The role of crawling predators in the decline and distribution of blue mussels in Norwegian coastal waters

Nadja Meister

Master of Science in Biology - Marine Biology
Department of Biological Sciences, University of Bergen
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Supervisors: Christian Jørgensen*, Tom J. Langbehn*, Øystein Varpe*
*Department of Biological Sciences, University of Bergen

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N.Meister

Nadja Meister

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Synthesis chapter

Scientific background

Blue mussels (*Mytilus* spp.) are widespread foundation species that facilitate healthy populations of many other species in the ecosystem through creating habitats, filtering water, or serving as prey for others (Figure 1) (Buschbaum et al. 2009, Norling & Kautsky 2007). They increase water quality by filter feeding that reduces nitrogen, phosphorus, organic particles, and sediments in the water column (Lindahl et al. 2005, SAPEA 2017, Timmermann et al. 2019). Blue mussels show alarming signs of decline across regions and ecosystems. In some regions they suffered due to climatic reasons, such as heat waves (Seuront et al. 2019), climate warming (Jones et al. 2010), and harsh winters (Carroll & Highsmith 1996). In other regions they declined due to harvesting (Baden et al. 2021, Beukema & Dekker 2007, Sorte et al. 2017), failed recruitment (Baden et al. 2021), predation by fishes (Šegvić-Bubić et al. 2011), or competition with invasive oysters (Baden et al. 2021). Additionally, ocean acidification (Sadler et al. 2018), hybridization of blue mussel species (Benabdelmouna & Ledu 2016), and parasites (Mortensen & Skår 2020) may negatively affect their persistence. Blue mussels are near threatened to critically endangered in all four European marine regions; Baltic Sea, North-East Atlantic, Mediterranean Sea, and Black Sea (Gubbay et al. 2016). In Norway and Sweden, they have largely disappeared from rocky shores while they continue to thrive on floating structures (Andersen et al. 2017, Baden et al. 2021, Christie et al. 2020). Proposed causes for the Scandinavian decline are climate change, pollution, disease, parasites, hybridization, and failed recruitment (Baden et al. 2021). While these are reliable drivers elsewhere, they cannot explain the blue mussel occurrence pattern seen in Norway. The only likely cause affecting rocky shores but not floating structures is a crawling predator, which is the thinking underlying the hypotheses tested in this thesis.

Although existing evidence and current literature remain inconclusive about whether predation, and if so which predator, is behind the blue mussel decline, we draw attention to the role of tributyltin (TBT), an organotin compound used in antifouling paints from the 1960s (IMO 2002). TBT caused imposex, the imposition of male organs on females, in marine gastropods, leading to sterilization and population declines (Bryan et al. 1987, Gibbs et al. 1987). Particularly impacted was the dogwhelk *Nucella lapillus* (Gastropoda), a well-studied crawling predator with blue mussels and barnacles as favourite prey (Connell 1961). Dogwhelks access blue mussels' flesh by drilling a hole through their shells with their micro-toothed radula (Carriker 1981). They dissolve the flesh with help of digestive enzymes and use their long proboscis to get it out of the hole (Carriker 1981). In Norway, high proportions of dogwhelks showed severe signs of imposex (Følsvik et al. 1999, Schøyen et al. 2019). TBT was phased out from the 1980s, culminating with a global ban in 2008 (IMO 2002). However, because it binds strongly to sediments it has continued to affect many areas and still remains in high concentrations in some areas, e.g., near large ports (Guðmundsdóttir et al. 2011, Ho et al. 2016). Where TBT has slowly degraded, dogwhelks have regained reproductive capability (Schøyen et al. 2019) and populations are recovering. For example, this was documented for the coast of southern England (Bray et al. 2012, Morton 2011), where dogwhelks increased 50-fold from 2003 to 2010 (Morton 2011). Many sites became recolonized, as shown for Isle of Cumbrae (Birchenough et al. 2002), and juveniles regained dominance (Evans et al. 1996). Even in Maine, where dogwhelks showed a persistent decline linked to warming, they peaked at 3-4 times normal density in 2007-2008 (Petraitis & Dudgeon 2020), indicating a population wave possibly linked to regained reproductive capability. In Norway, TBT levels are low now and 2017 was the first year that dogwhelks were free from imposex (Schøyen et al. 2019). This recovery might have affected community structure and dynamics in the intertidal.

Figure 1: The picture in the centre shows some of the biodiversity that blue mussels host, the pictures on the left show close-ups of the epibiotic growth on their shells, the pictures on the right show predators feeding on blue mussels; dogwhelks (*Nucella lapillus*), green crabs (*Carcinus maenas*), and common sea stars (*Asterias rubens*).

Other refugia than floating structures where blue mussels continue to thrive in Norway are low salinity habitats, wave and current exposed sites, cracks in rocks, and muddy bays (personal observation). In Norway, there are three *Mytilus* species coexisting and interbreeding; *M. edulis, M. galloprovincialis,* and *M. trossulus* (Brooks & Farmen 2013). The latter can cope with low salinities and outcompetes the otherwise dominant *M. edulis* in freshwater-influenced inner arms of Norwegian fjords (Brooks & Farmen 2013). Such habitats limit access for crawling predators with a low freshwater tolerance, such as sea stars (Binyon 1961) and dogwhelks (Stickle et al. 1985b). The warm-water species *M. galloprovincialis* is the least abundant, as its core distribution is in the Mediterranean Sea (Brooks & Farmen 2013). Nevertheless, it appears as far north as Svalbard (Mathiesen et al. 2017). Wave and current exposures trigger blue mussels to become more robust, e.g. through increased shell thickness (Akester & Martel 2000), and restrict feeding in many crawling predators, such as sea stars, crabs, and dogwhelks (Freeman & Hamer 2009, Menge 1983). Increased risk of dislodgement causes dogwhelks to seek refuge (Hughes & Burrows 1991), and makes them choosing smaller prey such as barnacles (Hughes & Dunkin 1984a). Compared to dogwhelks from sheltered sites, dogwhelks from exposed sites have shorter, squatter shells and larger apertures to reduce drag and resist dislodgement (J. H. Crothers 1985, Guerra-Varela et al. 2009). They are likely more resistant to rough weather than sea stars and crabs (Menge 1983). Blue mussels thrive in cracks of rocks, another microhabitat that is hardly accessible to predators (personal observation). Finally, muddy bays might protect blue mussels too. Soft bottoms serve as distribution barriers for dogwhelks (Colton 1916, Morgan 1972a). However, they provide home to the burrowing netted dogwhelk *Tritia reticulata*, another predator of blue mussels (Davenport & Moore 2002, Tallmark 1980), that was affected by TBT (Stroben et al. 1992). Dogwhelks develop directly from egg capsules (Colton 1916) and have, other than crabs and sea stars, no pelagic stage to reach floating structures. All this makes it more likely that dogwhelks may play a role in the Norwegian blue mussel decline.

Motivation, aim, and significance of the thesis

So far, the cause of the Norwegian blue mussel decline could not be identified. Proposed drivers of the decline, i.e., climate change, pollution, disease, parasites, hybridization, and failed recruitment, are reliable drivers in other regions, but it remains disputable how they could have skipped blue mussels thriving on floating structures. Predators are largely ignored, and their role in the Norwegian blue mussel decline remains unknown. An interesting candidate is the dogwhelk *N. lapillus* that recently regained full reproductive capacity in Norway (Schøyen et al. 2019). In other regions, dogwhelk populations increased rapidly as reaction to their recovery from pollution-induced sterility (Morton 2011). However, the magnitude of their increase and their impact on their blue mussel prey remains unknown in Norway. All this caught our curiosity, and the thesis is driven by the overarching research question: ***Are dogwhelk populations, recovering from TBT-induced sterility, driving the Norwegian blue mussel decline?***

In this thesis I aim to identify if a crawling predator could be behind the Norwegian blue mussel decline and if so, to investigate whether predation by dogwhelks can have effects of the observed magnitude and pattern. Additionally, I will assess other crawling predators that could play a key role in the decline. Based on these objectives and through multiple approaches, i.e., field monitoring, field experiments, and mesocosm experiments, I aim to answer the following, more specific research questions:

Q1: Are crawling predators behind the Norwegian blue mussel decline? **Chapter I**

Q2: What is the impact of dogwhelks on blue mussel mortality? **Chapter I**

Q3: Do dogwhelks have the feeding capacity to drive a country-wide blue mussel decline? **Chapter II**

Q4: Are Norwegian blue mussel refugia out of reach from dogwhelks? **Chapter II**

Q5: Which other crawling predators have high impacts on blue mussels? **Chapter II**

In Norway, blue mussel beds belong to the most important nature units (Bekkby et al. 2021). Beside their importance as foundation species (Buschbaum et al. 2009, Norling & Kautsky 2007), their potential to increase water quality through filter feeding is higher than any nutrient removal by land-based mitigation measures (Timmermann et al. 2019). Additionally, blue mussels are highly nutritious and blue mussel mariculture belongs to the most environmentally friendly marine food productions and has a nearly unlimited potential for growth (SAPEA 2017). In Norway, it has yet remained stable at ca. 2000 t blue mussels per year for more than a decade (Fiskeridirektoratet 2020). Identifying the cause(s) driving the Norwegian blue mussel decline is crucial and could in case of a crawling predator without a pelagic stage give green light for future investments in the development of Norwegian blue mussel mariculture, with blue mussels suspended on free-hanging ropes. Furthermore, changes in species composition and species abundance can drive cascading community shifts (Sorte et al. 2017). Knowing the cause may help choosing the right management strategies to conserve the remaining blue mussel populations, and thereby maintain their ecosystem functions as filter feeders and foundation species and prevent the ecosystem from shifting towards a new devaluated state.

Structure and approach of the thesis

This thesis is divided into three chapters. In this **synthesis chapter**, I already introduced the scientific background, motivation, aim, and significance of the thesis. I will now present the structure of the thesis including the function of each chapter and the approaches we chose to address the research questions. Subsequently, I will provide an overview and reflection of the results, limitations of the thesis, and end the chapter with an outlook for future research.

Chapter I "*Out of reach from crawling predators: blue mussel populations thrive on suspended structures but have declined elsewhere*" is a manuscript we submitted to the *ICES Journal of Marine Science*. The manuscript has already gone through one round of review, with positive reviewer feedback, and now has been resubmitted. In Chapter I we aimed to first identify if a crawling predator could be behind the Norwegian blue mussel decline (**Q1**) by using the literature to exclude proposed and elsewhere reliable drivers, by documenting the contrast of blue mussels being absent on structures touching bottom but present on nearby floating and free-hanging structures, and by determining blue mussel mortality in the field under exclusion of predators. In a second step, we aimed to identify the impact of dogwhelks on blue mussel mortality (**Q2**) by quantifying blue mussel and dogwhelk abundance on floating docks and rocky shores and by determining mortality of blue mussels accessible to dogwhelks but out of reach from other predators in the field. To address these aims, we collected data snorkelling on rocky shores, floating docks, and submerged trees on Norway's west coast around Bergen, and conducted a predator exclusion experiment with cages exposed in the rocky intertidal of small islands in Raunefjorden.

Chapter II *"The feeding and crawling potential of the dogwhelk Nucella lapillus"* presents a set of pilot experiments. We aimed to identify if dogwhelks have the feeding capacity to drive a country-wide blue mussel decline (**Q3**) by determining their feeding potential on a wide size spectrum of blue mussels in small mesocosms, and if Norwegian blue mussel refugia are out of reach from dogwhelks (**Q4**) by determining their crawling potential to cross soft bottoms and to crawl up chains and ropes that usually hold floating docks in place. In a last step, we aimed to identify other crawling predators that have high impacts on blue mussels (**Q5**) by assessing their feeding efficiency on blue mussels in small mesocosms and using information from the literature. To address these aims, we conducted seven pilot experiments in small (≤60 l) mesocosms at the Marine Biological Station Espegrend (MBSE).

Chapter I is a collaboration; all my supervisors helped me with fieldwork and setting up the caging experiment, I conducted the caging experiment and curated the data, I analysed the data and coded figures together with Tom Langbehn, I wrote the manuscript together with Christian Jørgensen, and all my supervisors contributed with inputs. Chapter II is my own work; I set up and conducted the pilot experiments, curated and analysed the data, coded figures, and wrote the chapter without much input from my supervisors. The synthesis chapter is also my own work. However, I believe that the ideas and views I convey in this thesis would not have been the same without the discussions I had with my supervisors. Therefore, and for consistency, I decided to use the personal pronoun “we” throughout the entire thesis.

Overview and reflection of the results

In **Chapter I** we show that blue mussels were largely absent on rocky shores and trees hanging into the water and touching the bottom, while they continued to thrive on floating docks and trees hanging freely in the water. Statistical analyses revealed that accessibility to crawling predators was a significant predictor of whether blue mussels were present or not. Additionally, the caging experiment confirmed that blue mussels continue to thrive when out of reach from predators. All this supports our hypothesis that a crawling predator is behind the Norwegian blue mussel decline (**Q1**) and provided the basis for the investigation about dogwhelks’ impact on blue mussels. Furthermore, we have not found a single dogwhelk on floating docks, but many on rocky shores. In the caging experiment that excluded other predators than dogwhelks, blue mussel mortality due to other causes than predation by dogwhelks was almost non-existent (< 1%), and it correlated positively with the average number of dogwhelks observed drilling or feeding. In conclusion, dogwhelks had a high impact on blue mussel mortality (**Q2**). This motivated us to look deeper into dogwhelks’ feeding potential.

In **Chapter II** we revealed that growing large does not protect blue mussels from being drilled by dogwhelks. Dogwhelks drilled and fed effectively on blue mussels of any size (up to 131 mm). They could handle small (≤ 20 mm) blue mussels within less than one day, and the fastest ones only needed one day to handle blue mussels up to 80 mm and 2.5 days for blue mussels sized 80-100 mm. Even small (12-13 mm) dogwhelks managed to drill medium-sized (27-32 mm) blue mussels. All this confirms that dogwhelks are effective predators of blue mussels and that they might have the feeding capacity to drive the Norwegian blue mussel decline (**Q3**). We cannot draw a firm conclusion due to small sample sizes in the pilot experiments as well as the uncertainty about the magnitudes of i) the increase of dogwhelk populations in Norway and ii) the decline of blue mussels in Norway. We also assessed dogwhelks’ potential to cross soft bottoms and to crawl up chains and ropes, that usually hold floating docks in place, over short distances (0.25 m). Dogwhelks’ progress was slowed down on mud compared to sand, and they more often managed to reach blue mussels on top of branches and concrete bricks than on top of ropes and chains. This tentatively suggests that muddy bays and floating docks, both habitats where we still observe blue mussels in Norway, are out of reach from dogwhelks (**Q4**), but larger sample sizes as well as the inclusion of hydrodynamics and larger crawling distances are needed to draw firm conclusions. Additionally, we found that many other species that feed on dead blue mussels, i.e., common periwinkles (*Littorina littorea*) and common sea urchins (*Echinus esculentus*), were not able to predate on live blue mussels, and that small sea stars had a low efficiency in handling medium-sized (40-60 mm) blue mussels. Other studies confirm that sea stars have relatively low consumption rates and suggest crabs as more efficient predators, on small to medium-sized blue mussels (Kamermans et al. 2009, Menge 1983). To identify which crawling predators other than dogwhelks have high impacts on blue mussels (**Q5**), we need further studies where we determine feeding efficiency of a variety of sea star and crab species, including diverse sizes of each species, on a wide size spectrum of blue mussels.

In **conclusion**, while Chapter I revealed that crawling predators are most likely behind the blue mussel decline and outlined dogwhelks' high impact on blue mussel mortality, Chapter II with its exploratory pilot experiments added evidence that dogwhelks likely have the feeding and crawling potential to play an important role in the decline. Therefore, the Norwegian blue mussel decline could in fact be the result of conservation success: the recovery of a crawling predator from ocean pollution. However, further studies are required to identify if dogwhelks have the capability to drive the country-wide decline without affecting blue mussels in refugia (i.e., floating docks, current and wave exposed sites, muddy bays, and low salinity habitats), and to more carefully assess alternative predators that could be behind the Norwegian blue mussel decline.

Limitations of the thesis

Most limiting was that neither the magnitude of the blue mussel decline nor the magnitude of the dogwhelk increase have been quantified in Norway. To our knowledge there are no comprehensive time series available, and the Institute of Marine Fisheries (IMR) has only recently started monitoring blue mussel populations. Therefore, it was impossible to establish a direct link between dogwhelks' recovery from pollution-induced sterility and the blue mussel decline that cooccur in Norway. Time was sparse and limited our capacity to monitor blue mussel occurrence and abundance to areas on the west coast of Norway around Bergen. Even though the pattern found was consistent throughout, it might not be representative for the whole of Norway. Additionally, rough weather limited the period field experiments could be run and the frequency we could inspect them at. Mesocosm experiments had a pilot design, they were exploratory and covered a wide range of questions, with the downside of few replicates per experiment that did not allow for statistical analyses and firm conclusions. Many questions were outside the scope of this master thesis but would be important to follow up to improve our understanding of the blue mussel decline, e.g. "Will blue mussel refugia continue to exist in the future and will they promote a shift in the dominating blue mussel species from *M. edulis* to *M. trossulus* or *M. galloprovincialis*?" We will address some of these questions in the following outlook for future research section.

Outlook for future research

During this thesis, questions arose that could not be answered by looking at the current literature and require further fieldwork and experiments. Some of these questions are relevant to understand the direction in which intertidal community structure and dynamics might evolve, and they are introduced here.

1) **When do wave action and currents hinder predators, such as dogwhelks, sea stars, and crabs, from feeding on blue mussels?**

   On the West coast of America the purple sea star *Pisaster ochraceus* defines blue mussels' lower distribution limit on rocky shores (Paine 1974). It is lower on exposed than on sheltered sites (Dayton 1971), showing that sea stars are limited in feeding by water dynamics (Menge 1983). Crabs are excluded from exposed shores where dogwhelks still persist (Hughes & Elner 1979). Dogwhelks may be less affected by harsh conditions than crabs and sea stars (Menge 1983). They adapt to exposed sites by developing shorter, squatter shells and wider mouths that reduce drag by waves and increase adherence strength (Crothers 1981, Guerra-Varela et al. 2009). Under unfavourable conditions, they switch to feed on smaller prey, prefer to stay in refuge, and feed less frequently (Burrows & Hughes 1991a, 1991b, Hughes & Burrows 1991). Wave exposed blue mussels are more robust than the ones at sheltered sites (Akester & Martel 2000), and thereby make it even harder for predators to access their flesh. However, the intensity at which hydrodynamic forces begin to prevent predators from feeding or exclude predators remains unknown.

2) **What will happen to blue mussel refugia in the future?**

   Will climate warming affect the persistence of refugia at exposed sites? Is it harder for dogwhelks to hold grip in warmer water? Warm water temperatures and feeding activity both increase respiration rates in dogwhelks (Stickle & Bayne 1982), and we would expect a trade-off between holding a firm grip, where the shell is tightly pressed against the ground, and high respiration rate, which requires water flow (as known from limpets, Hahn & Denny 1989). Looking into how dogwhelks' grip reacts to climate warming could help to predict what will happen to blue mussels that still thrive at exposed sites. Will the refugia increase (if dogwhelks lose grip with warming), be unaffected (if dogwhelks are unaffected by warming), or even decrease (if dogwhelks increase their prey handling efficiency with warming)?

