calculations for different months were done to have an overview of the evolution of the treatment effect on adults of *S. balanoides.* The analysis was done in June, August, September, and October as the last month of the experiment. It analyzed the effects of the treatments on the adult barnacle density inside the canopy-affected area (Figure 14), as the ratio of adult barnacles outside and inside the canopy-affected area. As the analysis of barnacle density inside the canopy-affected area and the ratio were equivalent, the results only showed the ratio analysis. Ratio analysis includes the relative effect of outside and inside the treatment areas, and therefore, gives higher precision of the experimental site.

The analysis of settlement panels was done only in May as there were no cyprids or recruits on the panels in other months. Furthermore, to test the quality of the treatments, wax tablets grazing marks analysis, limpet abundance between the treatments and canopy percentage was analysed using Welch *t*-tests. Wax tablets were only set out and analysed in June and July while limpet presence was studied comparing the first (May) and last month (October) of the experiment duration. Percentage of algae cover was analysed before the treatments were applied in the start of the experiment set up (May). The percentage of algae covered was analysed comparing the treatments where the canopy was present or removed.

F-test of equality of variance was applied in both settlement panels and removal experiments to test for shore height effect, presence of *A. nodosum* canopy and/or limpets *P. vulgata* effect on *S. balanoides* response. The effect size was also calculated for both experiments using the logarithm response ratio (LRR) (Durlak, 2009) (1) (and presented as a forest plot for each experiment.

$$\text{LRR} = \log \frac{mean\ Treatment}{mean\ Control} \qquad (1)$$

The effect of the treatments was determined following the recommendations by Durlak (2009): > 0.2 small effect, > 0.5 medium effect and > 0.8 as a strong effect. Boxplots were done using bootstrapping 95% confidence intervals (CIs) of 1000 iterations of the dataset.

3. RESULTS

3.1 Settlement panel experiment

3.1.1 Permanent settlement panels

There were no cyprids found on any of the permanent settlement panels. Recruit density on low-shore settlement panels was, on average, 56 times higher than on high-shore settlement panels (Welch two sample *t*-test: $t_{(9)} = 5.66$, $p < 0.001$, Figure 15). There was a very strong negative effect of shore-height on *S. balanoides* recruit density (mean LRR [95% CI] = -4.03[-6.02, -2.05]), which was independent of shore location, as indicated by a non-significant Block × Shore height interaction (Table 1).

Table 1. Summary of 2×2 ANOVA run on barnacle recruits on permanent settlement panels. Shore height was defined as fix factor and Block as random factor. Pooled residuals were calculated after verifying that $\delta^2 = 0$ (not significant at $\alpha = 0.25$). Pooled residual = Shore height × Block + Residual. The denominator for calculating the mean square (MS) of each source of variance is given in the "MS den" column. Headers are degrees of freedom (df), F-ratio (F) and *p-value (p)*.

Sources of variance	df	MS	F	p	MS den
Shore height	1	0.45	0.06	0.82	Pooled
Shore height × Block	1	0.05	0.02	0.90	Residual
Block	1	0.45	0.14	0.72	Residual
Residuals	16	3.30			
Pooled residuals	18	8.56			

On low-shore settlement panels, no barnacle recruits were found in the presence of the seaweed canopy. Therefore, no calculations using the LRR were done. However, an average of 17 barnacle recruits were found in the absence of *A. nodosum*. Canopy absence had a strong positive effect on barnacle recruit density (Welch two sample *t*-test: $t_{(9)} = 5.79$, $p < 0.001$, Figure 15). The effect of canopy on barnacle recruits was also independent of shore location, as indicated by a non-significant Block × Canopy interaction (Table 2).

Table 2. Summary of 2x2 ANOVA run on barnacle recruits on permanent low-shore settlement panels. Block was defined as random factor and Canopy as fix factor. Description of the columns and calculations as in Table 1.

Sources of variance	df	MS	F	p	MS den
Canopy	1	68.45	27.94	0.03	Pooled
Block × Canopy	1	0.45	0.17	0.69	Residual
Block	1	0.45	0.17	0.69	Residual
Residuals	16	2.70			
Pooled residuals	18	2.45			

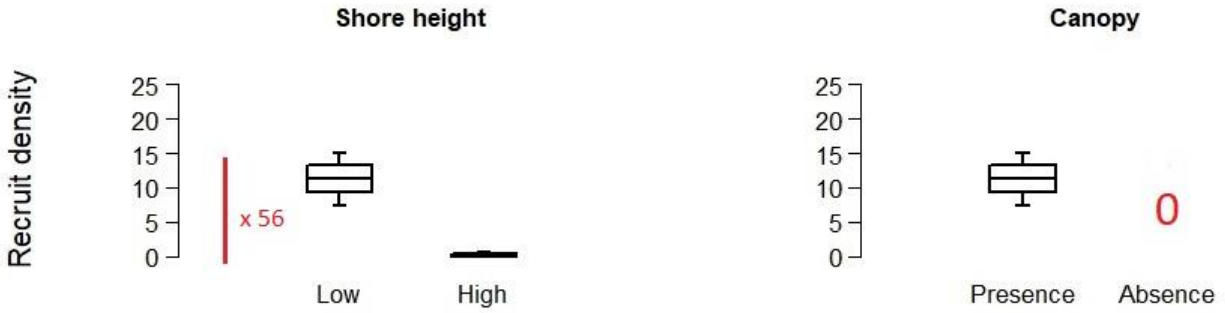

Figure 15. Boxplot showing the number of barnacle recruits of *S. balanoides* found on permanent settlement panels. Left plot difference between shore heigh (5 replicates): red number (×56) and line show the relative difference between the two treatments. Right plot comparison between presence and absence of canopy (5 replicates) on low-shore. There were no recruits found in the treatments with absence of canopy show as a 0 in the plot. The vertical whiskers described 95% bootstrapped confidence. The "boxes" are divided by a midline as the median dividing the upper and lower sizes as the 75 and 25 percentiles.

3.1.2 Monthly settlement panels

June was the only month with barnacle cyprids and recruits found on the monthly settlement panels. Shore height had a strong negative effect on both barnacle cyprid (mean LRR = - 2.15, Figure 16) and recruit density (mean LRR = - 3.26, Figure 16) of *S. balanoides*. Barnacle cyprid density on low-shore settlement panels was, on average, 10 times more than on high-shore settlement panels (Welch two sample *t*-test: $t_{(18)} = 6.21$, $p < 0.001$, Figure 17). Barnacle recruit density was also highly affected by shore height, with an average of 26 times more barnacle recruits lower than higher on the shore (Welch two sample *t*-test: $t_{(18)} = 4.46$, $p < 0.001$, Figure 17).

Lower on the shore, where the effect of *A. nodosum* was studied, barnacle cyprid density was 2.5 times higher in the absence of *A. nodosum* than in its presence (Welch two sample *t*-test: $t_{(18)} = 4.07$, $p < 0.001$, Figure 17). There was a strong negative effect of *A. nodosum* presence on barnacle cyprid density (mean LRR = - 0.96, Figure 16). Barnacle recruit density, on the other hand, was not affected by canopy presence (Welch two sample *t*-test: $t_{(17.39)} = -0.79$, $p > 0.440$, Figure 17). However, the LRR suggests a small positive effect of *A. nodosum* on barnacle recruit density (mean LRR = 0.23, Figure 16).