Could climate warming up to a certain level also be beneficial for blue mussels through creating larger freshwater refugia in Norway? We observe a decrease of salinity in Norwegian coastal waters for over half a century (Aksnes et al. 2009, Albretsen et al. 2012, Sætre et al. 2003), probably due to increased precipitation and increased runoff from rivers caused by warming (Sætre et al. 2003). Could *M. trossulus*, which tolerates low salinities, benefit from a future increase in brackish water habitats that limit the accessibility of predators with low freshwater tolerance, such as sea stars (Binyon 1961) and dogwhelks (Stickle et al. 1985b)?

3) **Will further constraints in blue mussel occurrence to refugia cause a shift in the dominating *Mytilus* species, such as from *M. edulis* to *M. trossulus* or *M. galloprovincialis*?**

Brooks and Farmen (2013) found predominantly *M. trossulus* on a floating structure in Møre and Romsdal, which contrasts with the otherwise much lower *M. trossulus* proportions found on rocky shores in Norway. Could this indicate interspecific differences in microhabitat preferences? DNA analysis of blue mussels from different microhabitats could help to address this question and to predict if we can expect a change in the dominating blue mussel species in the future. Do the three *Mytilus* species have different capabilities to persist during the Norwegian blue mussel decline? *M. trossulus* already dominates fjords and estuaries with brackish water (Brooks & Farmen 2013), but what about the other refugia?

4) **Do seasonal freshwater pulses i.e., snowmelt, glacier melt, and increased rainfall, prevent dogwhelks from invading and establishing themselves in habitats that are otherwise exposed to oceanic salinities?**

Blue mussels tolerate lower salinities than dogwhelks (Stickle et al. 1985a, Westerbom et al. 2002). During our fieldwork, we observed well-established blue mussel beds at a rocky site in Vestrepollen (Fanafjorden) where we measured 30.2 PSU (2 July 2022). At this site, we observed common sea stars and green crabs but not a single dogwhelk. What prevents dogwhelks from invading this site and feeding on blue mussels? The MBSE took CTD (conductivity, temperature, and depth) measurements in the nearby Kviturspollen during the last year (May 2021, September 2021, October 2021, December 2021, January 2022, and February 2022) and found surface salinities as low as 27 PSU during the winter. However, these are single point measurements and salinity could have dropped even lower, especially in Vestrepollen that is located closer to the estuaries. Dogwhelks' short term survival is limited by 15 PSU (Stickle et al. 1985a). However, dogwhelks reduce feeding with a decrease in oceanic salinities (Stickle et al. 1985b), and a positive energy budget can only be maintained at salinities >22.5 PSU (Stickle & Bayne 1987). Could it be that seasonal pulses of freshwater runoff cause long-lasting patterns such as the year-round absence of dogwhelks? Permanently installed salinity loggers and an introduction experiment with dogwhelks to such habitats could help to address these questions.

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Chapter I

Out of reach from crawling predators: blue mussel populations thrive on suspended structures but have declined elsewhere

Nadja Meister[1,*], Tom J. Langbehn[1], Øystein Varpe[1,2], Christian Jørgensen[1]

[1]Department of Biological Sciences, University of Bergen, Bergen 5020, Norway

[2]Norwegian Institute for Nature Research, Bergen 5006, Norway

*Corresponding author: tel: +47 45863434; e-mail: nme011@uib.no

Abstract

Blue mussels (*Mytilus* spp.) are declining around the world. In Norway, they thrive on floating structures, while on rocky shores they have widely disappeared. Proposed and elsewhere reliable drivers such as climate change, pollution, disease, parasites, hybridization, and failed recruitment would not discriminate between floating structures and rocks. Therefore, we hypothesize that crawling predators, unable to reach floating structures, drive the Norwegian decline. A known ferocious crawling predator without pelagic stage is the dogwhelk *Nucella lapillus*. We surveyed trees hanging into seawater and floating docks together with nearby rocky shores for blue mussels and dogwhelks, and conducted a predator exclusion experiment with caged blue mussels (40-80 mm). Blue mussels were present on all floating docks (65% cover), but only on 18% of rocky shores (≤5% cover). Similarly, they were found on 83% of trees without bottom contact, but only on 1% touching the seafloor. In cages, mortality due to other factors than dogwhelks was extremely low (< 1%) and confirms that blue mussels continue to thrive when out of reach from predators. An ecosystem with few blue mussels might be the result of a successful tributyltin (TBT) ban that led to the recovery of dogwhelks from pollution-induced sterility.

Keywords: invertebrate predators, population decline, predator recovery, refugia

Introduction

Blue mussels are widespread foundation species that create habitat and facilitate settlement and persistence of other species (Buschbaum et al. 2009). They provide invaluable ecosystem services by filter-feeding and thus removing nitrogen from eutrophic waters, and are a cheap, healthy, and sustainable source of marine protein (Lindahl et al. 2005, SAPEA 2017). Three blue mussel species, *Mytilus edulis*, *M. trossulus*, and *M. galloprovincialis*, coexist in Europe and sometimes interbreed (Brooks & Farmen 2013). The Mediterranean warm-water species *M. galloprovincialis* has its core distribution in southern Europe but occurs up to 70°N (Brooks & Farmen 2013). *M. trossulus* can cope with low salinity and dominates fjords and estuaries with brackish water (Brooks & Farmen 2013). All along the outer coast of Norway (58°N to 71°N), dominated by saline Atlantic water, *M. edulis* is the most common of the three species (Brooks & Farmen 2013), and it is even present in the Arctic archipelago of Svalbard at 78°N (Berge et al. 2005). Visual identification is impossible and molecular analysis is needed for species separation and hybrid detection (Brooks & Farmen 2013). Therefore, *Mytilus* spp. are often collectively referred to as blue mussels (Brooks & Farmen 2013), and we do so also in this study although our study area, Norway's west coast around Bergen, is where *M. edulis* typically dominates.

Blue mussels show a concerning decline across much of their distributional range. The last decade, blue mussels have been disappearing from many locations along the Norwegian coast (Andersen et al. 2017) and across other regions and ecosystems of the North Atlantic (Baden et al. 2021). The European red list of habitats shows that blue mussel beds across all four marine regions (Baltic Sea, North-East Atlantic, Mediterranean Sea, and Black Sea) are of conservation concern (near threatened to critically endangered) (Gubbay et al. 2016). In some regions, blue mussels have declined due to climate change and extreme climatic events. Blue mussels that are repeatedly exposed to air temperatures >31°C during low tide suffer increased mortality (Jones et al. 2010, Seuront et al. 2019). Rising temperatures and associated heat waves have led to mass mortalities along the northern French coast in summer 2018 (Seuront et al. 2019) and a 350 km poleward shift of the southern range margin along the east coast of North America from 1960 to 2006, where mussels previously were found south to Cape Hatteras (35°N) (Jones et al. 2010). At the other extreme, a harsh winter in 1988-1989 with air temperatures as low as −31°C wiped out blue mussels in the upper tidal zone along >1000 km of the Alaskan coastline, where they previously dominated (Carroll & Highsmith 1996). Future levels of ocean acidification may lead to thinner-shelled and slower-growing blue mussels that are more vulnerable to predation (Sadler et al. 2018).

In other regions, direct anthropogenic impact drove the decline. Global harvesting of wild blue mussels peaked in 1992-1993 at ca. 170 000 tonnes annually and triggered local declines of wild populations (Baden et al. 2021). Harvesting is one of the main drivers behind the >60% decline of local blue mussel populations along 450 km of the Gulf of Maine (~43°N) over the past 40 years (Sorte et al. 2017) and in the North-East Atlantic harvesting had removed most intertidal blue mussel beds in the Wadden Sea by 1990 (Beukema & Dekker 2007). Harvesting in the Wadden Sea was regulated from 1995 and further restrictions implemented on intertidal beds from 2004 and extended to subtidal populations from 2008, and as a result blue mussel beds have started to recover slowly (Baden et al. 2021, Beukema & Dekker 2007).

Species interactions appear to often play a role in the decline. *M. edulis* and *M. galloprovincialis* frequently interbreed and their hybrid offspring show reduced fitness and recruitment, which can negatively impact population persistence (Benabdelmouna & Ledu 2016). Jellyfish prey on pelagic blue mussel larvae and their blooms can cause recruitment failures (Baden et al. 2021). Wild fish aggregations, mainly from the families Sparidae, Atherinidae, and Mugilidae, caused large losses of young adults (ca. 35 mm) in blue mussel farms in Croatia (Šegvić-Bubić et al. 2011). Invasive Pacific oysters overgrew blue mussel beds in the Wadden Sea of Germany, Denmark, and Netherlands, forming "oyssel beds" (Baden et al. 2021). The parasite *Marteilia refringens* severely affects European flat oysters and recently a new *Marteilia* species, *M. pararefringens*, was found on blue mussels in England, Sweden, and Norway (Mortensen & Skår 2020); its impact, however, remains unclear (Mortensen et al. 2021). Blue mussels are superior when competing with barnacles for space and dominate the intertidal rocky shores, except when predators limit their distribution (Lubchenco & Menge 1978, Paine 1974).

In Norway, blue mussels are declining on the rocky shores along the coast while they continue to thrive a few meters away on buoys, floating docks, and ropes hanging from docks (Andersen et al. 2017, Christie et al. 2020). The same observations were made on the west coast of Sweden, where harvesting has virtually ceased and cannot be responsible for the ongoing extensive decline (Baden et al. 2021). Commercial production of blue mussels in Norway is dominated by aquaculture (Winther et al. 2010) while harvesting of wild populations for sale is restricted to a few locations near packaging plants in mid-Norway, and both biomass harvested and geographic scale are too small to cause the observed decline of wild stocks. Climate warming, ocean acidification, pollution, disease, parasites, hybridization, and failed recruitment are identified drivers of declines elsewhere and proposed causes for the Scandinavian decline (Andersen et al. 2017, Baden et al. 2021).

A key question is to what degree floating structures could relieve negative impacts from the suggested mechanisms. Norwegian summers are relatively cool, with water temperatures rarely and only locally exceeding the 25°C threshold, after which temperature starts to negatively affect blue mussel physiology and survival (Dowd & Somero 2013, Gazeau et al. 2014). Here and further north, the persistence of blue mussels is primarily determined by tolerating low air temperatures and ice scouring during winters (Clark et al. 2021). One key difference for a mussel living on a floating structure is that it is always submerged, in contrast to mussels in the rocky intertidal where air exposure involves intermittent feeding, higher and lower ambient temperatures, as well as access for terrestrial predators. Additionally, the formation of sea ice in calm bays or inlets can cause anoxic conditions below and thus lower survival and recruitment (Andersen et al. 2017). During the last two decades, coastal water temperatures have been increasing in Norway (Aksnes et al. 2019, Albretsen et al. 2012). Sea ice only occurred locally over small scales, and low temperatures have not been linked to the widespread decline (Andersen et al. 2017). All the other proposed causes would have equally affected mussels on rocks and floating structures.

Scandinavian research largely disregards harmful algal blooms, unfavourable weather conditions, competitors, and predators, even though these are identified threats to the European Union's blue mussel aquaculture (Avdelas et al. 2021). Particularly, biotic factors such as competitors and predators can affect blue mussels on rocks and floating structures unequally. Invasive Pacific oysters compete with blue mussels for space and lower recruitment by filter-feeding their larvae (Baden et al. 2021), but their distribution in Norway is largely limited to the southern coast (IMR 2020) and overlaps too little with the distribution of blue mussels to cause a large-scale decline. In Sweden and Norway, continually high densities of settlings in mussel farms and on floating structures exclude failed recruitment and predation on early life stages as drivers of the decline (Andersen et al. 2017, Baden et al. 2021). Birds such as eider ducks (*Somateria mollissima*) and oyster catchers (*Haematopus ostralegus*), fishes such as goldsinny wrasses (*Ctenolabrus rupestris*), common sea stars (*Asterias rubens*), green crabs (*Carcinus maenas*), and the predatory snails dogwhelk (*Nucella lapillus*) and netted dogwhelk (*Tritia reticulata*) feed on settled blue mussels and are known predators in Scandinavian waters (Andersen et al. 2017, Baden et al. 2021, Christie et al. 2020). Fishes and diving birds can reach blue mussels on floating structures and feed on them. It might be harder for birds to prey on mussels on the underside of floating structures, however, the sides of those structures are often equally covered with blue mussels (personal observation) and easily accessible. Therefore, we hypothesize that a crawling predator without pelagic eggs or larvae, unable to reach floating and free-hanging structures, must be behind the Norwegian blue mussel decline.

In this study, we quantified blue mussel abundance and related it to whether the habitat was accessible to crawling predators or not, and whether it was influenced by tidal cycles or not. We studied floating docks and nearby rocks, as well as fallen trees and branches hanging from the coastline into the water where some touch bottom while others hang freely in the water (Figure 1). Such trees usually experience the same tidal air exposure as the rocky shores where blue mussel declined, and are therefore of particular interest to evaluate potential climatic causes related to the above-surface environment. On the same floating docks and rocks, we also quantified the abundance of our prime suspect *N. lapillus*, which in contrast to the sediment burrower *T. reticulata* prefers hard substrate. Finally, and in response to our observations, we conducted a caging experiment in the field to investigate the feeding potential of *N. lapillus* on blue mussels and to which degree causes of mortality other than predation affect blue mussels. We compared feeding potentials of dogwhelks and the above-mentioned crawling predators by combining information from the literature.

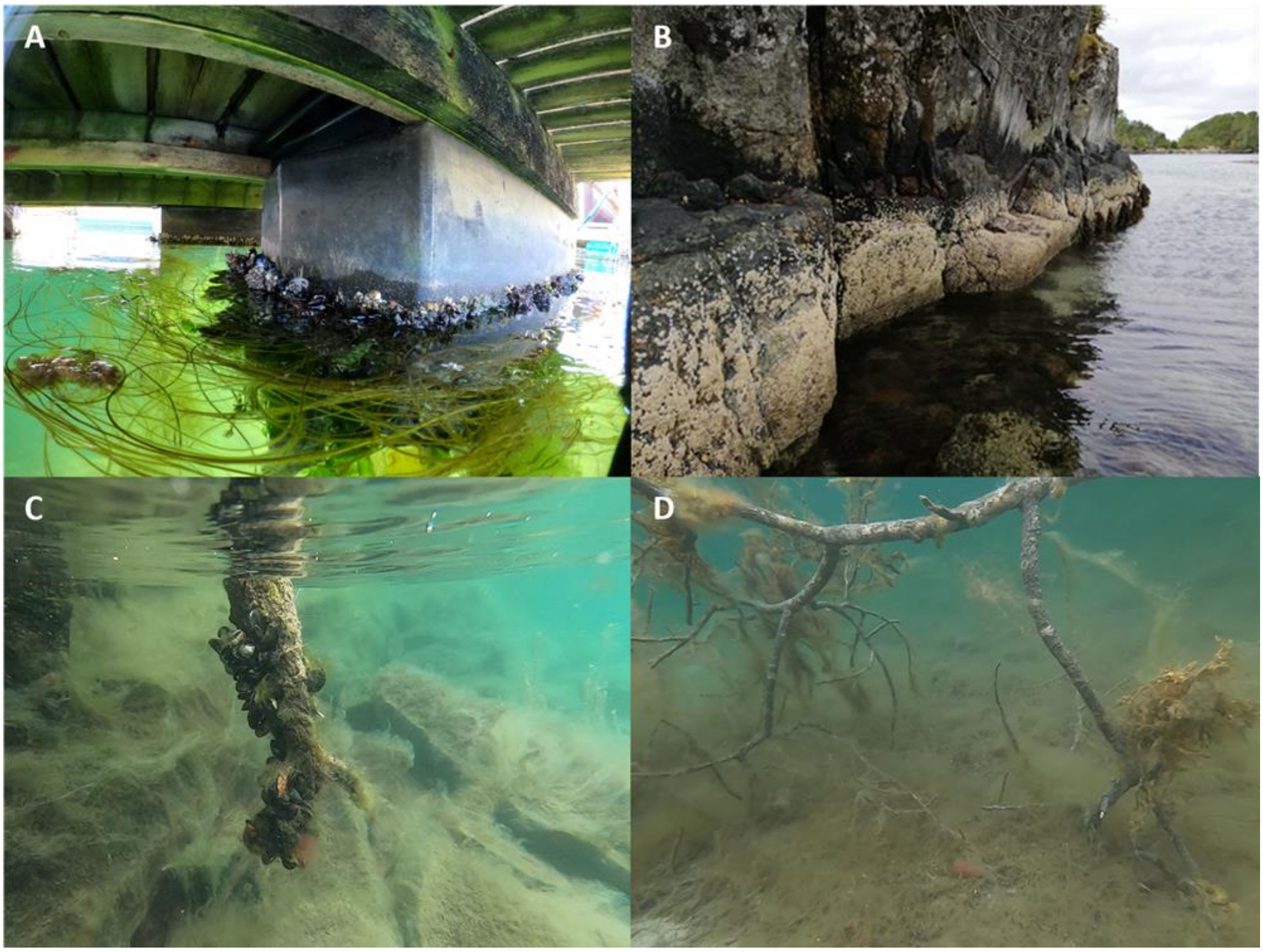

Figure 1: Floating dock with blue mussels (A), rocky shore without blue mussels (B), tree branch hanging freely with blue mussels (C), tree branch touching bottom without blue mussels (D).

Material and methods

Floating docks, rocky shores, and trees

We sampled floating docks and nearby rocky shores, as well as trees hanging from land into the sea, during a four-day long sailing trip 9-12 June 2021. From anchorages in Møkster, Fitjar, Våge (Tysnes), and Hagavik, we used a dinghy to reach and cover various sites in the areas (Figure 2). We chose a paired sample design to look at floating docks together with rocky sites a few meters away, with focus on blue mussels *Mytilus* spp. and dogwhelks *Nucella lapillus.* While we aimed to diversify the sampling areas, we did opportunistic sampling within these areas. We tried to cover all accessible floating docks but if there were several docks side by side, we skipped some randomly as we experienced that such docks usually showed a similar species cover. We snorkelled the entire dock and about 30 m of coastline nearby to record blue mussel and dogwhelk presence or absence. We estimated percent coverage of blue mussels and other species within square 0.1 m^2 frames and counted dogwhelks and species of low coverages within those frames. On floating docks, we placed frames randomly three times on submerged sides and/or undersides of the floats. On nearby rocks, we placed frames randomly in the intertidal. The aim was to get an overview of the average abundances of blue mussels and dogwhelks on floating docks and rocky shores (including man-made structures of rocks i.e., wharfs, piers, and breakwaters) a few meters away for direct comparison. Additionally, we recorded sizes of blue mussels using five different size classes (0-20 mm, 20-40 mm, 40-60 mm, 60-80 mm, ≥80 mm) by measuring some blue mussels *in situ*. Using a handheld salinometer we recorded local conditions (temperature, salinity) and noted GPS coordinates, wave and tidal exposure, depth, and predators observed. In the Våge and Hagavik areas, we found many trees hanging from land into the water and recorded whether blue mussels were present or absent on trunks and branches and if those were touching the bottom or were hanging freely in open water. In Godøysund, Våge, we systematically sampled all (81) trees within a predefined transect (Figure 2C) and analysed them separately. Additionally, we took pictures and videos under and over water using GoPros 7 and 8. We sampled 17 floating docks together with nearby rocks and 121 trees during the sailing trip. We added another 11 floating docks together with nearby rocks and two trees from fieldwork in Øygarden, Raunefjorden, Austrheim, Gulen, and Bergen areas during summer 2021. We covered those locations snorkelling from shore and motorboats using the same procedures as described above.

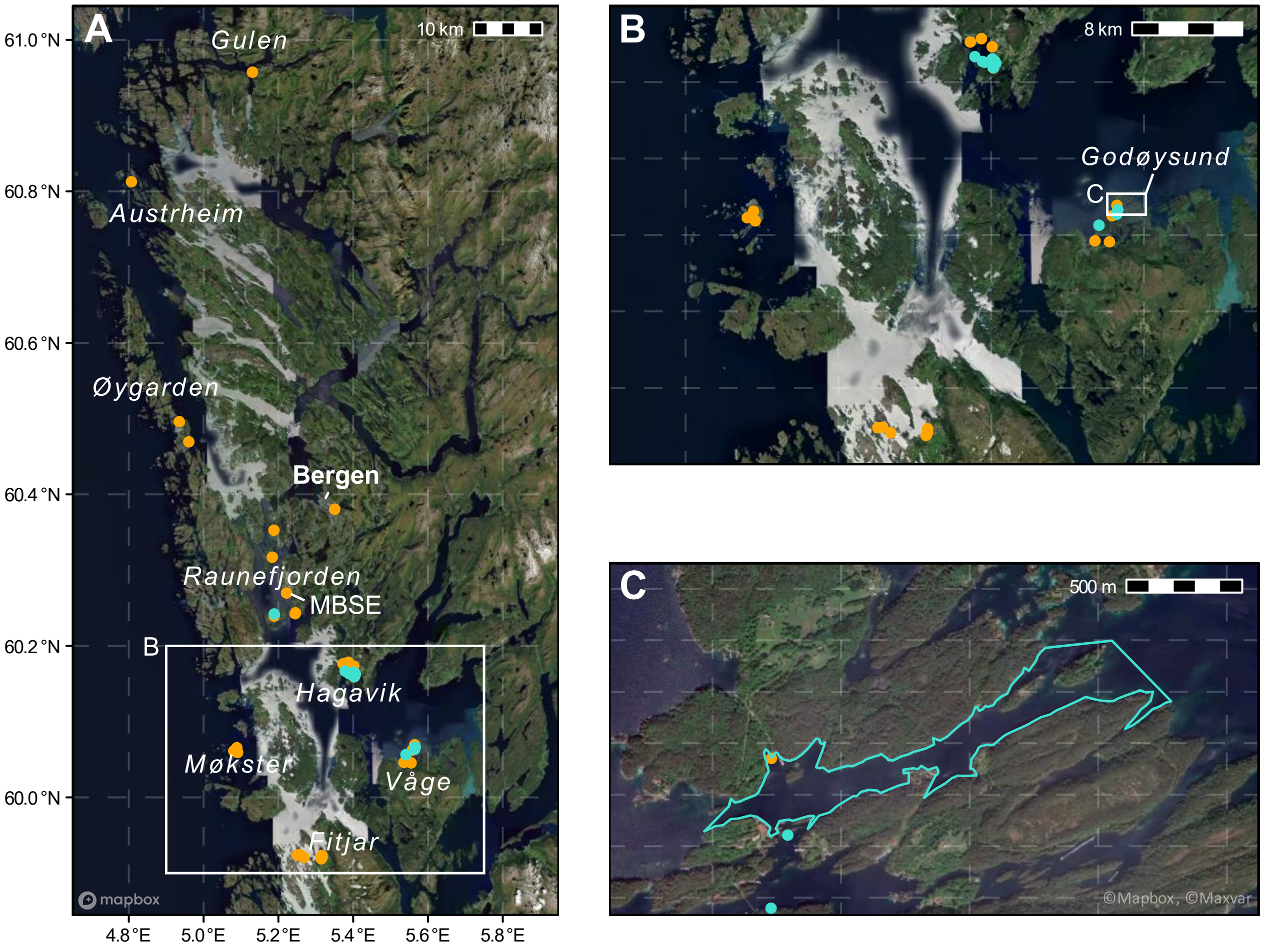

Figure 2: Map of the sampling sites (A) along Norway's west coast around Bergen, (B) close-up of more densely sampled area (white frame in panel A), and (C) further magnification of the tree transect in Godøysund (white frame in panel B). Floating docks together with nearby rocks are denoted by yellow dots and tree sites by turquoise dots. The area surveyed for the tree transect is also outlined in turquoise. Note that each tree site can contain several trees. Satellite images courtesy of ©Mapbox, ©Maxvar.

Caging experiment

In June 2021, we constructed 40 stainless steel cages with an edge length of 0.33 m, half with 8x8 mm and half with 28x28 mm mesh size. Prior to the experiment, we hung all cages from the dock at the Marine Biological Station Espegrend (MBSE) into seawater for 3 weeks to get rid of chemical and oil residues from the fabrication. We collected 880 blue mussels (40-80 mm) from floating docks of the MBSE. We cleaned them from barnacles and other organisms and split them randomly into groups of 22 individuals. We placed each group together with a rope into a beaker with constant seawater flow for minimum 10 days prior to the experiment to get them attached to the rope and minimize possible shell loss from large-meshed cages. We added two concrete bricks on the bottom of each cage to make them heavier and stretched the rope with blue mussels diagonally across the cage with the mussels resting on the bricks to minimize blue mussels having contact with the mesh and thereby with predators from outside the cage. Additionally, we collected adult dogwhelks (25-35 mm length) from rocky shores next to the MBSE and added 10 individuals to half of the small-meshed and half of the large-meshed cages, resulting in a two-by-two design: small- and large-meshed cages, and with or without dogwhelks added. Birds, fishes, sea stars, and crabs of sizes large enough to open medium-sized to large blue mussels, were excluded from all cages due to mesh size. Adult-sized dogwhelks could not pass through the small mesh, but they fitted through the meshes of the large-meshed cages. Therefore, small-meshed cages without dogwhelks served as a control to measure blue mussel mortality due to other factors than predation.

We set the cages up at 10 locations around eight small uninhabited islands in Raunefjorden within ~4.5 km from the MBSE in August (19.08.2021, location 1-5) and September (14.09.2021, location 6-10) 2021 (Figure S1). We placed the cages within the intertidal zone of gently sloping rocky shores with low to intermediate wave exposure. We avoided locations with high macroalgae density as these locations often have few dogwhelks. At each location, four cages, one of each category, were placed in a random order, all within a similar water depth and in homogeneous habitat. Locations were recorded with GPS coordinates and the cages distributed within a 10 m radius. A minimum distance of 1 m between the cages was maintained.

We visited the cages once a week, if weather conditions allowed, to document active predators. At one location (10) rough weather washed the cages into deeper water and we excluded these cages from analyses. After 8 weeks, we recovered the remaining cages and recorded if blue mussels were open, closed, or lost. Shells were analysed by recording number of drilling holes, number of drilling attempts (uncompleted holes), and if the shells showed other predation marks or were broken. Closed blue mussels without any completed drilling holes were identified as alive, all the others as dead. If shells of a dead blue mussel showed completed drilling holes the blue mussel was identified as predated by dogwhelks, else its cause of mortality was recorded as unknown. We subtracted lost blue mussels (mussels that disappeared from large-meshed cages) from sample sizes and excluded them from the analyses.

Data analysis

We conducted all analyses in R version 4.1.1 (R Core Team 2021). We generated maps using the packages “ceramic” (Sumner 2019) and “sf” (Pebesma 2018). For all other figures, we used “ggplot2” (Wickham 2016) and combined them using “patchwork” (Pedersen 2020). To test for difference between blue mussel presence and absence on floating docks versus nearby rocks, and trees touching bottom versus trees hanging freely in the water, we used Fisher's exact test for small sample sizes. To compare blue mussel densities within frames on floating docks and nearby rocks, we used an unpaired two-samples Wilcoxon test for not normally distributed data. We also pooled floating docks, rocky shores, and trees together and tested for the effects of accessibility to crawling predators and tidal exposure on blue mussel presence/absence by bootstrapping our data (1000 resamples) with "rsample" (Silge et al. 2022). We analysed the bootstrapped data by a one-way ANOVA with a Tukey HSD test. To statistically analyse the data from the caging experiment, we used two-way ANOVAs with Tukey HSD tests. We compared blue mussel mortalities and numbers of dogwhelks drilling/feeding between the four cage categories and tested for the effect of location. We tested if accessibility to adult dogwhelks is a predictor for blue mussel mortality by using an unpaired two-samples Wilcoxon test. Finally, we chose a second order polynomial regression model, which has a lower Akaike information criterion (AIC) than a linear regression model, to study relationships between blue mussel mortality and dogwhelk abundance within cages.

Results

We found that blue mussels were present on all (100%) visited floating docks but only on a few (18%) rocky shores nearby (Fisher's exact test, $p < 0.001$; Figure 3A). At one of the five rocky sites with blue mussels, blue mussels (≤100 mm) were patchily distributed below a freshwater surface layer, on the other four sites blue mussels (≤60 mm) were scattered within cracks in the rocks. We found large blue mussels (60-120 mm) on all floating docks.

Trees and branches hanging from land into the water showed the same pattern. Trunks and branches that hung freely in the water, without contact with the bottom, were almost always (83% of cases) inhabited by blue mussels. In contrast, blue mussels virtually never (only 1% of cases) occurred on trunks and branches that were in contact with the bottom (Fisher's exact test, $p < 0.001$; Figure 3B). Three out of a total of nine trunks/branches on which no mussels had settled despite not touching the bottom were barely submerged at high tide. In one other case the tree was free of any biofouling, suggesting that it had only very recently fallen into the sea. This pattern was consistent both in the transect in Godøysund, where we systematically surveyed all trees ($n = 81$), and every other site where we examined fallen and partly submerged trees for blue mussel settlement. The single tree that touched bottom and was covered with mussels was within the Godøysund transect at the location most exposed to rough wave action. Because observations within the transect (blue mussels on 81% of branches/trunks without bottom contact and 2% of the cases with bottom contact; Fisher's exact test, $p < 0.001$) aligned with observations elsewhere, we have pooled all tree observations (Figure 3B).

A closer look into floating docks and nearby rocks revealed that the observed difference in blue mussel occurrence was even stronger when considering percent coverage and abundance within the three frames per site (Figure 4AB). Here we found that floating docks and nearby rocky shores also significantly differed in terms of blue mussel densities (Wilcoxon test, $p < 0.001$). On floating docks, their coverage was often high, on average 65% (± 35% SD) but ranging from 5% to 100%. On rocks, blue mussels appeared only in low densities, the average coverage was around 1% (± 1% SD) and always ≤5%.

We found dogwhelks only on rocky shores and never on any floating structures (Fisher's exact test, $p < 0.001$; Figure 4CD). Dogwhelks were present on half of the rocky sites, and in more than a third, we found them in at least one of the three frames. The distribution of dogwhelks was very patchy and abundances within frames varied greatly, from 0 to 15 individuals on sites with dogwhelks. On one rocky site, we found both blue mussels and dogwhelks, both in low densities (0 within frames). Additionally, we observed sea stars and green crabs in low abundance at a few rocky sites, but no netted dogwhelks. A few small sea stars (diameter <100 mm) were also found on floating docks. Finally, when pooling floating docks, rocky shores, and trees together, we found that both the accessibility to crawling predators and tidal exposure significantly influenced blue mussel occurrence. The probability of blue mussels being present differed between all three habitats (Tukey HSD test; p values < 0.001): accessible to crawling predators and with tidal exposure (i.e.,

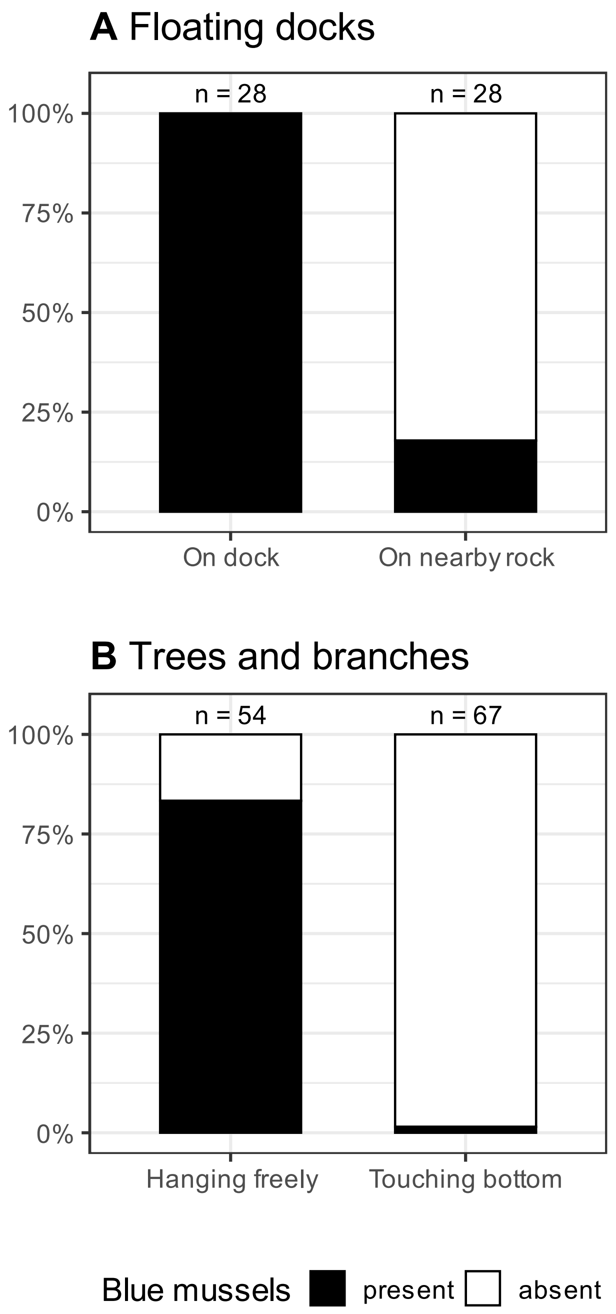

Figure 3: Blue mussel presence/absence (A) on floating docks and nearby rocks and (B) on trees and branches hanging freely in water and trees and branches touching bottom.

rocky shores and bottom-touching trees; 6.1±2.5%), inaccessible to crawling predators but with tidal exposure (i.e., free-hanging trees; 83±5.1%), and inaccessible to crawling predators and constantly submerged (i.e., floating docks; 100±0%).

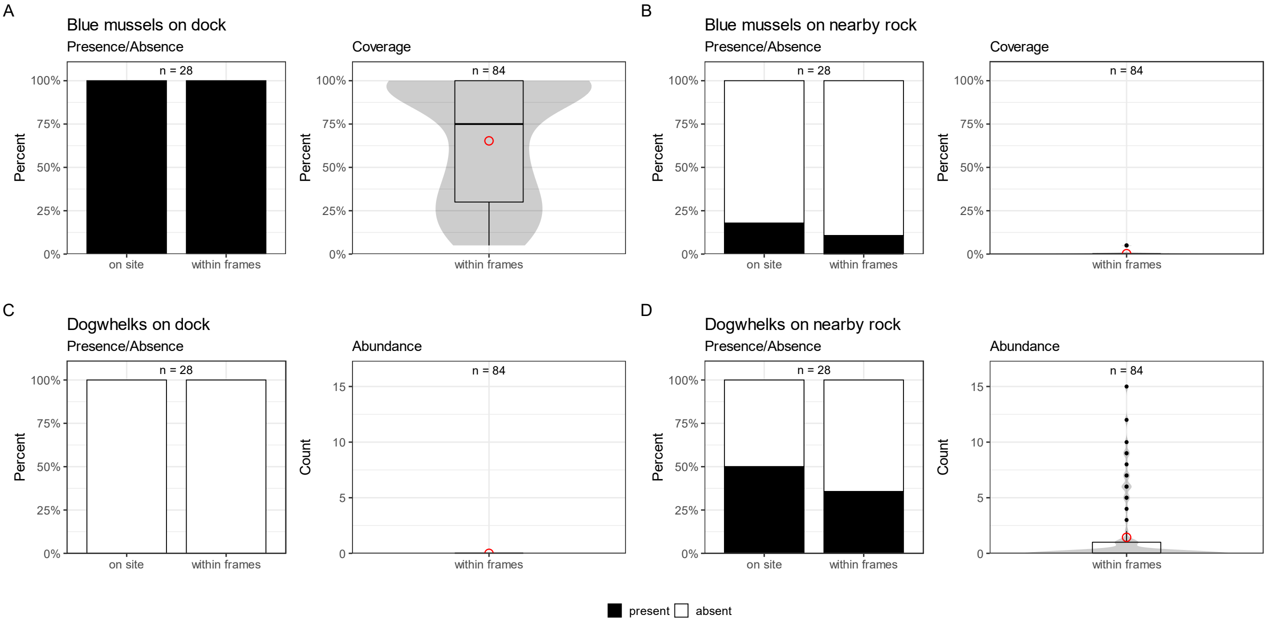

Figure 4: Presence/absence observations and percent coverage (within frames) on floating docks or nearby rocky shores for blue mussels (A and B) and dogwhelks (C and D) respectively. “On site” bars indicate presence/absence on the entire floating dock or within the 30 m rocky shore nearby, while “within frames” observations are limited to three randomly placed 0.1 m^2 frames on the floating docks or within the intertidal on the rocky shores nearby. Red circles in coverage and abundance plots indicate mean values. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. Outliers are >1.5 times the interquartile range beyond either end of the box and denoted by dots.

The caging experiment showed that dogwhelks predated on average about half of the blue mussels within 8 weeks, unless large dogwhelks were excluded from the cages (Figure 5). That large dogwhelks had access to cages was a significant predictor of blue mussel mortality (Wilcoxon test, $p < 0.001$). In small-meshed cages with 10 added dogwhelks, predation was most stable among locations ($\mu = 51\%$, $\sigma = 16\%$), and every dogwhelk fed on average 1.11 blue mussels during the experiment. In large-meshed cages, regardless of dogwhelks being added ($\mu = 49\%$, $\sigma = 32\%$) at the beginning of the experiment or not ($\mu = 49\%$, $\sigma = 39\%$), fluctuation among sites was higher. Predation ranged between 0% and 100% in large-meshed cages with dogwhelks added and between 0% and 95% in large-meshed cages without dogwhelks added. Overall, we lost 39 blue mussels, 20 from large-meshed cages with dogwhelks added and 19 from large-meshed cages without dogwhelks added. Blue mussels disappeared predominantly from cages with high predation. Noting that it is easier for two halves of a dead mussel to fall through the mesh than an intact bivalve, it is not unlikely that the missing individuals had been predated beforehand. Small-meshed cages without dogwhelks added also showed some mortality due to dogwhelk predation (μ = 8%, σ = 9%). This can be explained by our observations of dogwhelks drilling from the outside of the cages on blue mussels that had detached from the rope and ended up next to the mesh, or by small dogwhelks (10-15 mm length) entering the cages to feed. We also made these observations for some cages of the other categories. The proportions of blue mussels that died in cages where large dogwhelks were included from the start or could enter (small-meshed cages with dogwhelks added and large-meshed cages with and without dogwhelks added) do not significantly differ from each other (Tukey HSD test, p values > 0.9), but they all differ significantly from the proportion of blue mussels that died in cages where large dogwhelks were excluded (small-meshed cages without dogwhelks added; Tukey HSD test, p values < 0.003). Also, location (two-way ANOVA, $p = 0.009$) significantly influenced blue mussels' mortality. In total, only five blue mussels, <1%, died without being predated by dogwhelks during the 8 weeks. Two of these, both from large-meshed cages, had serrated edges that may have been predation marks from crabs. Another of these blue mussels, coming from a small-meshed cage, had broken shells looking as if it had been crushed by the concrete blocks, presumably during wave action. Only two dead blue mussels were free from any marks. Of all blue mussels predated by dogwhelks, 26% had additional drilling attempts (uncompleted holes) and 55% had more than one, up to seven, completed drilling holes. Drilling attempts were also found on a few, 6%, blue mussels alive.