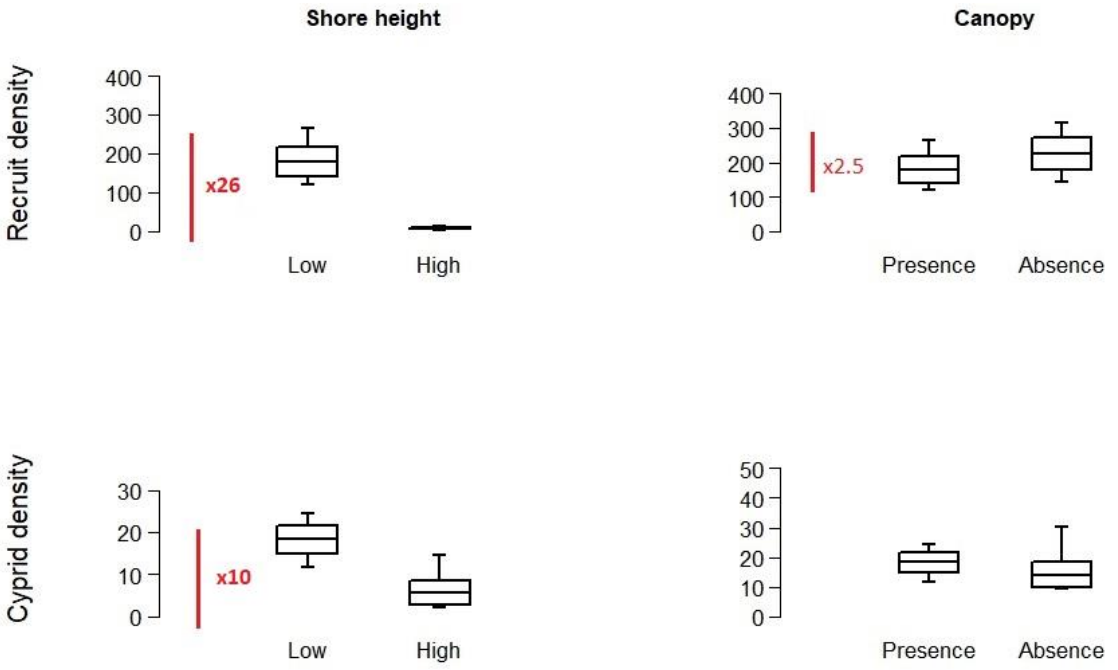

Figure 17. Barnacle recruits and cyprids density found in June: On the left, shore height effect and on the right the presence and absence of canopy *A. nodosum*. Description of the plot elements as in Figure 15.

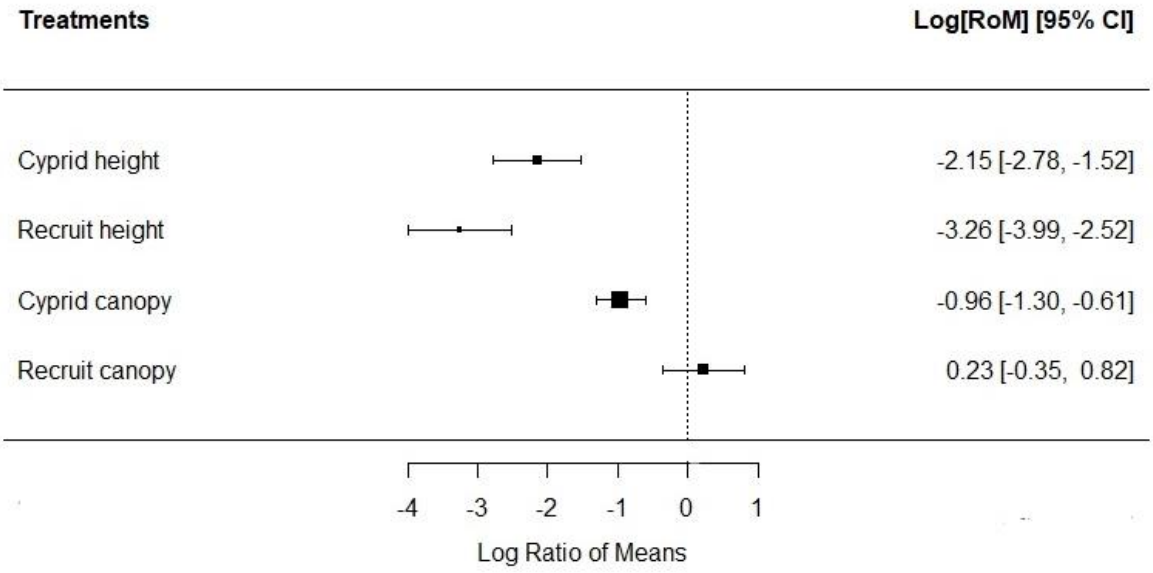

Figure 16. Effect of shore height (high vs. low) and canopy (presence vs. absence) on barnacle recruit and cyprid density in June. Each treatment is plotted as the estimate effect (box) with the 95% confidence interval (CI) displayed as the whiskers. Size of the boxes is proportional to the weight of the treatments in relation with the overall effect. Log ratio of means (Log [RoM]) and extreme values of the CI are expanded in the right column. Vertical dotted line represents the null values (Log [RoM]=1, no difference between treatments and control).

3.2 Removal experiment

3.2.1 Settlement panels

Barnacle cyprids and recruits on the settlement panels were only analyzed in May. Density of barnacle cyprids was affected by the different treatments (Table 3, Figure 18). Removal of *A. nodosum* had a strong positive effect (mean LRR = 1.21, Figure 19), with an average of 3.4 more cyprids on *A. nodosum* removal settlement panels (Figure 18). On the contrary, limpets removal had a small (mean LRR = 0.46, Figure 19) positive effect, with, on average, 1.5 times more barnacle cyprids present on settlement panels in plots where limpets had been removed (Figure 18). The combined effects of limpet and *A. nodosum* removal suggest an additive effect (mean LRR = 1.06, Fig. 5, Figure 19).

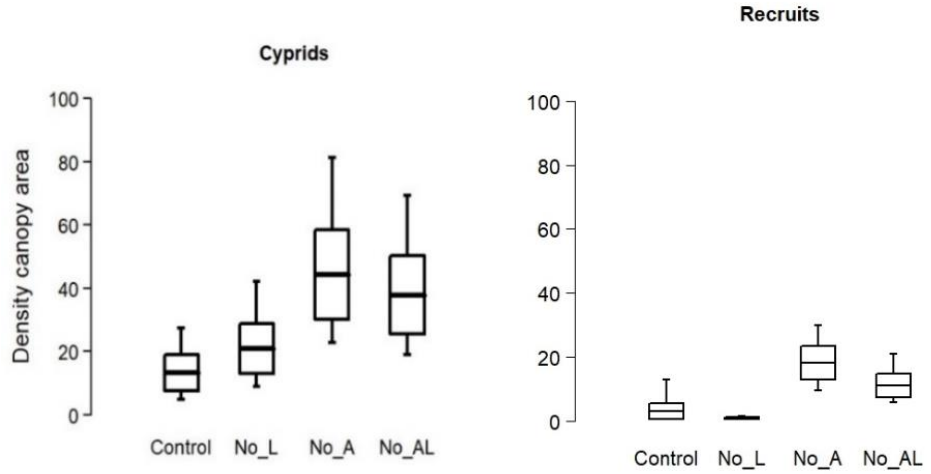

Figure 18. Differences in barnacle cyprids (left plot) and recruits (right plot) density between the control (no treatment) and the three treatments (3 replicates per treatment level) applied in May: No_L (*P. vulgata* removal), No_A (*A. nodosum* removal) and No_AL (*P. vulgata* and *A. nodosum* removal). Description of the plot elements as in Figure 15.

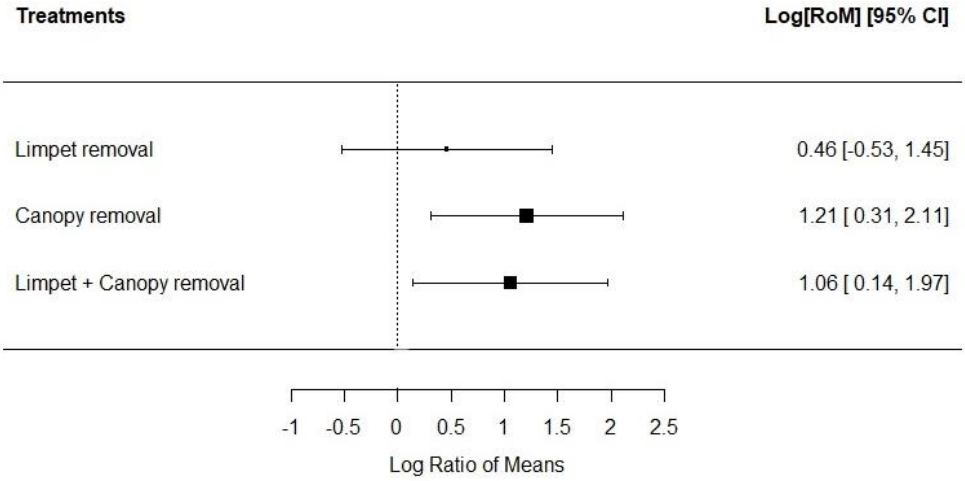

Figure 19. Effect of the three different treatments: Limpet (*P. vulgata* removal), Canopy (*A. nodosum* removal) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum* removal) on cyprids density in May after 5 weeks of panel incubation. Description of the plot elements as in Figure 16.

Barnacle recruit density was also affected by the treatments (Table 4, Figure 18). The number of barnacle recruits was strongly negatively affected by limpet removal (mean LRR = - 2.09, Figure 20) with an average of eight times less recruits on settlement panels with removal of limpets (Table 4, Figure 20). However, *A. nodosum* removal had a tiny positive effect on barnacle recruits (mean LRR = 0.09, Figure 20) with less than 1.1 times more recruits on settlement panels in plots where *A. nodosum* had been removed (Figure 18). The combination of both treatments had a small negative effect on the barnacle recruit density (mean LRR = -0.81, Figure 20, Table 4).

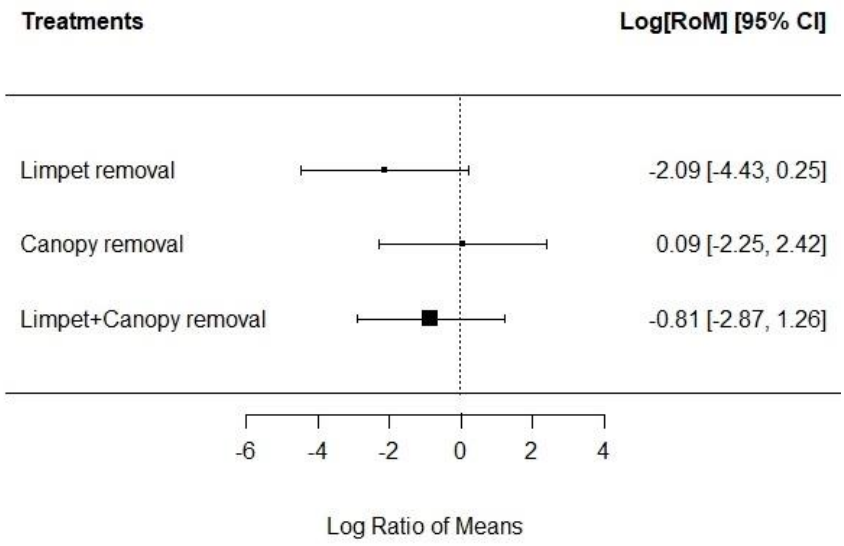

Figure 20. Effect of the three different treatments: Limpet (*P. vulgata* removal), Canopy (*A. nodosum* removal) and Limpet + Canopy (combined effect of removing *P. vulgata* and *A. nodosum*) on barnacle recruit density in May after 5 weeks of panel incubation. Description of the plot elements as in Figure 16.

A significant block effect for both barnacle cyprid (Table 3) and recruit density (Table 4) suggests that barnacle settlement and recruitment varied within the experimental site. Moreover, the effects of limpet removal on barnacle recruit density varied between blocks (significant treatment Limpet x Block interaction in (Table 4). The effect of limpet removal has a positive effect (strong in block I, III and I and very little in Block II) on barnacle recruit density (Table A1).

Table 3 Summary of 2x2 ANOVA run on barnacle cyprids set on settlement panels of the removal experiment in May. Block was defined as random factor while Limpet and Canopy as fixed factors. Description of the columns and calculations as in Table 1.

Sources of variance	df	MS	F	p	MS den
Limpet	1	20	0.07	0.934	Pooled
Canopy	1	27696	9.51	0.004	Pooled
Block	3	10511	0.02	0.021	Pooled
Limpet × Canopy	1	2394	0.82	0.370	Pooled
Limpet × Block	3	630	0.18	0.909	Residual
Canopy × Block	3	41	0.01	0.998	Residual
Limpet × Canopy × Block	3	1880	0.54	0.659	Residual
Residual	32	3493			
Pooled residual	41	2913			

Table 4. Summary of 2x2 ANOVA run on barnacle recruit density on settlement panels of the removal experiment during May. Block was defined as random factor while Limpet and Canopy as fixed factors. Description of the columns and calculations as in Table 1.

Sources of variance	df	MS	F	p	MS den
Limpet	1	204	0.72	0.45	Pooled
Canopy	1	15	0.13	0.73	Pooled
Block	3	236	1.94	0.14	Pooled
Limpet × Canopy	1	4	0.04	0.85	Pooled
Limpet × Block	3	284	2.34	0.09	Pooled
Canopy × Block	3	10	0.07	0.97	Residual
Limpet × Canopy × Block	3	6	0.04	0.98	Residual
Residual	32	142			
Pooled residual	38	122			

3.2.2 Canopy-affected area ratio (Figure 14)

Adult barnacles analyzed in October were significantly affected by the different treatments (Table 5, Figure 21). The removal of *A. nodosum* canopy had a strong positive effect (mean LRR = 1.64, Figure 22), increasing the adult barnacle density, on average, six times more than on its presence (Figure 21). Moreover, the effects of canopy removal on adult barnacle density do not vary between blocks (non-significant treatment Canopy x Block interaction in Table 5).

Removing *P. vulgata* had a relatively small (mean LRR = 0.41, Figure 22) effect on adult barnacle density which increased, on average, by 40% in plots from which limpets were removed. The combined effects of limpet and canopy showed an additive response on adult barnacle density (mean LRR = 1.84, Figure 22). The combination of both treatments was also independent of shore (= Block) location as indicated by the non-significant Block x Canopy x Limpet treatment interaction (Table 5). Furthermore, there was no significant shore (= Block) effect or interaction between Block and any of the treatments (Table 5).