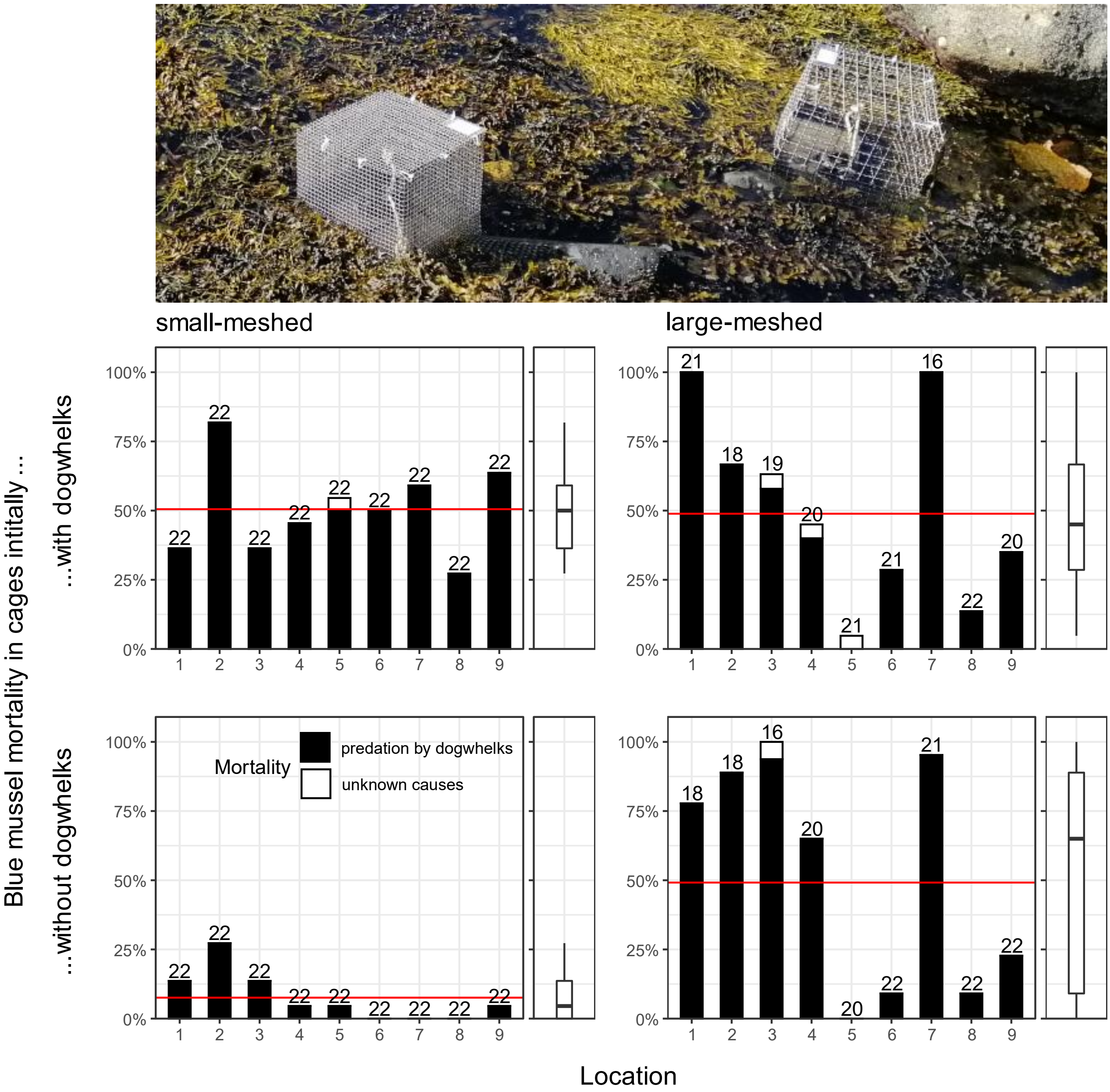

Figure 5: Blue mussel mortality (in %) in the four categories (from upper left to lower right): small-meshed cages with 10 dogwhelks added per cage, large-meshed cages with 10 dogwhelks added per cage, small-meshed cages without any dogwhelks added, and large-meshed cages without any dogwhelks added, after 8 weeks. Locations are comparable among categories. Mortality is divided into predation by dogwhelks (blue mussels that had completed drilling holes) and unknown causes (dead blue mussels without any completed drilling holes). The number of blue mussels that remained in each cage and contributed towards the analysis is on top of each bar, if no blue mussels went lost it equals 22. Red horizontal lines indicate mean mortalities within categories. Boxplots summarize data within categories. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. There are no outliers, observations >1.5 times the interquartile range beyond either end of the box. Some small dogwhelks managed to enter small-meshed cages and predated on blue mussels even in cages that were initially free from dogwhelks, explaining mortality from dogwhelks in the lower left panel.

Weekly visits revealed high active predator densities at some locations. Up to 19 dogwhelks were simultaneously handling blue mussels in large-meshed cages without dogwhelks added and 18 in large-meshed cages with dogwhelks added (Figure S2). In small-meshed cages with dogwhelks added, we observed a maximum of eight dogwhelks simultaneously handling blue mussels, and in small-meshed cages without dogwhelks added, a maximum of seven dogwhelks, all small enough to enter the mesh. The average number of active predators per visit was low ($\mu = 0.3$, $\sigma = 1.1$) for small-meshed cages without dogwhelks added and similarly higher (μ: 3.3-3.6) for the other three categories. For the latter, the number of active predators per visit was most stable for small-meshed cages with dogwhelks added ($\mu = 3.3$, $\sigma = 2.1$), indicating that dogwhelks were moving in and out through the large mesh (without dogwhelks added: $\mu = 3.6$, $\sigma = 5.2$; with dogwhelks added: $\mu = 3.5$, $\sigma = 4.2$). The numbers of dogwhelks per visit in cages where large dogwhelks were included or could enter (small-meshed cages with dogwhelks added and large-meshed cages with and without dogwhelks added) do not significantly differ from each other (Tukey HSD test, p values > 0.9), but they all differ significantly from the number of dogwhelks per visit in cages where large dogwhelks were excluded (small-meshed cages without dogwhelks added; Tukey HSD test, p values < 0.001). Also, location (two-way ANOVA, $p < 0.001$) and the interaction between location and cage category (two-way ANOVA, $p = 0.014$) significantly influenced the number of dogwhelks handling blue mussels. Comparing average numbers of dogwhelks drilling/feeding per visit with blue mussel mortalities within the same cages, we found a significant positive correlation (second order polynomial regression, $p < 0.001$; Figure 6). We did not observe any other predators than dogwhelks inside the cages, but we noticed a green crab just next to a large-meshed cage during one visit.

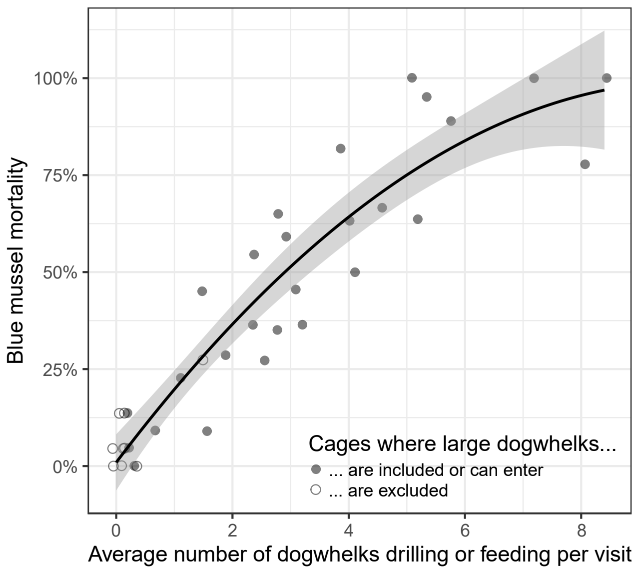

Figure 6: Correlation between average number of dogwhelks drilling or feeding per visit and blue mussel mortality (in %) in cages where large blue mussels were included or could enter and in cages where they were excluded. The black line is a second order polynomial regression with a 95% confidence interval ($p < 0.001$). Cages were visited 4-7 times, depending on weather conditions, during their 8 weeks in the field. Blue mussel mortality in cages excluding large dogwhelks is not always 0 as small dogwhelks managed to crawl in and out through the mesh.

Discussion

In this study we hypothesized that a crawling predator, unable to reach floating and free-hanging structures, drives the Norwegian blue mussel decline. Results from floating docks, rocky shores, and trees show that blue mussels continue to thrive in Norway when out of reach from crawling predators. All floating docks, as well as 83% of free-hanging trees and branches, were inhabited by blue mussels. In contrast, habitats accessible to crawling predators usually had no blue mussels. Only 18% of rocky shores and 1% of trees touching bottom were inhabited by blue mussels. We found that both the accessibility to crawling predators and tidal exposure predicted blue mussel occurrence. Blue mussels covered on average 65% (± 35% SD) of the submerged surface of the floating docks, whereas only 1% (± 1% SD) of the intertidal rocky shores. We did not find a single dogwhelk on any floating dock and the caging experiment confirmed that blue mussels continue to thrive when out of reach from predators. Blue mussels in cages where large dogwhelks were included or could enter experienced over six times higher mortality than blue mussels in cages where large dogwhelks were excluded, and also there, tiny dogwhelks were the cause of mortality. Blue mussel mortality in cages was positively related to the average number of dogwhelks drilling or feeding per weekly visit.

Proposed drivers of the Scandinavian blue mussel decline, such as climate change, pollution, disease, parasites, hybridization, and failed recruitment, have been attributed a role in blue mussel declines elsewhere but would affect blue mussels on floating structures to the same degree as blue mussels on any other substrate. The upper limit of blue mussels in the intertidal is controlled by thermal stress while air-exposed (Harley 2011) and duration of submergence to permit sufficient feeding. One could argue that constantly submerged blue mussels on floating docks are sheltered from temperature extremes and can feed continuously, compared to those on rocky shores experiencing air exposure during each tidal cycle. However, blue mussels on trees hanging from land into the water are subject to the tidal cycle, nevertheless they revealed the same pattern: blue mussels were absent on trunks and branches touching the seafloor but present on those hanging freely in open water. Pooling floating docks, rocky shores, and trees together, both accessibility to crawling predators and tidal exposure significantly influenced blue mussel occurrence. The influence of tide was due to lower occurrence of blue mussels on trees and branches without bottom contact (83±5.1%) compared to floating docks (occurrence of 100±0%); because most branches are markedly smaller habitats than a floating dock, the sheer difference in habitat size could also influence blue mussel occurrence and inflate the perceived effect of tidal influence. Already Suchanek (1978) observed that floating docks provide blue mussels with a refuge from predators and abundant food, and that the related California mussel (*Mytilus californianus*) on floating docks could reach a maximum size of 140 mm, in contrast to 40 mm or less on natural rocky shores. Our findings from the floating docks, rocky shores, and trees align with those of the caging experiment, where blue mussels continue to thrive when out of reach from predators. Mortality due to other causes than predation was almost non-existent in any of the cages. All this supports our hypothesis that a crawling predator, unable to reach floating and free-hanging structures, must be behind the Norwegian blue mussel decline.

Mobile subtidal predators are known to have high impacts on intertidal invertebrates: a range of predators feed efficiently on newly settled blue mussels during high tides (Rilov & Schiel 2006) and sea stars graze adult blue mussels too (Paine 1974). In the Wadden Sea, recent blue mussel declines are uncoupled from overharvesting and driven by frequent recruitment failures after warm winters (Beukema & Dekker 2007). Epibenthic predators, such as crabs and shrimps, are suggested to be behind these recruitment failures (Beukema & Dekker 2007) so that global warming can lead to increased predation pressure on bivalves (Beukema & Dekker 2005). On the east coast of North America, blue mussel settlings disappeared fully from eelgrass communities just a few weeks after initially high larvae settlement (Bologna et al. 2005). The low recruitment was linked to years with hot summers and high densities of benthic predators such as sea stars and crabs (Bologna et al. 2005). Common sea stars *Asterias rubens* and green crabs *Carcinus maenas* feed effectively on small blue mussels in Norway (Bodvin 1984, Christie 1983, Christie et al. 2020). Green crabs have increased in Scandinavia (Infantes et al. 2016), probably due to overfishing of top predators like cod *Gadus morhua* (Christie et al. 2020). Green crabs showed the potential to diminish blue mussel recruits drastically within few hours in mesocosms and could therefore, together with other mesopredators released from predation pressure, contribute to the Norwegian blue mussel decline (Christie et al. 2020). Green crabs grab blue mussels with their chelae and use the larger one to crush their shells (Elner & Hughes 1978). They eat small blue mussels (Christie et al. 2020) and size of preferred prey correlates positively with size of green crab, mostly restricted to shells <40 mm (Elner & Hughes 1978).

Reports from the public show that well-established blue mussel beds in Norway, where collection occurred for more than a decade, disappeared over 1-2 years, starting from 2015 (Andersen et al. 2017). This suggests that large adult mussels also died, and that focus must extend beyond the juvenile life stage. Common sea stars can handle larger blue mussels than green crabs (Dolmer 1998), but their consumption rate is much lower (Kamermans et al. 2009). They open small blue mussels with short force impulses that increase rapidly in strength, and handle larger mussels through exhaustion of the posterior adductor muscle by applying force for an extended period (Norberg & Tedengren 1995). Another strategy they use is to besiege the mussel, waiting for it to open its valves; a small gap between the valves is enough for them to insert their stomach into the cavity and digest the mussel inside its shell (Norberg & Tedengren 1995). Small sea stars could possibly have entered large-meshed cages and be responsible for the death of the two blue mussels without any predation marks. *A. rubens* has pelagic larvae (Barker & Nichols 1983) and floating structures are therefore not completely isolated from it. We even observed a few small sea stars (diameter <100 mm) on floating docks. In this study, blue mussels found on rocks were either in low salinity habitats or grew protected in cracks, factors that limit the access of predators and both sea stars (Binyon 1961) and dogwhelks (Stickle et al. 1985b) have low tolerance to freshwater.

Dogwhelks *Nucella lapillus* are distributed all along the Norwegian coast (Schøyen et al. 2019) except for freshwater-influenced inner parts of fjords (Brattegard 1966) and they mainly prey on blue mussels and barnacles (Colton 1916). Dogwhelks secrete inorganic acid to soften their prey's shell while drilling with their micro-toothed radula (Carriker 1981). Once the hole is completed, they inject digestive enzymes and insert their long proboscis to feed on dissolved flesh not immediately accessible (Carriker 1981). They successfully drill blue mussels as large as 131 mm (personal observation). The caging experiment confirmed that dogwhelks feed effectively on medium-sized and large blue mussels (40-80 mm) under natural conditions and that they managed to decimate blue mussels within a few weeks. We expect dogwhelks to have an even higher impact on blue mussel beds with small individuals, as feeding rates on juvenile blue mussels are much higher (Freeman & Hamer 2009). More than half of the empty blue mussel shells collected in southern England over a two years study from 2006 to 2008 were drilled (Morton 2011). In Alaska, it was a predatory snail, *Nucella lima*, that hindered blue mussels from regaining spatial dominance after their mass mortality in winter 1988-1989 (Carroll & Highsmith 1996). Another factor that makes dogwhelks a likely suspect in the recent blue mussel decline is the fact that they are recovering worldwide from pollution-induced sterility (Schøyen et al. 2019). Tributyltin (TBT) was developed in the 1960s and widely used in antifouling paints on ships from the 1970s (IMO 2002). This organotin compound triggers imposex, the imposition of male organs on females, in *N. lapillus* and many other marine gastropods (Bryan et al. 1987, Gibbs et al. 1987). In the 1980s, high TBT concentrations were found worldwide and as a consequence several countries, including Norway in 1989, restricted the use of TBT to commercial vessels (IMO 2002). TBT became globally banned in 2008 (IMO 2002). It is now reduced to low levels in the environment and 2017 was the first year imposex was not found any more in *N. lapillus* along the Norwegian coast (Schøyen et al. 2019). Increasing predator populations could have large effects on their prey. More indirect mechanisms, for example through non-consumptive effects where blue mussel larvae avoid settling in areas with waterborne dogwhelk cues (Ehlers et al. 2018), can further affect local distribution and population dynamics.

Another predatory gastropod that was affected by TBT pollution is the netted dogwhelk *Tritia reticulata* (Stroben et al. 1992). It is found along most of Norway's coastline, but its core distribution is further to the south (GBIF 2022c, OBIS 2022c). It can be found from the Canary Islands to Norway, throughout the Mediterranean, Black Sea, and North Sea (GBIF 2022c, OBIS 2022c). Although this species is common around rocky shores, it prefers patches of soft sediment (Tallmark 1980). Unlike *N. lapillus*, but like most other members in the family Nassariidae (also known as mud snails), they are burrowers with a preference for organic substrate (Davenport & Moore 2002, Tallmark 1980). While they are occasionally found in *Mytilus* beds, they might be attracted because mussel beds act as sediment traps (Tallmark 1980). *T. reticulata* is euryhaline and often found in the intertidal where freshwater streams run into the sea (Barnett et al. 1980). In Norway, this is one of the few refugia where blue mussels still thrive (personal observation). Further, *T. reticulata* is more often described as scavenger than as carnivore, as it lies buried in the sediment until triggered by the scent of carrion (Crisp 1978, Davenport & Moore 2002, Tallmark 1980). All this suggests that *T. reticulata* is not a likely culprit for the observed large-scale decline of blue mussels in Norway.

The above-mentioned predator-prey interactions are complex. Blue mussels have a high phenotypic plasticity and respond to waterborne predator cues. If dogwhelks are around, mussels grow thicker shells (Sherker et al. 2017); if they sense sea stars, they invest in a stronger adductor muscle (Freeman 2007, Reimer & Tedengren 1996); and if crabs are present, they increase their byssus production to attach themselves more firmly to the substrate (Côté 1995, Leonard et al. 1999). Mussels even show active defence by trapping dogwhelks with byssus threads and leave them immobilized (Farrell & Crowe 2007, Petraitis 1987). Predators also interact with each other. Predation attracts scavengers, such as the polychaete worm *Eulalia viridis* (Morton 2011) and the common whelk *Buccinum undatum* (Christie 1983), and co-consumption by two species can more efficiently reduce blue mussel abundance (Christie et al. 2020). However, green crabs also prey on dogwhelks (Hughes & Elner 1979) and suppress dogwhelks' feeding activity through non-consumptive effects (Bourdeau & Padilla 2019, Quinn et al. 2012) in the same way as sea stars (Gosnell & Gaines 2012). Changing environmental conditions can cause shifts in the dominance of intertidal predator species (Menge 1983). Such changes in species composition and species abundance can drive cascading community shifts (Sorte et al. 2017).

Conclusion

Data collected on floating docks, rocky shores, and trees reveal that accessibility to crawling predators is a significant predictor for blue mussel occurrence: blue mussels were present on floating docks and free-hanging trees and branches, whereas they were largely absent on rocky shores and bottom-connected trees and branches. The caging experiment confirmed that blue mussels continue to thrive when out of reach from predators. All our data support our hypothesis that the Norwegian blue mussel decline is driven by a crawling predator. The caging experiment revealed that dogwhelks feed effectively on medium-sized and large blue mussels. Blue mussel mortality in cages correlated positively with the average number of dogwhelks observed drilling or feeding. Dogwhelk populations recovering from pollution-induced sterility could play an important role in the Norwegian blue mussel decline and might be responsible for a new ecosystem state with few blue mussels.