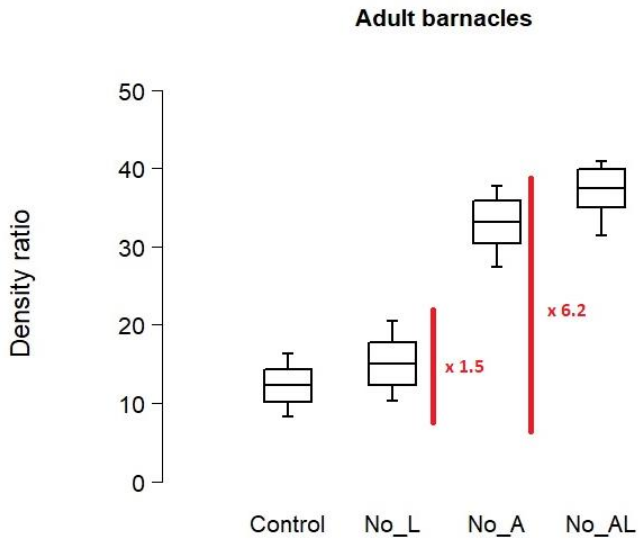

Figure 21. Differences of the ratio (outside/inside canopy-affected area) in adult barnacle density between the control and the three treatments in October. Description of the plot elements as in Figure 15.

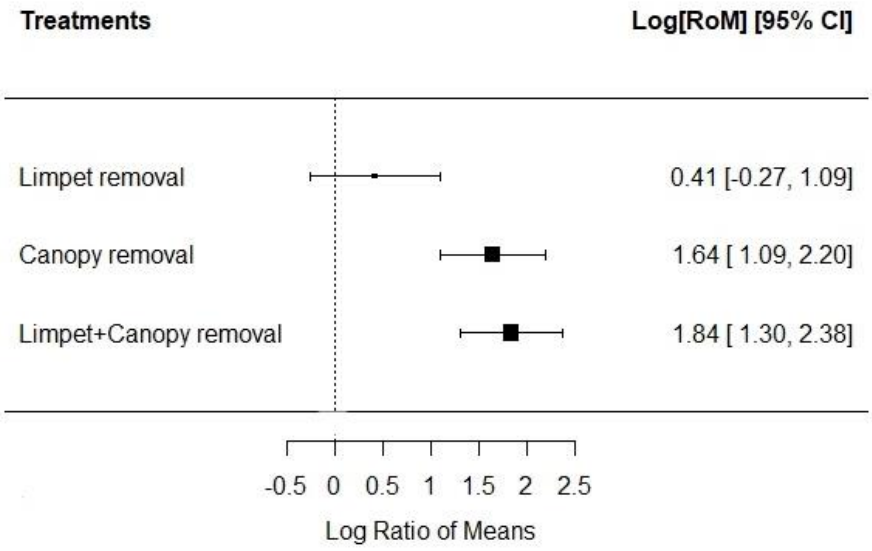

Figure 22. Effect of the three different treatments: Limpet (*P. vulgata*), Canopy (*A. nodosum*) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum*) on barnacle adult density inside the canopy-affected area during October. Description of the plot elements as in Figure 16.

Table 5. Summary of 2× 2 ANOVA run on the ratio between adult barnacles set outside and inside the canopy-affected area (Figure 14). Block was defined as random factor while limpet and canopy as fixed factors. Pooled residuals were calculated after verifying that $\delta^2 = 0$ (not significant at $\alpha = 0.250$). Pooled residual = Shore height × Block + Residual. The denominator for calculating the mean square (MS) in each source of variance is given in the "MS den" column. Degrees of freedom (df), F (F-ratio) and p-value (p).

Sources of variance	df	MS	F	p	MS den
Limpet	1	1680	2.77	0.103	Pooled
Canopy	1	26555	43.71	0.001	Pooled
Block	3	492	0.81	0.467	Residual
Limpet × Canopy	1	728	1.20	0.280	Pooled
Limpet × Block	3	654	1.07	0.372	Residual
Canopy × Block	3	393	0.65	0.590	Residual
Limpet × Canopy × Block	3	770	1.27	0.301	Residual
Residual	32	606			
Pooled residual	44	608			

Barnacle adults analysed in June (Figure B1) and August (Figure B2) had analogous treatments effect as in October, when the experiment was exposed to the treatments the longest time.

3.2.3 Outside canopy affected area

No significant differences between any of the treatments (Figure B3) with very little effect of the treatments (canopy and/or limpet removal) on the density of adult barnacles (Figure B4).

3.3 Treatment quality

3.3.1 Limpet abundance

During the whole experiment, abundance of limpets inside the canopy-affected area (Figure 14) on control plots was, on average, 2.6 times higher than in plots where limpets had been removed (Welch two sample *t*-test: $t_{(325)} = -7.1$, $p < 0.001$, Figure 23). The removal of limpets was strongly effective (mean LRR [95% CI] = - 0.94 [- 0.17, - 1.71]). However, the effect in the first month (May) of limpet removal was not significant (Welch two sample *t*-test: $t_{(44)} = 0.42$, $p = 0.67$, Figure 23) and its removal was very little effective (mean LRR [95% CI] = - 11[- 0.63, 0.40]).

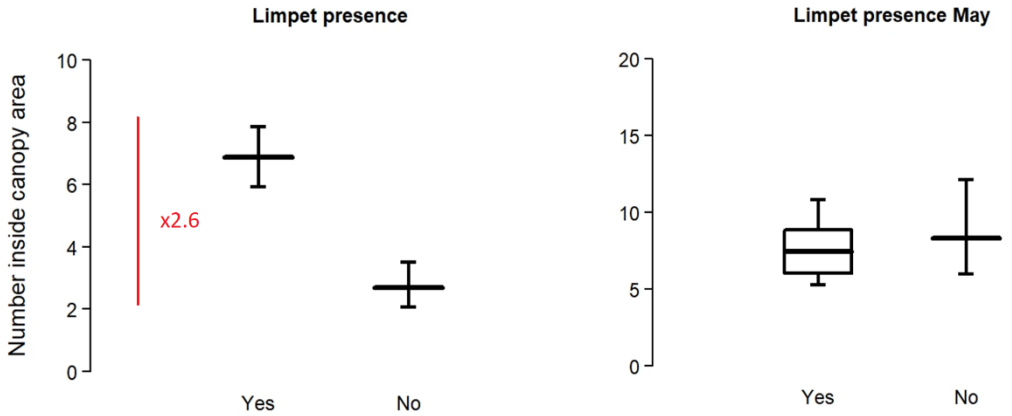

Figure 23. Number of limpets (*P. vulgata*) present during the whole experiment duration (left plot) and during the first month (May) in the treatments where they were removed (No) vs where they were presence (Yes). Description of the plot elements as in Figure 15. Sample size n = 24 experimental units.

3.3.2 Grazing marks

Both months present variation in the area scratched between the treatments (Figure 24). There was a significant difference on the grazing area with an average of five times more area scratched in treatments with presence of limpets than in treatments where limpets were removed during both months (Welch two sample *t*-test: $t_{(70)}$ = -6.79, p < 0.001, Figure 25). In addition, the absence of limpets had a strong negative effect on the scratched area found in both June (mean LRR [95% CI] = - 2.32 [- 3.09, - 1.55] and July treatments (mean 95% CI] = - 2.33 [- 3.10, - 1.55]).

Figure 24. Amount of area scratched between the different treatments Limpet (*P. vulgata*), Canopy (*A. nodosum*) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum* in June (left plot) and July (right plot). Description of the plot elements as in Figure 15.

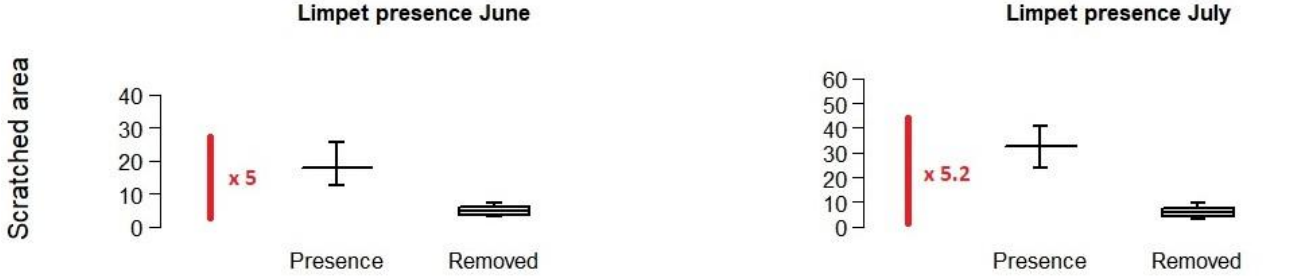

Figure 25. Amount of area scratched between treatments with presence of limpets and treatments where the limpets were removed in May (left plot) and June (right plot). Description of the plot elements as in Figure 15.

3.3.3 Percentage algae cover

The percentage of algae covered between the treatments were the canopy was present or removed was non-significant (Welch two sample *t*-test: $t_{(92)} = -3.61$, $p < 0.001$, Figure 26).

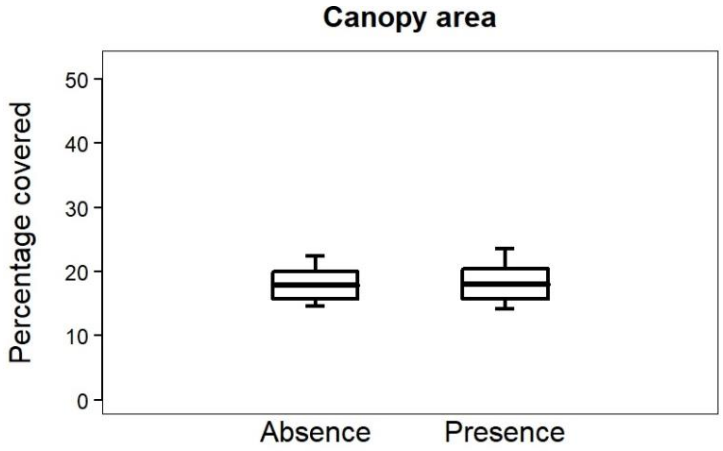

Figure 26. Percentage of algae covered before the treatments of presence and absence of canopy where applied. Description of the plot elements as in Figure 15.

3.4 Comparative studies on limpet effects

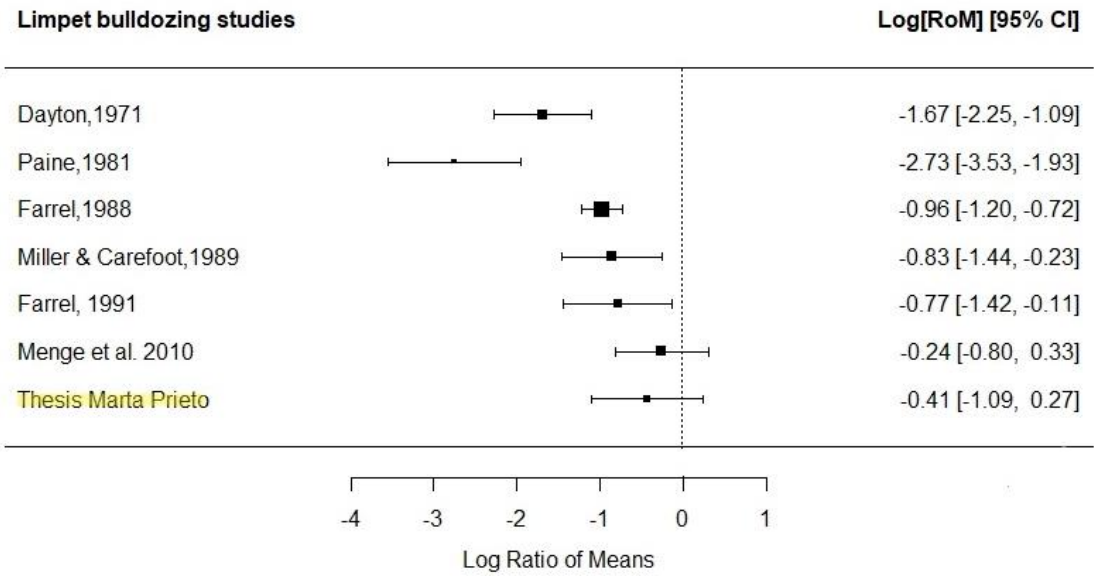

Figure 27. Forrest plot representing the different limpet (*Lottia digitalis*) effects on barnacles (*Balanus glandula*) studied in the US pacific coasts vs the analysis done in this experimental study of limpet *P. vulgata* effect on barnacles *S. balanoides* in Northern Norway shores (underline in yellow). Description of the plot elements as in Figure 16.

4. DISCUSSION

4.1 Summary of results

The analysis showed that *S. balanoides* cyprids and recruits were negatively affected by shore height and canopy presence. The results indicate that high intertidal zones have much stronger negative effects on *S. balanoides* cyprids and recruit survival than the presence of seaweed canopies in low intertidal zones. Cyprid density increased where canopies and limpets were removed and, apparently, limpet removal has a small positive effect on *S. balanoides* recruit density. Presence of *S. balanoides* adults was also negatively affected by seaweed canopy whiplash and limpets bulldozing effects. Canopy presence had a strong negative effect on *S. balanoides* adults while limpet presence had a small negative effect. The combined effects of seaweed-canopy and limpet removal on *S. balanoides* adults clearly suggest an additive effect.

4.2 Barnacle (*Semibalanus balanoides)* phenology

Semibalanus balanoides started to settle on the shore during the first week of May. The settlement timing window was between May and June as cyprids were found on settlement panels deployed on the shore in both months. The time and intensity of phytoplankton blooms is an essential factor to determine how many cyprids will be available to settle in the substrate (Jenkins et al., 2000). The phytoplankton bloom is an important food source supply for early recruits and therefore seems to coincide with the timing of larvae development (Jenkins et al., 2000). In northern Norway waters the phytoplankton spring bloom usually starts in April and finishes around May/early June with the freshwater run-off from snow and ice-melting (Wassmann et al., 1996). To the best of my knowledge, there are no studies reporting barnacle phenology in the Tromsø region. However, there is information of *S. balanoides* phenology from other latitudes. In temperate regions, like the coast of Massachusetts, USA, settlement timing of *S. balanoides* starts in mid-January with the peak of cyprids abundance in February and early March (Pineda et al., 2001). Studies on coasts of Great Britain showed that settlement of cyprids peaks in April/May in the western coasts and in May/June in the eastern and northern coast of UK, varying from year to year (King et al., 1993). Moreover, studies in Nova Scotia and Canada indicated that cyprids abundance also peaks during May/June in these locations (Ellrich et al., 2016).