Data availability statement

When the manuscript is accepted, all data will be available in a public repository such as datadryad.org.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Author contributions

All authors designed the study, participated in field excursions and setting up experiments; NM conducted the caging experiment; NM curated the data; NM and TJL analysed data and coded figures with input from all co-authors; NM and CJ wrote the manuscript with input from all co-authors. All authors have consented to their authorship and have approved the manuscript for publication.

Conflict of interest

The authors declare no conflicts of interest.

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Supplementary figures

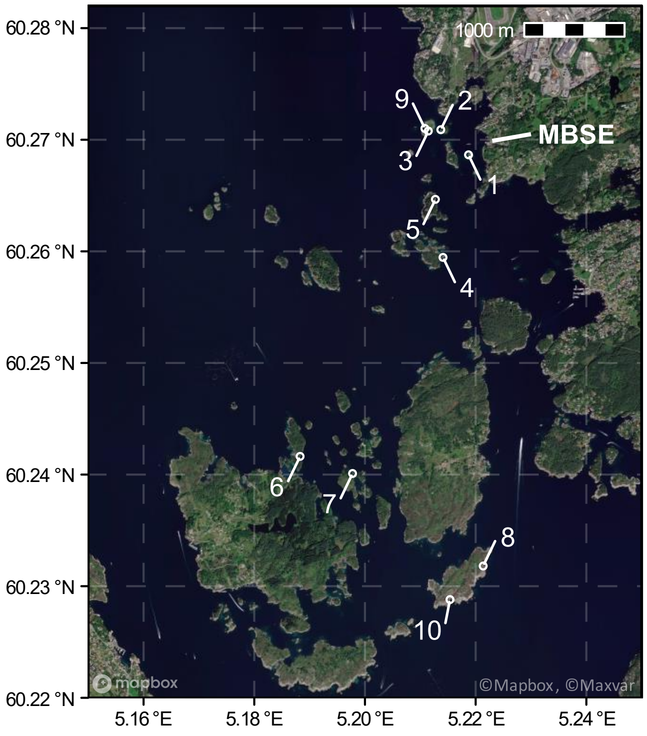

Figure S1: Cage locations in Raunefjorden within ~4.5 km from the Marine Biological Station Espegrend (MBSE). At location 10, we had to stop the experiment due to rough weather dragging the cages into deeper water, it is therefore excluded from analyses. Satellite images courtesy of ©Mapbox, ©Maxvar.

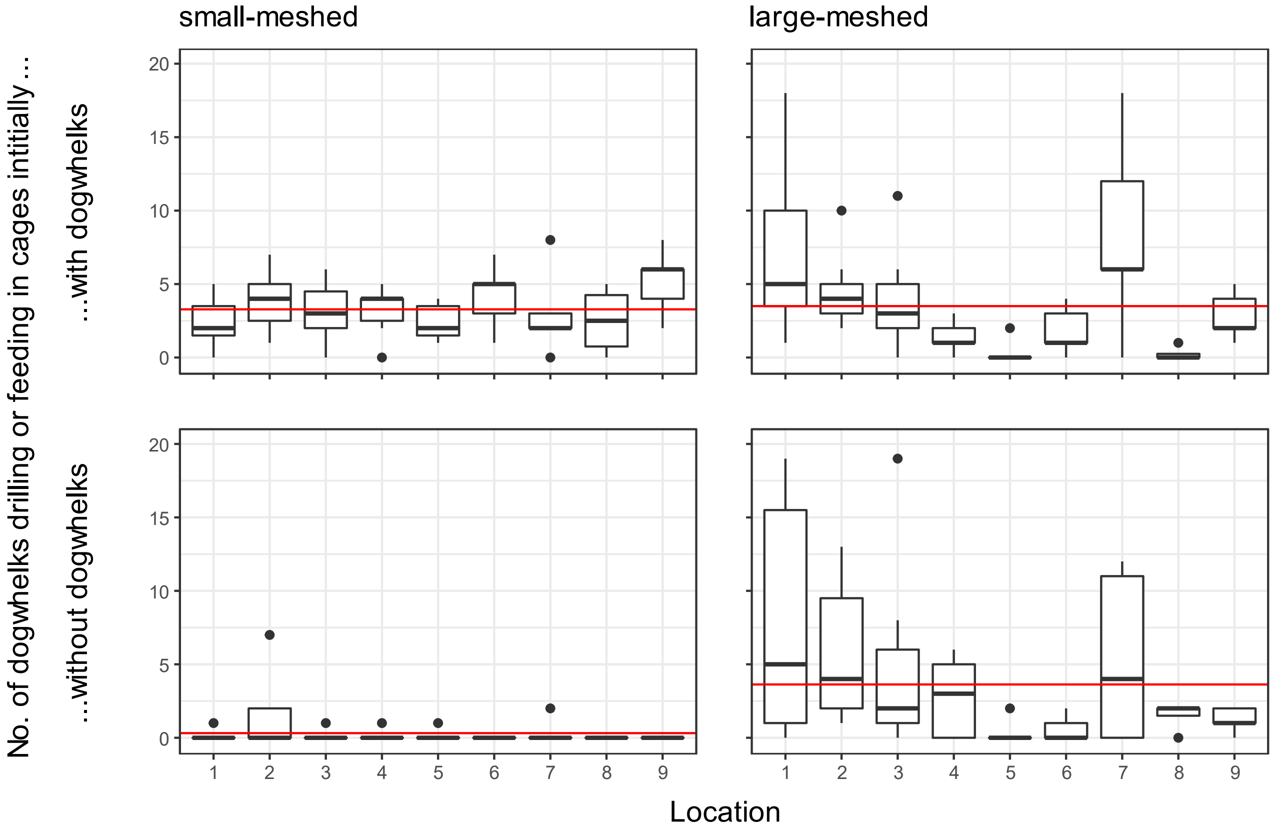

Figure S2: Number of prey-handling dogwhelks observed in each cage per visit for the four categories: small-meshed cages with 10 dogwhelks added per cage, large-meshed cages with 10 dogwhelks added per cage, small-meshed cages without any dogwhelks added, and large-meshed cages without any dogwhelks added. Cages were visited 4-7 times, depending on weather conditions, during their 8 weeks in the field. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. Outliers are >1.5 times the interquartile range beyond either end of the box and denoted by dots. Red horizontal lines indicate mean numbers of prey-handling dogwhelks within categories.

Chapter II

The feeding and crawling potential of the dogwhelk *Nucella lapillus*

Introduction

Background

Blue mussels (*Mytilus* spp.) continue to thrive on floating and free-hanging structures in Norway despite their large-scale decline on rocky shores (Chapter I). The only likely cause creating such a pattern is a crawling predator without pelagic eggs or larvae, unable to reach blue mussels on floating and free-hanging structures (Chapter I). Scanning floating docks, rocky shores, and trees hanging from land into the sea for blue mussels revealed that whether crawling predators can access the habitat is key to determining blue mussel occurrence, and predator exclusion experiments confirmed that blue mussels continue to thrive when out of reach from such predators (Chapter I).

The dogwhelk *Nucella lapillus* is a known ferocious crawling predator on blue mussels (Colton 1916). Dogwhelks feed predominantly on small (ca. 25 mm) blue mussels (Hughes & Dunkin 1984a), but they also have high feeding impacts on medium-sized and large (40-80 mm) blue mussels (Chapter I). They secrete inorganic acid to soften blue mussels' shell while drilling with their micro-toothed radula (Carriker 1981). They preferably drill at the most accessible position, the thin postero-dorsal quadrant, or the most nutritious position, the antero-dorsal quadrant over the digestive gland (Hughes & Dunkin 1984a, Morton 2010). Once the hole is completed, they inject digestive enzymes and insert their long proboscis to feed on dissolved flesh not immediately accessible (Carriker 1981). Dogwhelks ingest up to three times faster when feeding on blue mussels exposed to warm temperatures and air during low tide, but too hot temperatures, sea water ≥20°C or air ≥28°C, reduce whelks' feeding rates (Stickle et al. 1985b, Yamane & Gilman 2009). To avoid thermal extremes during low tides, the related Northern striped dogwinkle *Nucella ostrina* plans ahead; it feeds preferably on the sides of the rocks that are shaded during low tides (Hayford et al. 2015), and avoids extreme low tides around midday (Hayford et al. 2018). Such choices of microhabitats are based on the semi-lunar tidal cycle and can thermoregulate snails and therefore buffer them from warming (Hayford et al. 2021).

In addition to dogwhelks’ complex feeding behaviour, the evolutionary arms race between prey and predator is highly dynamic. Blue mussel larvae avoid to settle in areas where they sense waterborne dogwhelk cues (Ehlers et al. 2018). They use a long byssus thread to sail through the water and can reel themselves in for settlement when they get in touch with a suitable structure (De Blok & Tan-Maas 1977), but if they sense dogwhelks they can detach and relocate (Ehlers et al. 2018). Blue mussels exposed to dogwhelks increase shell thickness (Sherker et al. 2017) and byssus thread production (Farrell & Crowe 2007). They actively defend themselves by trapping dogwhelks with byssus threads, which leaves them immobilized (Farrell & Crowe 2007, Petraitis 1987). The risk of being trapped and facing a slow death by starvation is lower along the margins than within the blue mussel beds (Davenport et al. 1996) and could explain the reduced dogwhelk densities towards the centre of the beds (Petraitis 1987). Blue mussel mortality is highest along margins of the beds and blue mussels move up to 0.1 m per month to take over the favoured safer spots in the centre of the beds (Nicastro et al. 2008). However, blue mussels are capable to repair drilling holes within a few weeks if dogwhelks are removed before they inject digestive enzymes that cause lethal damage (George et al. 2022). Dogwhelks prefer the prey, blue mussels or barnacles, that they are used to feed on and that usually appears in higher relative abundance (Burrows & Hughes 1991b, Hughes & Dunkin 1984b). They become more efficient in handling a prey species with practice (Dunkin & Hughes 1984, Hughes & Dunkin 1984a).

Dogwhelks are distributed all along the Norwegian coast (GBIF 2022b, OBIS 2022b) and highly suspect in the blue mussel decline as they recently recovered in Norway from pollution-induced sterility (Schøyen et al. 2019). Tributyltin (TBT) is an organotin compound used in antifouling paints on ship hulls since the 1960s (IMO 2002). It triggers imposex, the imposition of male organs on females, in marine gastropods, which at later stages can result in sterilization through the blockage of the oviduct by vas deferens formation (Bryan et al. 1987, Gibbs et al. 1987). A few ng/l of TBT is enough to induce sterilization in dogwhelks, leading to population declines (Bryan et al. 1987). A stepwise TBT ban started in many European countries with restrictions on small vessels (< 25 m) in the 1980s (1989 in Norway) (IMO 2002). In 2008, TBT became globally banned (IMO 2002). As a result, decimated dogwhelk populations started to recover worldwide (Synthesis chapter) and 2017 was the first year dogwhelks were free from imposex in Norway (Schøyen et al. 2019). Recent population boosts might have increased dogwhelks’ energetic demands with cascading effects on their blue mussel prey. Therefore, we hypothesize that dogwhelks, released from TBT-induced reproductive depression, are behind the Norwegian blue mussel decline.

In Norway, blue mussels continue to thrive when out of reach from predators, but they decline drastically in the presence of dogwhelks (Chapter I). While Chapter I provided evidence that a crawling predator is most likely behind the Norwegian blue mussel decline and outlined dogwhelks' high impact on blue mussel mortality, dogwhelks' feeding and crawling potential to cause a decline of the observed magnitude and pattern remains unknown. In the present study, we aimed to start filling this knowledge gap by conducting pilot experiments in small (≤60 l) mesocosms at the Marine Biological Station Espegrend (MBSE). These experiments assessed i) dogwhelks' feeding capacity to drive a country-wide blue mussel decline and ii) if Norwegian blue mussel refugia are out of reach from dogwhelks. A set of pilot experiments focused on the former and investigated dogwhelks' efficiency to drill and feed on blue mussels of various sizes, if growing large protects blue mussels from dogwhelks, if juvenile dogwhelks can handle medium-sized blue mussels, and if dogwhelks can switch to feed on other bivalves when their main prey (blue mussels and barnacles) becomes scarce.

Not only floating and free-hanging structures but also low salinity habitats, current and wave exposed sites, muddy bays, and cracks in rocks provide refuge for blue mussels in Norway (personal observation, Synthesis chapter). Dogwhelks have no pelagic stage, they lay eggs in little capsules preferably placed within cracks or below macroalgae in the intertidal (Colton 1916). To feed on blue mussels on floating docks, they would need to crawl up chains or ropes that hold floating docks in place. Even though we have not found a single dogwhelk on floating and free-hanging structures during our fieldwork (Chapter I), we need to investigate their potential for reaching blue mussels on floating structures. Therefore, we set up pilot experiments testing dogwhelks' abilities to crawl up chains and ropes. We compared the results with dogwhelks' abilities to crawl up concrete bricks and branches that represent structures where blue mussels largely disappeared, such as rocky shores and trees hanging from land into the sea and touching bottom. Additionally, we conducted a pilot experiment testing dogwhelks' ability to cross soft bottoms, a refugium where blue mussels continue to thrive on small rocks and associated macroalgae in Norway (personal observation). In addition to analysing dogwhelks' feeding and crawling potential to cause the Norwegian blue mussel decline, we aimed to identify alternative crawling predators with high impacts on blue mussels.

Structure

This exploratory study contains seven pilot experiments. Each pilot experiment had a different focus: #1 focused on predation rates of adult dogwhelks; #2 on the ability of dogwhelks to crawl up vertical structures; #3 on the ability of dogwhelks to cross soft bottoms; #4 on the drilling capacity of juvenile dogwhelks; #5 on the ability of dogwhelks to drill large blue mussels; #6 on potential alternative prey for dogwhelks; and #7 on potential alternative predators of blue mussels. The aim of conducting pilot experiments was to get a broad insight into dogwhelks' behaviour, to identify which experimental set-ups work well and how we can improve them for future studies, as well as to point out the direction of indicative trends, rather than to conduct statistical analyses and obtain firm conclusions. As all pilot experiments were conducted at the MBSE under similar conditions, we continue the chapter with a general material and methods section and go subsequently step-by-step through all pilot experiments by looking at experiment-specific methods, results, natural history observations (only for some of the pilot experiments), and discussions. In a general discussion section, we pool all results together, discuss limitations, and how these could be overcome in future studies. We end the chapter with a short conclusion.

General material and methods

Experiments

In June and July 2021, we set up experiments in 64 beakers outside at the MBSE. All beakers received constant seawater input, pumped from 10m depth in Raunefjorden, right outside the station (Figure 1). To ensure that the flow rate in all beakers was similar, all water hoses were cut to the same length and fitted with a regulating valve that allowed for manual adjustments of the water flow. We used 16 round 20-liter beakers for the walkway experiment, 42 round 7.5-liter beakers for the predation rate, alternative predator, alternative prey, small dogwhelk, and large blue mussel experiments, and six 0.35 x 0.5 x 0.35 m aquaria for the substrate experiment. We collected blue mussels from floating structures of the MBSE and dogwhelks from rocky shores nearby. We cleaned blue mussels' shells from barnacles and other biofouling and kept dogwhelks without food for 5-10 days prior to the experiments to clear their digestive tracts and generate hunger. We measured dogwhelks' length, from apex to siphon canal, and blue mussels' length, from anterior to posterior end, to the nearest mm. We used thin stainless-steel wire to secure blue mussels to objects, so that they could not change their position within the beakers but still were able to open their valves to filter feed.

The first experiments started on the 23rd of July 2021 and the last ones ended on the 17th of November 2021. We ran multiple replicates within this time, each replicate contained new blue mussels and dogwhelks. We inspected experiments and documented results at least three times per week (usually on Mondays, Wednesdays, and Fridays). Additionally, we recorded salinity and temperature with a handheld salinometer. With help of a webcam, we kept daily track of the water pump and assured that beakers were continuously provided with oxygenated and nutritious sea water. We covered all beakers with mosquito nets to prevent dogwhelks from escaping. Once the dogwhelk left its prey, we recorded if the blue mussel was completely eaten or just parts of it, and we collected the shells and labelled them for future analyses. We cleaned the beakers and aquaria once per month, during periods when dogwhelks were not feeding.

Figure 1: Experimental set-up at the Marine Biological Station Espegrend. Constant sea water supply from 10 m depth provided the 64 beakers and aquaria with nutrients and oxygen.

Data analysis

We calculated minimum prey handling times by taking the number of days between the date we first observed a dogwhelk drilling or feeding and the date we last observed the dogwhelk drilling or feeding if the action resulted in a completed drilling hole. We added i) half of the number of days between the last date we checked the experiment before we first observed the dogwhelk drilling or feeding and the date of the first drilling or feeding observation, and ii) half of the number of days between the date of the last drilling or feeding observation and the date we first observed the dogwhelk to not drill or feed anymore (Figure 2). This gave us as precise estimates of prey handling times as possible. We used the same method to calculate starving and prey approaching times, taking the average of the maximum and the minimum possible starving or prey approaching time spans, respectively.

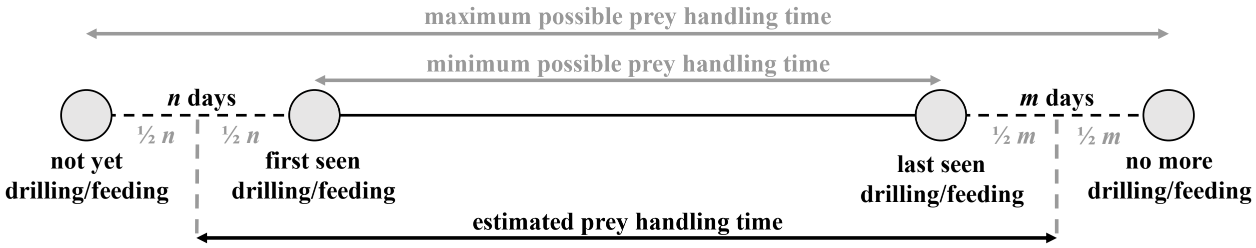

Figure 2: The estimated prey handling time was calculated by taking the minimum possible prey handling time and adding i) half of the number of days between the last date we checked the experiment before we first observed the dogwhelk drilling/feeding and the date of the first drilling/feeding observation, and ii) half of the number of days between the date of the last drilling/feeding observation and the date we first observed the dogwhelk to not drill/feed anymore. The estimated prey handling time is also the average of maximum and minimum possible prey handling times.

We conducted all analyses in R version 4.1.1 (R Core Team 2021). We calculated time spans between dates using “lubridate” (Grolemund & Wickham 2011). We produced figures using “ggplot2” (Wickham 2016) and combined them using “patchwork” (Pedersen 2020). We did not apply any statistical analyses due to the small sample sizes of the pilot experiments.

Pilot experiments

Pilot experiment 1 – Predation rates

Methods

We placed one dogwhelk and four blue mussels from the same size class at the bottom of each beaker. All dogwhelks were between 25 and 35 mm and blue mussels within one of five size classes: 0-20 mm, 20-40 mm, 40-60 mm, 60-80 mm, and 80-100 mm. The aim was to determine predation rates on different sized blue mussels. During our inspections, we recorded whether dogwhelks were feeding or drilling on blue mussels or not. With help of this data, we reconstructed the time dogwhelks spent before drilling, while drilling and feeding, and in between handling two blue mussels. We removed, measured, and labelled predated blue mussels. The experiments ended when all four blue mussels were eaten, and new replicates were set up.

Results

Adult dogwhelks increased their prey handling time i.e., the time spent drilling and feeding, with size of their blue mussel prey (Figure 3). Dogwhelks required 0.5 to 4.5 days (μ = 1.7 days, σ = 0.8 days) to handle blue mussels up to 20 mm, 1-12 days (μ = 5 days, σ = 2.8 days) for blue mussels sized 20-40 mm, 2-24.5 days (μ = 9.9 days, σ = 6.3 days) for blue mussels sized 40-60 mm, 1-42.5 days (μ = 12.4 days, σ = 8.9 days) for blue mussels sized 60-80 mm, and 2.5-52.5 days (μ = 23.8 days, σ = 18 days) to handle the largest blue mussels (80-100 mm). We excluded one blue mussel (60-80 mm), that died during the experiment without being predated, from the analyses. Salinity was rather constant throughout the experiment at 31.1-32.4 PSU. Water temperature was always above 13°C and peaked towards the end of August with 16.5°C.

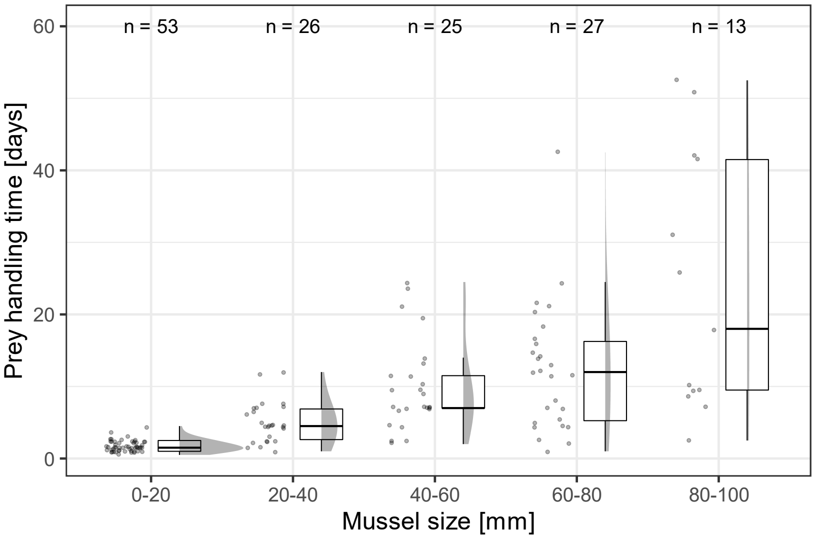

Figure 3: Number of days adult dogwhelks spent handling a single blue mussel from different size classes: 0-20 mm, 20-40 mm, 40-60 mm, 60-80 mm, 80-100 mm. Numbers on top indicate the number of observations per blue mussel size class. Dots represent single observations and the grey curved areas their density distributions. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile.

There was no clear trend in starving times i.e., the time a dogwhelk spent before it started drilling a blue mussel (Figure 4). Starving times were similar for all sizes of blue mussels but slightly shorter for the smallest blue mussels (0-20 mm: μ = 5.1 days, σ = 9.4 days; 20-40 mm: μ = 12.4 days, σ = 10.8 days; 40-60 mm: μ = 15 days, σ = 13.4 days; 60-80 mm: μ = 7.3 days, σ = 9 days; 80-100 mm: μ = 13.2 days, σ = 10.7 days). Furthermore, we found no clear difference in dogwhelks’ starving times before feeding on their first, second, third, or fourth blue mussels (Figure 4).

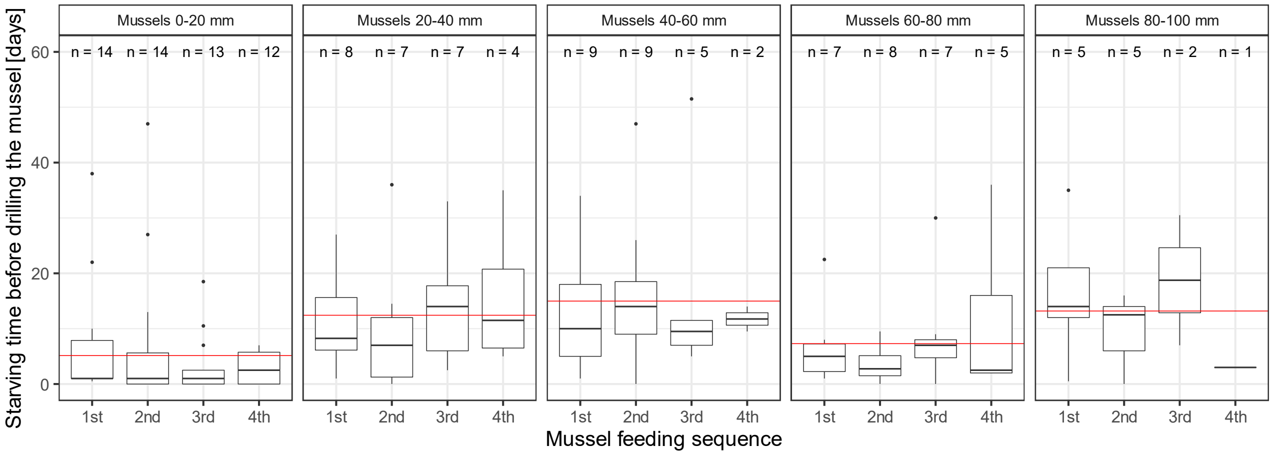

Figure 4: Starving times, the time a dogwhelk spent before it started drilling a blue mussel, in days across the different size classes and for each of the four blue mussels within a replicate. Numbers on top indicate the number of observations per blue mussel size class. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. Outliers are >1.5 times the interquartile range beyond either end of the box and denoted by dots. Red horizontal lines indicate mean starving times within categories.

The total time an adult dogwhelk needed to drill and feed all four blue mussels, starting when the dogwhelk was positioned on the first blue mussel and ending when it left the fourth blue mussel, increased with blue mussel size (Figure 5). Only 24 dogwhelks out of 45 replicates managed to consume all four blue mussels and were included in this analysis. On average, dogwhelks spent 21 days (± 15.1 days SD) to consume four 0-20 mm blue mussels, 68.8 days (± 13 days SD) for four 20-40 mm blue mussels, 78.5 days (± 14.8 days SD) for four 40-60 mm blue mussels, 73.8 days (± 13 days SD) for four 60-80 mm blue mussels, and 97 days for four 80-100 mm blue mussels. The times spent on blue mussels sized 20-80 mm were not markedly different from each other. When feeding on the smallest (0-20 mm) blue mussels, dogwhelks managed to feed up to

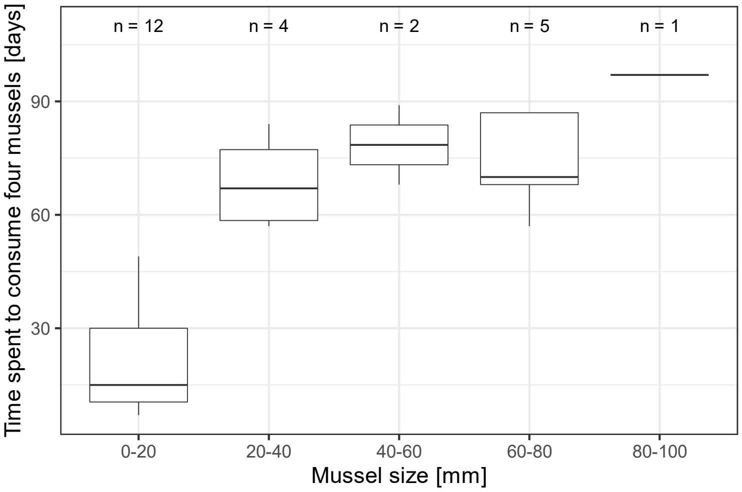

Figure 5: Time, number of days, that an adult dogwhelk spent to consume four blue mussels of a certain size class in a row. Numbers on top indicate the number of observations per blue mussel size class. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. There are no outliers, observations >1.5 times the interquartile range beyond either end of the box.

three blue mussels within the maximum three days between two successive observations. There was no apparent size preference within size classes: 21% of dogwhelks started to feed on the smallest of the four blue mussels first, 25% on the second smallest, 37% on the second largest, and 17% on the largest.

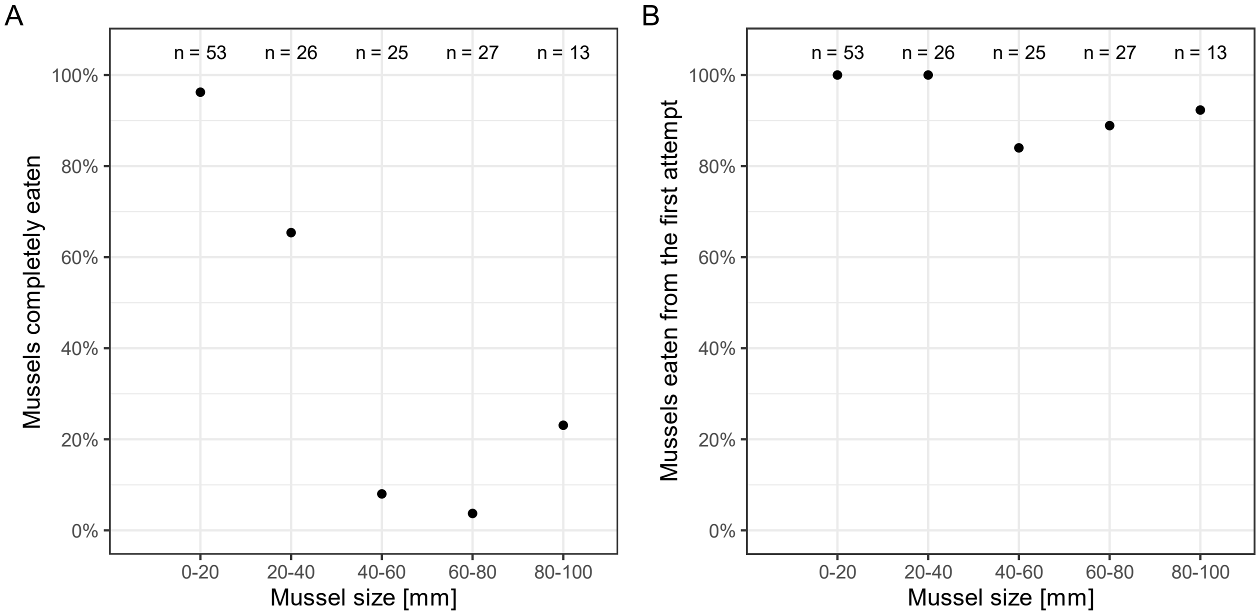

Figure 6: Percentage of blue mussels per size class that was completely eaten by dogwhelks without any leftovers of flesh (A), and percentage of blue mussels that was successfully drilled during dogwhelks' first attempt and subsequently eaten (B). Numbers on top indicate the number of observations per blue mussel size class.

Dogwhelks often left drilling holes behind without eating all the flesh inside the shells (Figure 6A). Small to medium-sized blue mussels were an exception; 96% of dogwhelks feeding on blue mussels sized 0-20 mm managed to eat the flesh completely, and 65% of dogwhelks feeding on blue mussels sized 20-40 mm. This percentage dropped for larger blue mussels, to 8% and 4% for 40-60 mm and 60-80mm blue mussels, respectively. It slightly increased for the largest, 80-100 mm, blue mussels to 23%. Dogwhelks usually managed to complete their first drilling attempt and to feed successfully on the blue mussel, but sometimes, when drilling on medium-sized to large (40-100 mm) blue mussels, they needed a second or third attempt at a different position on the shell to successfully make a hole (Figure 6B). When blue mussels were only partly eaten, it was the foot, posterior adductor muscle, and mantle margin that were left over (Figure 7).

Figure 7: Blue mussel abandoned by dogwhelk after feeding. Left behind are foot, posterior adductor muscle, and part of the mantle.

Natural history observations

A few dogwhelks laid up to 13 egg capsules during the experiment. Egg capsules were yellow coloured and approximately 5 mm long (Figure 8). They were laid on top of blue mussels or along the walls of the beakers.

When not feeding on blue mussels, dogwhelks preferred to stay close to the mosquito nets covering the beakers, on the interface of water and air. Some even managed to crawl upside-down across the mosquito nets.

Figure 8: Dogwhelks' egg capsules laid on top of a previously drilled and eaten blue mussel.

Once drilled, blue mussels that were only partly eaten and left behind did not always open their valves immediately. Especially large blue mussels often took a few (up to 7) days until their posterior adductor muscles lost strength and their valves started to open.

Two blue mussels of the smallest size class were eaten without being drilled. Dogwhelks likely injected enzymes through the opening of the valves. Another blue mussel of the same size class had a narrow semi-circular hole next to the opening.

One dogwhelk managed to complete a drilling hole, but it probably got removed by the blue mussel (80-100 mm) before it injected its digestive enzymes. Therefore, the blue mussel survived the first drilling attempt. However, the dogwhelk immediately started a second drilling attempt and was successful. It consumed the blue mussel completely. Unfortunately, we could not distinguish between the two drilling events as the dogwhelk was continually positioned on the blue mussel during the inspections. The dogwhelk needed ca. 7.5 weeks from starting to drill the first hole until finishing to feed through the second hole. Within this time, the blue mussel started repairing the first drilling hole (Figure 9).

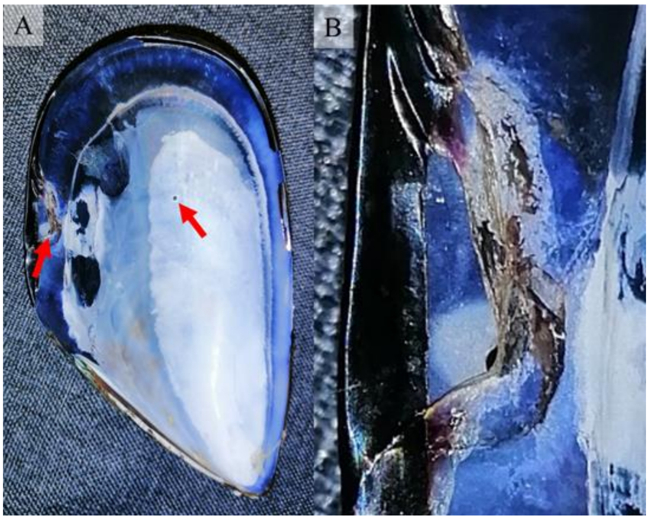

Figure 9: (A) A blue mussel (82 mm) with two drilling holes, which are marked with red arrows, and (B) a close-up on the drilling hole where the blue mussel started repairing the shell damage.

Blue mussels first cover the drilling hole with an organic membrane, and subsequently deposit calcite crystals and aragonite tablets to repair the shell damage (George et al. 2022). This process takes 7-10 weeks (George et al. 2022).

Discussion

Our results showed a positive correlation between prey handling time and blue mussel size. This was most likely triggered by the increased shell thickness of larger blue mussels, which results in prolongated drilling times (Hughes & Dunkin 1984a). It is not surprising that prey handling times of a certain blue mussel size class overlapped with the ones of blue mussels one size class smaller and larger, as blue mussel size classes were continuous and overlapping by 1 mm. Additionally, some blue mussels, primarily small ones that were not immediately drilled, grew during the experiment, so that some that were previously on the upper border of a size class had entered the next size class before being drilled. Nevertheless, they were counted in their original size class due to their function in the experimental design (one dogwhelk with four blue mussels), which could also have contributed to an overlap between the prey handling times of bordering size classes. However, we recorded a clear gradual increase of prey handling time with blue mussel size. Temperature and salinity showed little fluctuation throughout the entire experiment. Both stayed close to the optimal conditions, 15°C and 30 PSU, that result in highest ingestion and feeding rates in dogwhelks (Stickle et al. 1985b). Miller (2013) calculated feeding rates of juvenile dogwhelks (12-15 mm) on small blue mussels (10-17 mm) under conditions similar to the ones in this study (i.e., starving of dogwhelks prior to the experiment, similar temperature range, and no tidal cycles) and found that drilling and ingestion combined take about 1-3 days, which is very similar to our results for the smallest blue mussel size class (0.5-4.5 days, $\mu = 1.7$ days). Also, other conditions were beneficial: there were no predators or competitors for dogwhelks, no waves or strong currents causing dislodgement of dogwhelks, and no desiccation stress as dogwhelks were constantly submerged. All these factors may have contributed to elevated feeding rates. On the other hand, aerial exposure during low tides can increase dogwhelks' feeding rates up to three times (Stickle et al. 1985b).

We have not found any clear trend in dogwhelks' starving times i.e., the time before consuming the first blue mussel or in between consuming successive blue mussels, regarding blue mussel size. For the smallest blue mussels (0-20 mm) the time a dogwhelk waited until it started drilling and feeding was slightly less than for larger blue mussels. This might be explained by our results that showed that dogwhelks usually ate small blue mussels completely and left flesh in larger blue mussels behind. This is a known behaviour (Morton 2011) and the reason for it could be that the dogwhelks' guts fill up quickly because dogwhelks are able to ingest food faster than they digest (Burrows & Hughes 1991a), as well as by dying blue mussels that start to open their valves, which could make it harder for dogwhelks to suck the remaining tissue out of the drilling hole. We did not observe any dogwhelk positioned on the inside of valves to feed on the remaining tissue, which could confirm that their guts were full after feeding through the drilling holes. Often, we found the foot, posterior adductor muscle, and mantle margin left behind. These are the same organs that another blue mussel drilling marine gastropod, the banded dye-murex *Hexaplex trunculus*, usually leaves behind (Peharda & Morton 2006). The banded dye-murex is distributed in the Eastern Atlantic and Mediterranean: from France to Spain, Portugal, Morocco, Madeira Island, and Canary Islands (GBIF 2022a, OBIS 2022a), and therefore not further considered in this study. Similarly, in their study about dogwhelks' feeding behaviour on blue mussels, Hughes and Dunkin (1984a) found that the discarded flesh is predominantly from the mantle and foot. This might reflect differences in solubility and nutritional value of body parts. Additionally, they found that the percentage of mussel flesh extracted by adult dogwhelks decreased from 90% for 10 mm blue mussels to 60% for 40 mm blue mussels (Hughes & Dunkin 1984a).

In contrast to our findings, Bayne and Scullard (1978) found an allometric relation between prey size and duration of the post-feeding phase i.e., the time during which the meal was digested and the dogwhelk moved from one prey to another. However, this might be the case because their study only included small blue mussels ≤ 25 mm. Such blue mussels were in our experiment usually completely eaten and could therefore also have affected starvation times. However, we did not study the effect of prey size within the smallest, or any other, size class. Bayne and Scullard (1978) also found that an increase in water temperature (up to 20°C) shortened the post-feeding phase and caused elevated feeding rates during summer. In general, we would have expected constant starving times over all prey size classes before feeding the first blue mussel, as all dogwhelks started under similar conditions; they were kept without food for 5-10 days prior to the experiment. It is likely that the thin shells of blue mussels from the smallest size class motivated dogwhelks to start drilling earlier, as dogwhelks can sense shell thickness (Hughes & Dunkin 1984a, Morton 2011). But we cannot explain the fluctuation of starving times before consuming the first blue mussels across the other size classes, and we would need larger sample sizes to draw clear conclusions.