4.3 Relative effect of height vs seaweed canopy presence

4.3.1 Barnacle settlement

In June, cyprid density was negatively affected by shore height, with about 10 times more barnacle cyprids on the low shore than on the high shore. Furthermore, barnacle cyprid density was also negatively affected by canopy presence, with 2.5 time more barnacles in the absence of *A. nodosum* than in its presence. The results suggest that the effect of shore height was stronger than the effect of canopy presence on cyprid density.

The effect of physical stress limiting the survival of *S. balanoides* cyprids has been widely studied (Wethey, 1984). On high shore levels, barnacles are exposed to desiccation and heat stress as major stress factors that limit their survivorship (Wethey, 1984). In the Arctic, ice friction moved by wind flow can also be a main factor decreasing barnacle population on high exposed shores (Marfenin et al., 2013). Moreover, lower cyprid density found on high shores could be related to the decision of barnacles to settle in a less stressful environment (Clare, 2011; Marfenin et al., 2013). Seaweed canopies have also been shown by other studies to limit barnacle settlement and survivorship. During high tides, *A. nodosum* is swung by water motion hitting the substrate repeatedly and thereby detaching settling barnacles and attached cyprids from the substrate (Beermann et al., 2013). Furthermore, in wave-exposed shores where *A. nodosum* is more frequently and intensely moved by the waves can enhance the whiplash effect on barnacle settlement than on wave sheltered shores (Leonard, 1999). In contrast, most studies done in sheltered shores showed that *A. nodosum* may ameliorate physical stress (Jenkins et al., 1999a; Davies et al., 2008). Beermann et al. (2013), for instance, found that on wave-sheltered temperate mid-intertidal habitats positive (maintenance of moisture and cooling) and negative (whiplash) effects of *A. nodosum* on barnacle recruitment balance each other out. The study also suggests that the negative effect of *A. nodosum* whiplash will prevail on habitats with high physical stress (Beermann et al., 2013). My study was set on an Arctic mid-intertidal wave exposure shore (high-stress physical conditions). As Beermann et al. (2013) suggested, the data of this study revealed that the negative effect of *A. nodosum* whiplash effect in wave exposure shoreline was much stronger than the stress amelioration effect on barnacle recruitment survival.

In this experimental study, the presence of *A. nodosum* affected the cyprid settlement success less than the effect of shore height. One possible explanation for this observation seems possible. As mentioned before, *A. nodosum* can ameliorate environmental stress by providing

a shade environment on wave sheltered shores and hot days as well as a stress factor by whiplash. While heat stress and desiccation caused by high shores limits affect consistently on hot days over an entire area, the effect of whiplash is highly dependent on the canopy movement by wave action, punctually on the specific area that the canopy occupied. In addition, whiplash effect will only act in combination with wave action. Therefore, on calm days with no wave exposure during the settlement window, cyprids can settle successfully, avoiding whiplash effect. During my experiment, settlement timing took place during May/June, a period with days of relatively calm weather (personal observations) which could have reduced settlement mortality by canopy whiplash.

4.3.2 Barnacle recruitment

Recruit density was also negatively affected by shore height. In June, barnacle recruit density was, on average, 26 times higher at low-shore than at high-shore. In addition, the high shore's negative effect increased during time as recruit density in October was around 56 times higher on low-shore than on high-shore. This negative effect of shore height indicates that recruit survivorship was relatively stronger affected by environmental stress high on the shore than settlement success. Some potential causes for these results may be plausible. On one hand, during June, when barnacle metamorphose to recruits, temperatures were the highest recorded in the experiment duration, up to 30 ºC at high intertidal ("HOBO UA-002-64 Pendant Temp/Light, Onset Computer, Bourne, Massachusetts, USA"). These high temperatures may create a strong post-settlement barnacle mortality. On the other hand, at some point barnacles will settle in locations where the conditions are not adequate for their development (Jenkins et al., 2000). The reason for this includes the food limitation (Jarrett, 1997). Cyprids are nonfeeding organisms that rely on their food storage to survive and therefore, need to settle when food reserves are no longer available (Jarrett, 1997). For this reason, barnacle cyprids can be found on stress environments such as high intertidal shores. However, post-settlement barnacle success, and therefore recruit survivorship, will be dependent on settlement on sites with the most successful conditions for survival.

Ascophyllum nodosum seaweed canopy presence showed a positive effect on barnacle recruitment, opposite to the negative effect that it had on settlement barnacle success. These contradictory effects may be related to the whiplash resistance by the different barnacle stages. Metamorphosis from barnacle cyprids to recruits usually takes place within a day, not lasting longer than three days (Jarrett, 2000; Connell, 1961). Furthermore, over time, barnacle recruits get more resistant to whiplash effect (Jenkins et al., 1999b). Mortality of recruits of, for

instance, *Semibalanus balaniodes* were higher in the first five days of settlement after which recruits were more resistant, with 51% of barnacle survival to whiplash effects in comparison to recently metamorphosed recruits and cyprids with 4% and 7% of survival respectively (Jenkins et al. 1999b).

4.4 Limpet bulldozing effect

4.4.1 Barnacle settlement and recruitment

In June, limpets (*P. vulgata)* had a small negative effect on barnacle settlement success with, on average, 1.5 times more barnacle cyprids on plots with limpets absent than in limpet presence. On the contrary, recruit density was higher in plots with limpet presence than in plots where limpets had been removed. Some explanations for these observations appear to be possible. First, limpet bulldozing effect is mainly effective during the settlement period, when cyprids and early recruits are less adequately attached to the substrate (Ellrich et al., 2020). During this time, limpets have a strong negative effect on settlement success, however, limpet bulldozing effect was rather small in this study. Due to the lack of measure at the exact time barnacles were settling, which takes place within a day or two (Jarrett, 2000; Connell 1961), the strongest negative effects of limpets on settling barnacles may have also been unmeasured. Secondly, limpets like *P. vulgata* can have a positive effect under the presence of recruits, reducing microalgae abundance which may have significant localized negative effects on barnacle recruitment (Hawkins, 1983). Microalgae abundance can be a barrier for recruitment survival, limiting their post-settlement attachment success (Menge et al., 2010). Therefore, limpets positively influence recruitment survival by removing microalgae abundance on the substrate.

4.4.2 Adult barnacles

Limpets had very little negative effect on adult barnacle density, increased around 40% in plots from which limpets were removed. However, based on the findings of similar studies done in US Pacific coasts (Dayton, 1971; Paine, 1981; Farrel, 1988; Miller & Carefoot, 1989; Farrel, 1991; Menge et al., 2010) the effect of limpets (*Lottia digitalis*) bulldozing showed a strong negative effect on adult barnacle (*Balanus glandula)* density in comparison to this study. Overall, the results showed by the studies done in the US Pacific coasts, a temperate region, exhibit a strong negative effect (mean LRR of -1.2) of limpets on barnacle survival. In contrast, the thesis results done on an Arctic intertidal region showed a much lower effect (mean LRR

of -0.41) (Figure 27). These differences provide evidence of the contrasting effects between ecological intertidal interactions in temperate and Arctic regions and therefore, the difficulty to extrapolate results obtained on temperate shores to Arctic ecosystems. Nevertheless, it must be taken into consideration that those temperate studies were done on species (*L. digitalis* and *B. glandula)* with similar ecological role as those studied in the Arctic region (*P. vulgata and S. balanoides*), but different species could have different ecological and behavioral patterns that make them more affected by bulldozing detachment. For example, some barnacle species show differences on strengths attachments to the substrate which may explain the different sensitivity to bulldozing detachment (Miller & Carefoot, 1989).

The low limpet effect on adult barnacles could also be explained by other factors. On one hand, limpet bulldozing effects may be less effective by movement restriction. Surface heterogeneity created by barnacles can limit limpet mobility and, under extreme conditions like ice-covered substrates, reduce the food availability (Miller & Carefoot, 1989). A study done on the Isle of Man (UK), *Patella vulgata* limpets living around a barnacle cover substrate spent less time active, carrying out shorter and less "trips" each day than limpets on smooth substrates (Santini et al., 2000). On the other hand, limpet grazing activities could also be limited by predation risk. Coleman et al. (2004) show that predation risk may enhance limpet detachment and aggregation which could lead to altered feeding impact of limpets on algae. As it is known, *P. vulgata* is eaten by a large variety of predators such as fish, crabs, starfish, other gastropods, octopi, birds, and humans (Silva et al., 2008). A study done on southwest England shores showed that most common predator were crabs *Necora puber*, *Carcinus maenas*, and *Cancer pagurus* and small fishes such as blennies (Silva et al., 2008). Another study done in Kimmeridge Bay, UK states oystercatcher *Haematopus ostralegus* as a strong limpet predator (Coleman et al., 1999). Some of those species (like the oystercatcher and crabs *C. maenas* and *C. pagurus)* are found in the Arctic region (Parr et al., 2014) and are possible predators of *P. vulgata*. However, the results did not show a reduction of limpet abundance during the experiment that could indicate an effect of predators preying on limpets. Therefore, it would not be expected that limpet grazing activity was limited by predators.

4.5 Canopy-limpet interactive effects

Adult barnacles were strongly affected by *A. nodosum* removal, with six times more barnacle density in the absence of the canopy than in its presence. However, the removal of *P. vulgata*

had a relatively small effect on adult barnacles, with 40% more barnacles in the absence of limpets than in its presence. The combined effect of *A. nodosum* and *P. vulgata* presence on adult barnacles resulted in an additive effect, contrary to the hypothesis suggestion of an interactive effect of canopy presence and limpets bulldozing activities having extra pressure on barnacle survival. Several explanations for this result seem possible. First, the location of the study in a highly wave-exposed shore could explain the restricted limpet movements. Unfortunately, I was not able to measure the wave force on the experimental site as the equipment was lost just after it was set up on the field. However, this loss seems to indicate that the shore was under strong wave actions. Limpets in wave-exposed shores are susceptible to be dislodged by strong waves. Consequently, they reduce its mobility and enhance the attachment to the substrate to prevent the detachment (Grenon & Walker, 1981; Vieira & Bueno, 2019). Second, canopy whiplash effect in wave-exposed shores is repeatedly hitting the surveyed area while bulldozing effects, in the canopy-affected area, occur intermittently as they move around being unlikely to cross the same area multiple times. Therefore, canopy whiplash effect might be much more persistent based on the size and frequency of the waves.

Third, differences in temperatures between temperate and Arctic regions could also explain the unexpected limpet and canopy additive effect on adult barnacle density. Cold air and water temperatures have been observed to reduce grazing activity rates on *P. vulgata* (Redfern et al., 2021). For example, Santini et al. (2004) showed that lower temperature ranges experience in the Isle of Man, UK during spring (air temperatures 9.9 ℃ to -0.9 ℃ and water temperatures 9.9 °C to 7.9 °C) decrease feeding activities by reducing radula motions (Santini et al., 2004). In my study, air temperatures in May range from 11.2 ℃ to -1.7 ℃ and water temperatures range from 10.4 ℃ to 4.6 ℃. These temperatures, similar to the ones measured by Santini et al. (2004), suggest a reduction of limpet movements and its effect on adult barnacles. Furthermore, in temperate regions, with months that can reach really high temperatures, seaweed-canopy acts as an ameliorator, keeping a moisture microclimate that can alleviate species, like *P. vulgata,* from desiccation and heat stress. However, in Arctic regions, where temperatures are essentially low, seaweed-canopy cannot offer species like limpets a benefiting environment by reducing the effects of low temperatures. Therefore, in the Arctic intertidal, seaweed-canopy may not act as an ameliorator species which could explain the additive effect found between *A. nodosum* and *P. vulgata* in the study. The functional role of *A. nodosum* canopy in the Arctic intertidal seems to differ from the studies done on temperate regions where canopy presents beneficial effects in other intertidal species, like the limpets.

4.6 Limitations of the study

The primary limitation to the generalization of these results is that the study was prescribed on a high physical stress gradient of the theorical model by Bruno et al. (2003). The predictions of the model on the right end of the physical stress gradient suggest that stress amelioration will have a strong positive effect on the community interactions (Bruno et al., 2003) (Figure 1B). In this study, seaweed *A. nodosum* canopy was contemplated to be a stress amelioration species reducing physical stress by limiting understory water loss and temperature variability for other intertidal species like barnacles and limpets (Beermann et al., 2013). However, the results showed seaweed canopy presence as a strong negative effect on the survival of barnacle density and did not show significant positive effect on limpet presence. The differing result expected from the model could be explained by the position of the Arctic region assumed in the model that may be set even higher on the physical stress gradient where stress amelioration is not effective anymore. The Arctic intertidal presents extreme air and water temperature changes, strong solar light seasonally, ice-scouring, freezing of the intertidal and freshwater from snow melting, among others (Gili & Petraitis, 2009; Høgslund et al., 2014). As so, the Arctic intertidal region could be described as one of the highest physical stressed environments.

The design of the current study is also subject to limitations. During the methodological process, removal of limpets was performed throughout the experiment but with some periods of about three weeks between each removal event. This intermittent removal could have affected the limpet treatment results. However, treatments' quality results showed the effectiveness of limpet removal with 2.6 times higher abundance of limpets in control treatments than in plots where limpets were removed. Moreover, the study did not measure limpets' grazing activity at the time of barnacle settlement when bulldozing effect is suspected to have the strongest negative effect on barnacle survival (Ellrich et al., 2020). The results of the removal experiment are also limited by the presence of block effect (= shore) in barnacle recruit density on the settlement panels during May, which could limit the comparison of the treatments between shores.

Further outlook

Arctic intertidal ecology is highly unknown with mainly observational studies done (Fritz et al., 2017; Thyrring & Peck, 2021). With extreme environmental conditions, ecology of the Arctic coastal regions may also differ to temperate zones, where most ecological studies have been

performed. A study done by Jenkins et al. (2000) showed differences in the settlement timing of *S. balanoides* between NW Europe coasts with a window from March to June. Such differences shall be even higher in Arctic intertidal regions. Therefore, future experiments should focus on the study of the exact settlement and recruitment timing of *S. balanoides* in this Arctic experimental intertidal zone. Moreover, the limpet bulldozing effect could be studied in the settlement cyprids peak when barnacles are more vulnerable to limpet-induced detachment.

There are many studies from NE and NW Atlantic coasts which focus on barnacle-seaweed canopy, barnacle-limpet, or limpet-seaweed canopy ecological interactions. However, as I can recall, there is no information about the interactive effects between canopy and limpets on barnacle density. The additive effect found on this study between the two species suggests that the seaweed canopy ecological role in the Arctic differs from temperate regions. Most studies done in temperate regions suggest that canopy ameliorates limpet's desiccation and heat stress which would enhance the negative effect that both species have on the barnacles. For this reason, it could be a further step to study the canopy-limpet relation and its effect on barnacle density in temperate regions to determine if canopy ecological role differs between temperate and Arctic intertidal regions.