Our results showed that the time to consume all four blue mussels was short ($\mu = 21$ days) for the smallest blue mussels (0-20 mm), but about equally prolongated for larger blue mussels (20-80mm, $\mu = 68.8$-78.5 days), and even longer for the largest blue mussels (80-100 mm, $\mu = 97$ days). This could be explained by the thicker shells of large blue mussels that prolong drilling times (Hughes &

Dunkin 1984a), but the sample sizes were too small to draw a clear conclusion. Prey handling times that positively correlated with prey sizes supported the overall increase of time to consume four blue mussels with prey size. Additionally, dogwhelks never needed a second drilling attempt to successfully drill small blue mussels (<40 mm), but sometimes a second or third attempt to access the flesh of larger blue mussels (>40 mm). Multiple attempts might be needed to drill thicker shells when dogwhelks started drilling at an inconvenient, thick-shelled, position or due to active defences of blue mussels. But it could also be that dogwhelks needed to gain practice in drilling blue mussels, as they came from rocky shores next to the MBSE where blue mussels were absent and barnacles seemed to be their main prey. Practice can increase their success rate by increased drilling on either the most accessible position, the postero-dorsal quadrant, or the most nutritious position, the antero-dorsal quadrant (Hughes & Dunkin 1984a, Morton 2010). The latter is not only beneficial because it gives straight access to the digestive gland, but also because it does not immediately affect the adductor muscles (Hughes & Dunkin 1984a). It delays gaping of the drilled blue mussel, especially if it is a large one, and thereby keeps exploiting dogwhelks, that feed through the valve openings, away for longer (Hughes & Dunkin 1984a). We often observed that the valves of drilled large blue mussels opened with a delay, up to 7 days after the drilling event. Some dogwhelks laid eggs during the experiment, which likely added additional variance to the results.

Pilot experiment 2 – Walkways

Methods

In the walkway experiment we tested dogwhelks' ability to climb up four different materials: branches, nylon ropes, chains, and rocks/concrete bricks. Dogwhelks had to climb vertically 0.25 m to reach and feed on blue mussels. We set each of the four treatments up with four simultaneous replicates in separate beakers (Figure 10). We hung the ropes and chains into the beakers through holes in the middles of the mosquito nets so that they barely touched the bottoms. We removed all side branches from the branches and placed one branch per beaker between the bottom and the mosquito net, sticking out from the middle of the net for fixation. We mounted rocks up to 0.25 m high piles, but after one round of replicates (end of August), we replaced them with 0.25 m tall concrete bricks for better comparison with the other vertical structures. We excluded data from rock piles from the analysis. We attached one blue mussel with thin stainless-steel wire after 0.25 m of chain, rope, and branch or on top of a rock pile and concrete brick. We used blue mussels from 45 to 65 mm and dogwhelks from 25 to 35 mm. During inspections, we recorded if dogwhelks were located on the blue mussel drilling or feeding, crawling on the walkway, or neither. Once a dogwhelk left the blue mussel after feeding, the experiment ended, and we set up a new replicate. After four weeks all experiments ended regardless of dogwhelks feeding or not. We calculated prey approaching times, the time from the start of the experiment until the dogwhelk was positioned on the blue mussel and started drilling. We used the most precise estimations of dates dogwhelks started to drill, as explained in the general material and methods section.

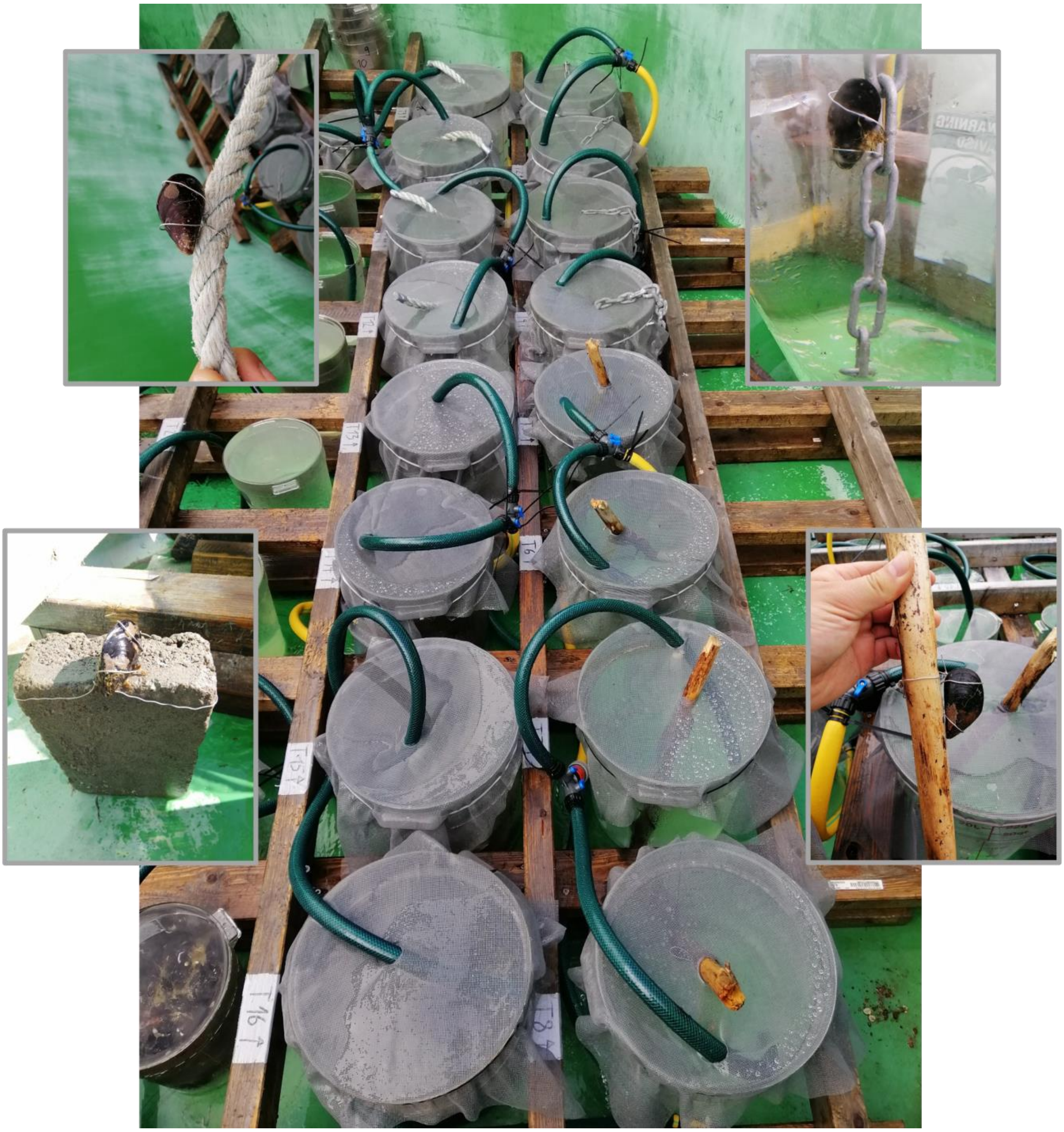

Figure 10: The set-up of the walkway experiment with four simultaneous replicates of each treatment: rope, chain, concrete brick, and branch.

Results

We found that adult dogwhelks preferred to crawl up concrete bricks and branches rather than ropes and chains (Figure 11A). In 75% cases dogwhelks managed to crawl up concrete bricks and started drilling on blue mussels, in 71% cases they overcame branches, in 42% cases ropes, and only in 31% cases chains. However, dogwhelks spent about the same time to crawl up these walkways, on average 12.9 days (± 11.1 days SD) for concrete bricks, 12.1 days (± 9.2 days SD) for branches, 11.8 days (± 7.6 days SD) for ropes, and 13.8 days (± 2.5 days SD) for chains (Figure 11B). One dogwhelk died after three weeks of the experiment. We included this dogwhelk from a chain replicate in the analysis because we do not know when it last fed prior to the experiment and therefore, its death might have resulted from not being able to reach a food source.

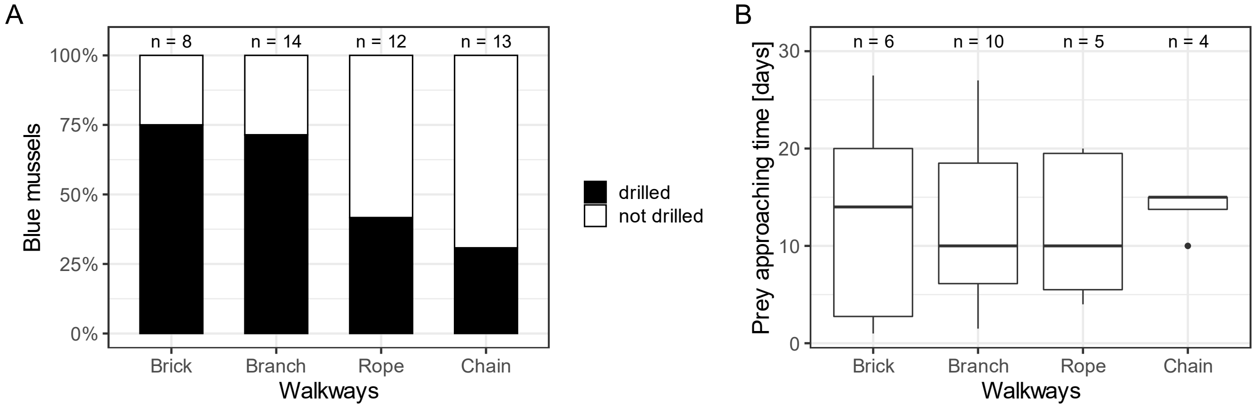

Figure 11: Percentage of blue mussels drilled by dogwhelks that managed to crawl up the different walkways (A) and the time (number of days) these dogwhelks needed until they reached their blue mussel prey (B). Blue mussels were attached to the four walkways: bricks, branches, ropes, and chains, after 0.25 m of distance from the bottom. Numbers on top indicate the number of observations per walkway. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. Outliers are >1.5 times the interquartile range beyond either end of the box and denoted by dots.

Natural history observations

We observed active defences of blue mussels against dogwhelks drilling on them. In three cases, twice on a branch and once on a chain, we observed how blue mussels reacted to drilling dogwhelks by wiggling out of the wire and thereby shaking off the dogwhelks. But the dogwhelks fought back, drilled complete holes on new positions of the shells, and killed the blue mussels. In a fourth case the same happened, but when the dogwhelk was back on the blue mussel, the blue mussel fought back once more by attaching hundreds of byssus threads from the branch to the top of the dogwhelk shell before it escaped once more by moving up on the branch to the top where the mosquito net sealed the beaker (Figure 12). The dogwhelk stayed immobilized flipped over for one week before we ended the experiment. The dogwhelk did not recover.

Figure 12: The result of a blue mussel using its active defenses, byssus threads, to flip over and immobilize a dogwhelk that faces a slow death by starvation.

Discussion

Our results showed that dogwhelks managed to crawl up short distances on all four walkways: concrete bricks, branches, ropes, and chains. However, they reached blue mussels more often on concrete bricks and branches than on ropes and chains. This might reflect the walkways' properties; bricks are the sturdiest, followed first by branches, then by ropes, and last by chains. Chains are potentially most difficult to climb as there is movement between the links in the chain. We do not know if dogwhelks could overcome larger distances of ropes and chains, especially in the sea where the water is not as static as in the beakers and would cause these walkways to move. During our fieldwork, we did not observe any dogwhelks on floating docks held in place by ropes or chains, but other crawling predators with pelagic larvae, such as sea stars, were present (Chapter I). Tides change the amount of tension on ropes and chains holding floating docks in place, and other hydrodynamic forces such as currents and waves increase the dislodgement of dogwhelks, especially during drilling and feeding (Burrows & Hughes 1991b, Hughes & Burrows 1991, Hughes & Dunkin 1984a). Harsh hydrodynamic conditions limit feeding and promote a change towards smaller prey, barnacles (Burrows & Hughes 1991b), and cause dogwhelks to seek refuge (Hughes & Burrows 1991). Additionally, waves reduce dogwhelks' sensitivity towards predator cues (Freeman & Hamer 2009) and increase their mortality (Etter 1989). Wave exposed blue mussels are thicker and have more cylindrical shaped shells with lower shell height / shell width ratios, larger dysodont teeth, thicker hinge ligaments, and are overall more robust than sheltered blue mussels (Akester & Martel 2000). Their thicker shells could increase prey handling times and thereby increase the risk of dislodgement during drilling. Wave exposed dogwhelks are also adapted, they have shorter and squatter shells that reduce drag by waves and larger apertures that increase adherence strength to resist dislodgement (Crothers 1981, Guerra-Varela et al. 2009). Hydrodynamic forces such as tides, waves, and currents might make it more difficult for dogwhelks to crawl up vertical surfaces in the field, especially if those surfaces are flexible, such as ropes and chains. It is likely that this would result in reduced prey handling efficiency due to higher risk of dislodgement.

Pilot experiment 3 – Substrates

Methods

We covered the bottoms of three aquaria with ~0.1 m sand and of another three with ~0.1 m mud, both collected in the Raunefjorden area. We tested dogwhelks' ability to crawl over those two substrates. We placed two flat stones on the substrate of each aquarium with a 0.25 m distance between them (Figure 13). We then placed a dogwhelk onto one of these stones and secured a blue mussel with thin stainless-steel wire to the other. We used blue mussels between 40 and 50 mm and dogwhelks from 25 to 35 mm. During inspections, we recorded the dogwhelk's position (substrate, glass wall, stone, mussel) to later calculate the time it used to approach and handle a blue mussel. The experiment ended when the dogwhelk finished feeding or after four weeks.

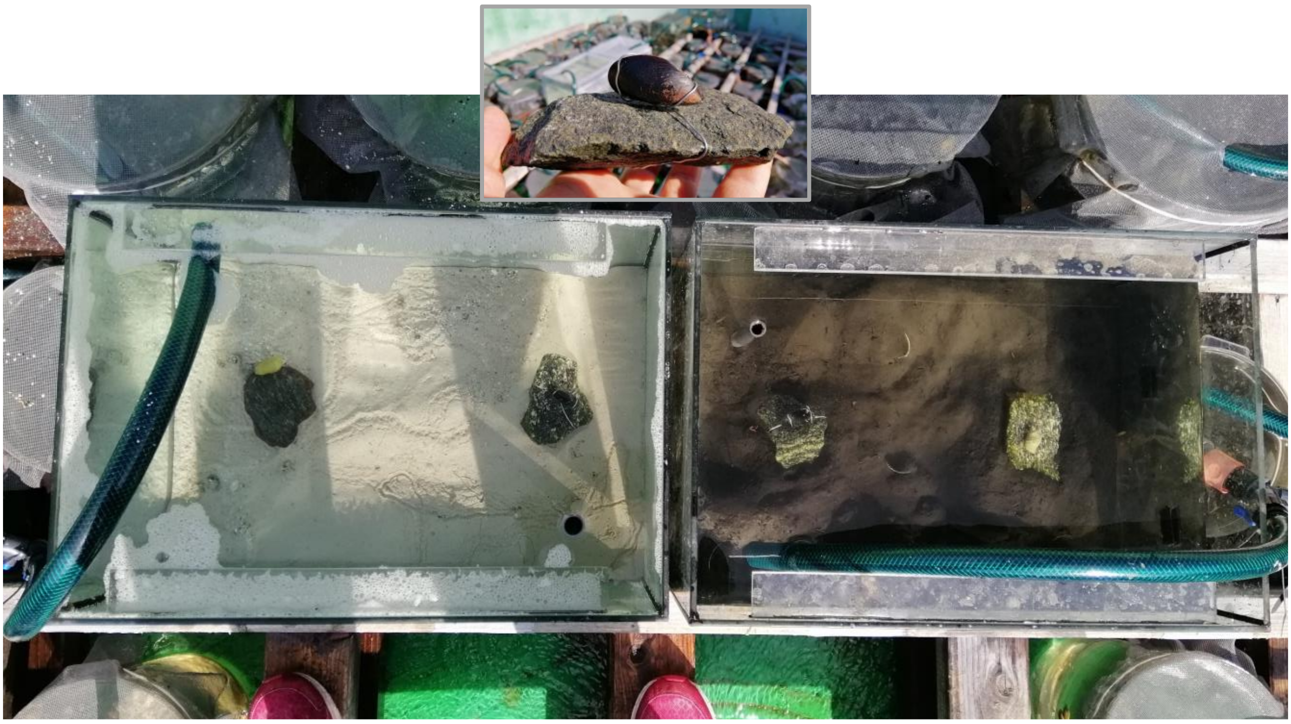

Figure 13: The set-up of the substrate experiment with the two treatments: sand and mud. Blue mussels were secured to flat stones with stainless-steel wire and dogwhelks were placed on stones 0.25 m apart from blue mussels.

Results

Similar proportions of dogwhelks managed to cross mud (64%) and sand (56%) to feed on blue mussels (Figure 14A). However, their prey approaching times were markedly different. It took them on average 12.3 days (± 7.7 days SD) to crawl over mud to reach their blue mussel prey compared to 4.3 days (± 4 days SD) over sand (Figure 14B).

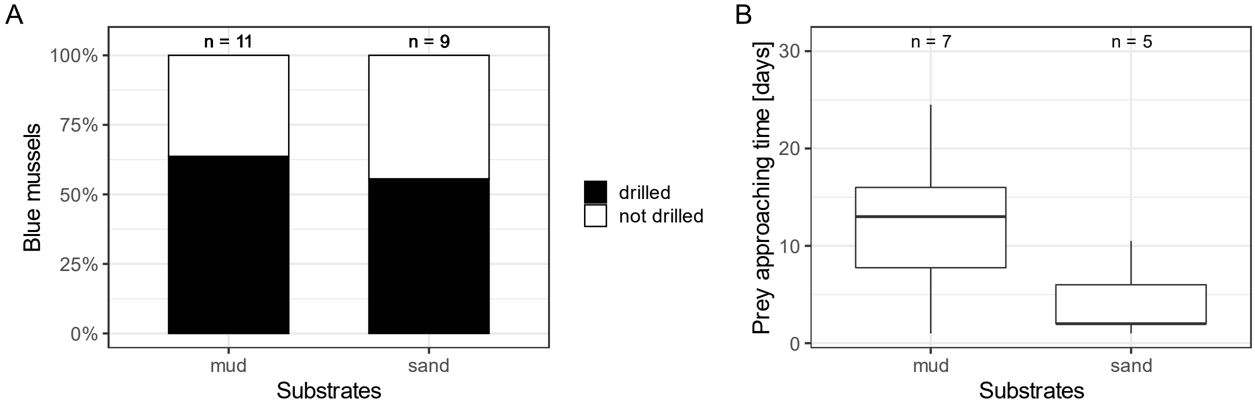

Figure 14: Percentage of blue mussels drilled by dogwhelks that managed to crawl 0.25 m over mud or sand (A) and the time (number of days) those dogwhelks needed until they reached their blue mussel prey (B). Numbers on top indicate the number of observations per treatment. Boxes indicate 25%, 50%, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range below the 25th percentile and on the largest value within 1.5 times the interquartile range above the 75th percentile. There are no outliers, observations >1.5 times the interquartile range beyond either end of the box.

Natural history observations

One dogwhelk dug itself through the layer of mud and crawled along the glass bottom of the aquarium to reach the blue mussel. All other dogwhelks were either seen crawling on the substrate or left visible tracks in the substrate (Figure 15). Dogwhelks did not always immediately approach their prey.

Figure 15: The track a dogwhelk left behind in sand.

While collecting mud for the experiment in a shallow bay in Raunefjorden, we found three netted dogwhelks *Tritia reticulata* in the sediment. *T. reticulata* is another predator of blue mussels that was severely affected by TBT (Stroben et al. 1992). It prefers to live in soft sediments (Davenport & Moore 2002, Tallmark 1980), and is therefore unlikely a candidate that triggered the decline of blue mussels on rocky shores in Norway (Chapter I).