4.8 Conclusion

By analyzing the effects of biotic and abiotic factors on the barnacle *S. balanoides* on the Arctic intertidal shore of Kvaløya island in northern Norway, this thesis has shown that barnacles are highly negatively affected by desiccation on high shores in comparison to the lower whiplash effect. Additionally, the results showed that limpet bulldozing had a small negative effect on barnacles, contrary to the strong negative effect shown in studies done in temperate regions. Thus, the new approach of studying an interactive effect between seaweed canopy and limpets expected from the current literature resulted in an additive effect on barnacle abundance. These results suggest that the facilitation by canopy is more likely to happen in temperate regions, where species are more exposed to a warmup intertidal. The following step should focus on studying the seaweed canopy-limpet relation on temperate regions to test the multiplicative effect that both species may have on barnacle density as the literature suggests. In addition to the results of my study, this further research could explain how species seem to have different ecological roles in the ecosystems depending on its distribution along the latitudinal gradient. Furthermore, with the lack of Arctic intertidal studies and the strong effect predicted by climate change on these regions, further general research is needed for a better understanding of the ecological relations of intertidal species on a highly extreme understudied environment.

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6. ANNEX

Annex A.

Table A1. Summary of Welch two-sample t-tests run on barnacle recruit density on the settlement panels during May to test for significance on the effectiveness of the presence of limpets between Blocks. Degrees of freedom (df), t (t-value), p (p-value) and LRR (Log response ratio). In Block III the LRR = Infinity and the denominator (treatment) = 0.

Sources of variance	df	t	p	LRR
Block I	10	-1.06	0.31	0.43
Block II	5	-0.53	0.18	0.05
Block III	5	1.15	0.30	Inf
Block IV	10	0.48	0.64	1.6

Annex B.

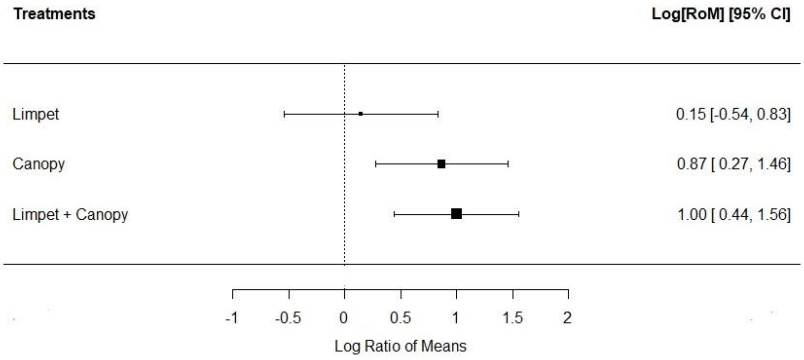

Figure B1. Forest plot showing the effect of the two treatments and its combination on barnacle adults during June. Limpet (*P. vulgata*), Canopy (*A. nodosum*) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum*). Each treatment is plotted as a box with the 95% confidence interval (CI) displayed as the horizontal line. Mean Log response Log [RoM] ratio and extreme values of the CI are described in the right column. Vertical dotted line represents the null values.

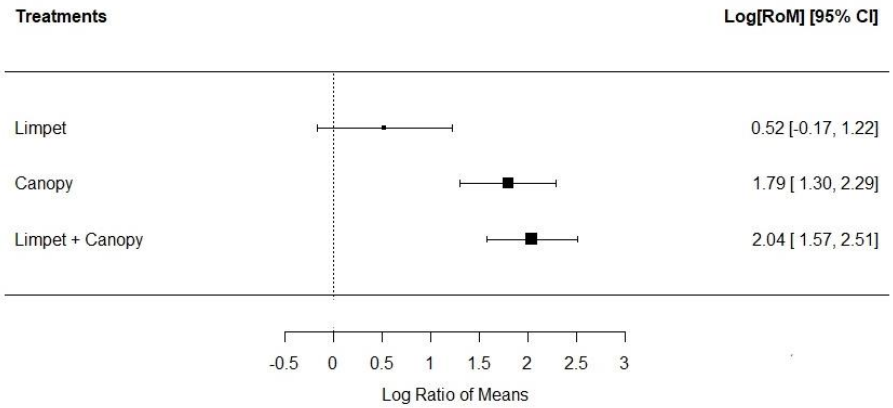

Figure B2. Forest plot showing the effects of Limpet (*P. vulgata*), Canopy (*A. nodosum*) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum*) on adult barnacle density during August inside the canopy-affected area (Figure 14). Description of the plot data and symbols as in Figure B1**.**

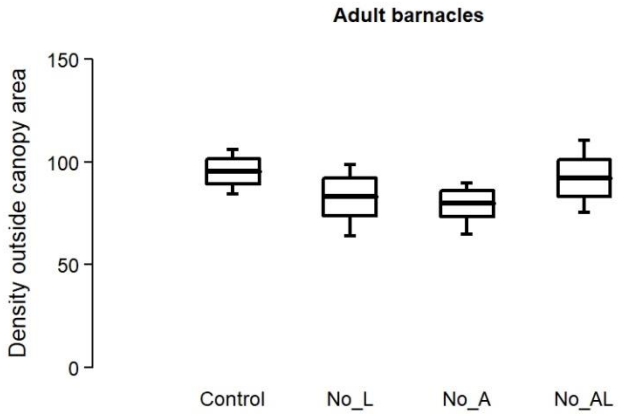

Figure B3. Boxplot of the differences in adult barnacle density between the control and the three treatments during October: No_L (*P. vulgata* removal), No_A (*A. nodosum* removal) and No_AL (*P. vulgata* and *A. nodosum* removal) outside the canopy-affected area (Figure 14). Description of the plot data and symbols as in Figure 15.

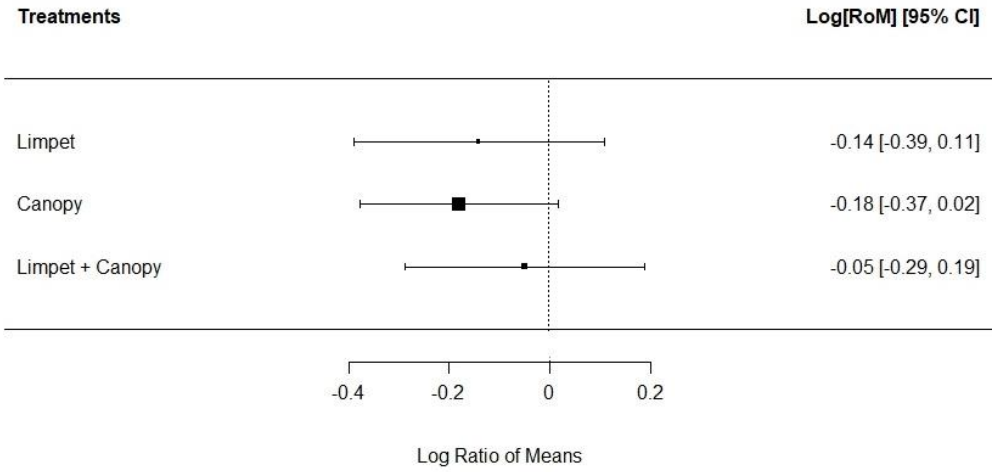

Figure B4. Forest plot showing the effects of Limpet (*P. vulgata*), Canopy (*A. nodosum*) and Limpet + Canopy (combined effect of *P. vulgata* and *A. nodosum*) on adult barnacle density in October outside the canopy-affected area (Figure 14). Description of the plot data and symbols as in Figure A1.