Discussion

Our results showed that dogwhelks managed to crawl over short distances on soft sediments, such as mud and sand. This contrasts with earlier studies that listed mud and sand as distribution barriers (Colton 1916, Morgan 1972a). However, dogwhelks' crawling abilities are likely distance dependent.

We would need to test their ability to crawl for longer distances on sand or mud without the possibility of resting in between on a stone or the glass walls of the aquarium to determine to which extent dogwhelks are limited to hard substrates. Another reason why their distribution is restricted to hard substrates could be that they have no motivation for crossing soft bottoms as their main prey species, blue mussels and barnacles, are usually sessile on solid surfaces (Connell 1961). However, Colson and Hughes (2004) found far greater dogwhelk movements than expected from a slow-crawling species without pelagic stage. When looking at genetic structure, they found that dogwhelks must have passed some potential barriers such as sandy or estuarine areas (Colson & Hughes 2004). But it remains unclear if this happened by dogwhelks crawling or passive transportation of juvenile dogwhelks by currents and rafting (Colson & Hughes 2004).

Our results showed that dogwhelks needed ca. three times more time to approach prey on mud than on sand. This could reflect dogwhelks' difficulties to crawl over mud and may explain why blue mussels thrive in muddy bays (personal observation). However, sample sizes were too small to draw clear conclusions. It might be that the dogwhelks in aquaria with mud were by chance less hungry than the ones in aquaria with sand, especially since some dogwhelks just passed the blue mussels without starting to drill and feed. The prey approaching time on mud (μ = 12.3 days) was similar to the ones of the walkway experiment (pilot experiment 2; bricks: μ = 12.9 days, branches: μ = 12.1 days, ropes: μ = 11.8 days, chains: μ = 13.8 days). However, these approaching times were lower than the starving times in the predation rate experiment (pilot experiment 1) for mussels of a comparable size (μ = 15 days for blue mussels sized 40-60 mm), and the prey approaching time on sand was even lower (μ = 4.3 days). It remains unclear why dogwhelks with blue mussels immediately available took longer to start drilling than the ones that had to cross substrates or walkways in order to reach their blue mussel prey.

Pilot experiment 4 – Small dogwhelks

Methods

We tested the ability of four small dogwhelks (12-13 mm) to drill and feed on medium-sized blue mussels (27-32 mm). Dogwhelks usually reach maturation after two years at a minimum size of 25 mm (Connell 1961, Hughes & Dunkin 1984a) and therefore, we assumed that the small dogwhelks in this experiment were juveniles. Additionally, the small dogwhelks all had thin-lipped shells, which is another sign of immaturity (Connell 1961, Moore 1936). We placed each dogwhelk together with one blue mussel into a beaker and recorded their prey handling times as described in the general material and methods section above. Additionally, we recorded if dogwhelks needed single or multiple drilling attempts to access the flesh, and if they consumed it partly or completely. The experiments ended when the dogwhelks finished feeding.

Results

Juvenile dogwhelks needed on average 14.4 days (± 6.8 days SD) to handle medium-sized blue mussels. The fastest finished within 7 days, whereas the slowest took more than three times longer (Table 1). They all consumed their blue mussels completely. Two juveniles managed to access the flesh within the first drilling attempt, whereas the other two needed a second drilling attempt (Figure 16). During inspections, it was not possible to distinguish between the two drilling events because the dogwhelks were continually positioned on the blue mussels. Therefore, the prey handling times for the latter two juvenile dogwhelks also included the time spent on their first drilling attempt, which could explain the prolonged prey handling time (23 days) for one of these juvenile dogwhelks.

Figure 16: A juvenile dogwhelk (13 mm) together with the drilled shell of its blue mussel prey (31 mm). The shell shows a drilling hole at the thinnest position, the postero-dorsal quadrant, as well as a drilling attempt in the antero-ventral quadrant.

Table 1: Four juvenile dogwhelks, their size [mm], the size of their blue mussel prey [mm], if single or multiple feeding attempts were needed, if the blue mussel was consumed partly or completely, and the number of days it took the dogwhelks to handle (drill and feed) their prey.

ID	size dogwhelk (mm)	size blue mussel (mm)	feeding attempt(s)	eaten	prey handling time (days)
1	13	28	single	completely	16
2	13	27	multiple	completely	11.5
3	13	31	multiple	completely	23
4	12	32	single	completely	7

Discussion

Our results showed that juvenile dogwhelks (12-13 mm) successfully drilled and fed on medium-sized (27-32 mm) blue mussels. Miller (2013) calculated predation rates of juvenile dogwhelks (12-15 mm) on small blue mussels (10-17 mm) under conditions similar to the ones in this experiment (i.e., starving of dogwhelks prior to the experiment, similar temperature range, and no tidal cycles) and found that drilling and ingestion combined take ca. 1-3 days. This is markedly shorter than in our study, where juvenile dogwhelks needed between 7 and 23 days (μ = 14.4 days) to handle a blue mussel. The increase of shell thickness with blue mussel size is responsible for longer drilling times (Hughes & Dunkin 1984a), and thereby most likely the reason for the longer prey handling times we observed. Compared to adult dogwhelks from the predation rate experiment (pilot experiment 1), which needed between 1 and 12 days (μ = 5 days) to handle blue mussels of similar size (20-40 mm), juvenile dogwhelks were slower in handling prey. In contrast to the adult dogwhelks, of which only 65% managed to completely eat their blue mussel prey, all four juveniles ate their prey completely. This contrasts with the fact that larger dogwhelks have larger gut volumes than small dogwhelks and thereby can feed for longer periods and on higher quantities of food (Burrows & Hughes 1991b). Adults never needed a second drilling attempt to successfully access the flesh, however half of the juveniles did. Even in the field where they had both barnacles and blue mussels available, we observed juvenile dogwhelks (10-15 mm) feeding on medium-sized to large (40-80 mm) blue mussels (Chapter I). This is in contrast with the study by Morton (2010), who observed that juveniles <13 mm exclusively feed on barnacles. Juveniles become more efficient in handling blue mussels while they grow and gain practice, which increases their success rate by increased drilling on either the most accessible position, the postero-dorsal quadrant, or the most nutritious position, the antero-dorsal quadrant (Hughes & Dunkin 1984a, Morton 2010). The lack of practice is another factor that could explain why some juveniles needed a second drilling attempt to succeed and why juveniles were slower than adult dogwhelks in handling their blue mussel prey.

Pilot experiment 5 – Large blue mussels

Methods

We tested the ability of two adult dogwhelks to drill and feed on the largest blue mussels we have found (125 mm and 131 mm; Figure 17). We chose dogwhelks between 25 and 35 mm and placed each together with one blue mussel into a beaker to record their prey handling times as described in the general material and methods section. Additionally, we recorded if dogwhelks needed single or multiple drilling attempts to access the flesh, and if they consumed it partly or completely. The experiments ended when the dogwhelks finished feeding or after eight weeks.

Figure 17: Large (131 mm) blue mussel with adult-sized (28 mm) dogwhelk.

Results

One dogwhelk managed to drill its blue mussel, whereas the other tried twice but both times gave up before completing the hole (Table 2). The dogwhelk that managed to drill through the shell of a blue mussel as large as 131 mm needed 46.5 days to handle its prey. It only managed to consume a small part (~10%) of the blue mussel. After the dogwhelk finished feeding and after we removed the remaining tissue from the shell, we discovered that the dogwhelk drilled through the shell twice, at the antero-ventral quadrant of each shell half. This was not visible during inspections since the dogwhelk was continually positioned on the shell of the blue mussel. Therefore, the prey handling time for the dogwhelk feeding on this large blue mussel included twice the time needed to complete a drilling hole.

Table 2: Two large blue mussels, their size [mm], the size of their dogwhelk predators [mm], if single or multiple feeding attempts were needed, if they were consumed partly or completely, and how many days it took the dogwhelks to handle (drill and feed) them. Note that only one dogwhelk (ID 2) was successful in drilling and feeding within the period of eight weeks.

ID	size blue mussel (mm)	size dogwhelk (mm)	feeding attempt(s)	eaten	prey handling time (days)
1	125	31	multiple	-	-
2	131	28	single	partly	46.5

Discussion

Our results showed that even the largest blue mussels (131 mm) can be drilled by dogwhelks. While growing large protects blue mussels from being eaten by green crabs (*Carcinus maenas*) (Elner & Hughes 1978), it does not prevent dogwhelks from drilling through their shells. This makes dogwhelks an effective predator that could be responsible for the disappearance of some well-established blue mussel beds in Norway. The fact that blue mussels are not able to grow out of the predation window makes them as a sessile species much more vulnerable and might be a reason why they developed active defences against dogwhelks; when dogwhelks are around, blue mussels increase byssus thread production and actively trap dogwhelks with these threads (Farrell & Crowe 2007, Petraitis 1987). However, dogwhelks prefer to feed on smaller blue mussels than the ones predicted to be the most profitable (Hughes & Dunkin 1984a). This might be due to prolonged drilling times for larger blue mussels, leading to the devaluation of larger mussels (Hughes & Dunkin 1984a). Longer drilling times increase the risk of competing dogwhelks stealing flesh or displacing the occupant, predation, dislodgement by waves, and desiccation (Hughes & Dunkin 1984a). However, under favourable (weather) conditions dogwhelks avoid small prey to maximize their energy gain (Hughes & Burrows 1991).

Pilot experiment 6 – Alternative prey

Methods

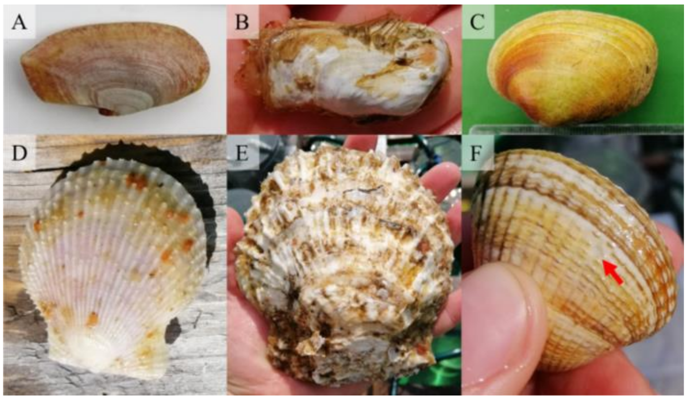

Figure 18: *Gari fervensis* (A), *Hiatella arctica* (B), *Venerupis corrugata* (C), *Chlamys varia* (D), *Ostrea edulis* (E), and *Cerastoderma edule* (F). *C. edule* has a drilling attempt from a dogwhelk, which is marked with a red arrow.

We collected bivalves i.e., Faroe sunset shells (*Gari fervensis*; Figure 18A), wrinkled rock borers (*Hiatella arctica*; Figure 18B), pullet carpet shells (*Venerupis corrugata*; Figure 18C), variegated scallops (*Chlamys varia*; Figure 18D), European flat oysters (*Ostrea edulis*; Figure 18E), and common cockles (*Cerastoderma edule*; Figure 18F), in shallow waters next to the MBSE. *H. arctica*, *C. varia*, and *O. edulis* were attached to a floating dock, whereas *G. fervensis*, *V. corrugata*, and *C. edule* were buried in the sand. We cleaned their shells from biofouling and measured their diameter at the widest position to the nearest mm. We placed each bivalve in a beaker with four adult-sized (25-35 mm) dogwhelks to observe if these bivalves serve as alternative prey source for dogwhelks. The beakers did not contain any substrate and therefore, the bivalves were fully exposed to the dogwhelks. Experiments ended when the bivalves were consumed or after four weeks. We set replicates up with the species of bivalves that were available.

Results

Table 3: Bivalves, their size, and if they were eaten, alive, or dead without being eaten after the four weeks exposed to dogwhelks.

ID	bivalve	bivalve size [mm]	bivalve state
1	*Cerastoderma edule*	40	eaten
2	*Cerastoderma edule*	41	alive
3	*Ostrea edulis*	127	alive
4	*Hiatella arctica*	39	alive
5	*Hiatella arctica*	25	alive
6	*Chlamys varia*	50	alive
7	*Chlamys varia*	70	alive
8	*Gari fervensis*	26	alive
9	*Venerupis corrugata*	33	dead
10	*Venerupis corrugata*	50	alive

Dogwhelks showed little interest in other bivalves than blue mussels. They only predated one *C. edule* (Table 3). All *O. edulis*, *H. arctica*, *C. varia*, *G. fervensis*, and one out of two *V. corrugata* were still alive after the four weeks of the experiment. One *V. corrugata* died after two weeks without being predated. Dogwhelks did not feed on the dead *V. corrugata*. We only observed dogwhelks besieging and drilling on *O. edulis* and one out of two *C. edule*. Dogwhelks did not manage to drill through the shell of *O. edulis*, even though we observed all four drilling on it. They also did not manage to drill through the shell of *C. edule*. After five days of the experiment, one dogwhelk started to drill on *C. edule* for four days before it left the shell with an incomplete drilling hole behind. Two days later, *C. edule* was dead with three dogwhelks inside its valves feeding on its flesh. Three days later, the flesh was entirely consumed. The shell showed two drilling attempts but no hole through it.

Discussion

Our results showed that dogwhelks are able to predate thick-shelled bivalves such as *C. edule*. Their flexibility to change prey species could help them to persist during periods without blue mussels and barnacles. This was the case at an English pebble bank called Old Den, where dogwhelks switched to feed on *C. edule* after the disappearance of their main prey (Morgan 1972a). Morgan (1972b) observed up to 20 dogwhelks feeding on a single *C. edule* in the laboratory. Usually only one dogwhelk penetrated the shell by drilling (Morgan 1972b). The others aggregated after *C. edule* released body fluid due to tissue damage and took flesh from between the valves (Morgan 1972b). This is similar to the behaviour we observed, where only one dogwhelk tried to drill a hole, but several dogwhelks came to feed once *C. edule* died and opened its valves. Even though the drilling event did not end in a complete hole, it might have stressed the mussel enough to start gaping and thereby allowing another dogwhelk to penetrate through its valve opening (Hughes & Dunkin 1984a, Morgan 1972b). Other known bivalve-prey species for dogwhelks are *H. arctica*, *O. edulis,* and *Lasaea rubra* (John H Crothers 1985). In this experiment, dogwhelks did not drill on *H. arctica*, but they showed interest in *O. edulis* even though it was large (127 mm) and thick-shelled. They continually besieged and drilled on it, but without success. *L. rubra* only grows up to 3 mm (Ballantine & Morton 1956) and we did not consider testing it as potential prey. Dogwhelks did not feed on the dead *V. corrugata* even though it would have been easy prey. Perhaps they could sense that *V. corrugata* was ill and therefore avoided it. However, we could not find any reports of dogwhelks feeding on *V. corrugata*.

Pilot experiment 7 – Alternative predators

Methods

We collected potential predators, such as common periwinkles (*Littorina littorea*), common sea urchins (*Echinus esculentus*), and common sea stars (*Asterias rubens*), in the intertidal next to the MBSE and measured their diameter at the widest position to the nearest mm. We chose these three species because during our fieldwork, we observed them feeding on blue mussels. However, only common sea stars are known to predate effectively on blue mussels (Bodvin 1984, Christie 1983, Enderlein & Wahl 2004). We placed the potential predators in beakers with four blue mussels (20-40 mm or 40-60 mm) and observed their behaviour for either 4 or 12 weeks. We recorded the number of blue mussels that were predated within this time. Due to common periwinkles' small size and low predation expectations, we placed six common periwinkles within the same beaker and added relatively small (20-40 mm) blue mussels.

Results

Only common sea stars fed on blue mussels (Table 4). Both common periwinkles and common sea urchin did not access blue mussels' flesh. The common sea urchin left scratches on the posterior shell margins of all four blue mussels, and two blue mussels had rasped edges after four weeks, preventing them from closing their valves tightly. Two out of three common sea stars managed to predate blue mussels, both were ~80 mm and each ate two blue mussels during the 12 weeks of the experiment (Figure 19). The one that did not feed, despite repeatedly spending several days besieging a blue mussel, was the smallest (~60 mm) common sea star in the experiment.

Figure 19: Small (80 mm diameter) common sea star besieging a blue mussel.

Table 4: Potential predators, the number of predators in the beaker, the size [mm] of the predator(s), the number of blue mussels in the beaker, the size of the blue mussels [mm], the number of blue mussels eaten, and the duration of the experiment [weeks].

ID	potential predator	no. predators	size predator(s) (mm)	no. blue mussels	size blue mussels (mm)	no. blue mussels eaten	experiment duration (weeks)
1	*Littorina littorea*	6	15-22	4	20-40	0	4
2	*Echinus esculentus*	1	120	4	40-60	0	4
3	*Asterias rubens*	1	80	4	40-60	2	12
4	*Asterias rubens*	1	60	4	40-60	0	12
5	*Asterias rubens*	1	80	4	40-60	2	12

Discussion

The results tentatively showed that intertidal species that feed on blue mussels often have lower impacts on them than dogwhelks. Common periwinkles were not able to kill blue mussels, even though they like feeding on dead blue mussels (personal observation). That common periwinkles are not dangerous to blue mussels can also be seen in blue mussels' selective use of active defences. Blue mussels use their byssus treads more frequently to trap dogwhelks than common periwinkles (Farrell & Crowe 2007, Petraitis 1987) and produce more than twice as many byssus threads when dogwhelks are around compared to common periwinkles (Farrell & Crowe 2007). However, common periwinkles might reduce freshly settled blue mussels through grazing and bulldozing (Wahl & Sonnichsen 1992). The common sea urchin did also not manage to access the flesh of blue mussels. However, it left scratches on the posterior shell margins of all four blue mussels and rasped edges on two. We observed that the common sea urchin experienced difficulties reaching the blue mussels that stayed on the bottom next to the wall of the round beaker, because it was too large and could not bend its body to enter this space. It would have been interesting to continue the experiment in a larger beaker to determine if common sea urchins are able to access blue mussel's flesh when having more time and space available. However, the common sea urchin was very inefficient in handling prey and would most likely not have been able to kill the blue mussels. Blue mussels do not react to waterborne cues of common sea urchins (Côté 1995).

Other crawling species that live in the intertidal predate blue mussels. We observed small (80 mm) common sea stars feeding on blue mussels. Common sea stars are well-known predators of small blue mussels in Norway (Bodvin 1984, Christie 1983), but have low consumption rates (Kamermans et al. 2009). The two small common sea stars that fed consumed both two medium-sized (40-60 mm) blue mussels within 12 weeks, and thereby had lower consumption rates than dogwhelks (Pilot experiment 1). The smallest (60 mm) common sea star did not manage to open medium-sized shells. Therefore, a minimum size might be required for common sea stars to succeed. Blue mussels react to waterborne predator cues with high phenotypic plasticity. If they are exposed to sea stars, they invest in a stronger adductor muscle (Freeman 2007, Reimer & Tedengren 1996) and firmer attachment to the substrate (Dolmer 1998). The latter can also be observed in blue mussels exposed to crabs i.e., edible crabs (*Cancer pagurus*) and green crabs (*Carcinus maenas*), as well as an increase in shell thickness (Côté 1995, Leonard et al. 1999). Green crabs have a much higher consumption rate than common sea stars (Kamermans et al. 2009), but are mostly restricted to feed on blue mussels <40 mm (Elner & Hughes 1978). Therefore, they might not be responsible for the disappearance of well-established blue mussel beds. Nevertheless, they may play an important role in the Norwegian blue mussel decline, as suggested by Christie et al. (2020).

Feeding behaviours are complex, especially in the field where predators additionally interact with each other. Sea stars also consume whelks and suppress their feeding behaviour through non-consumptive effects (Gosnell & Gaines 2012). The same is true for crabs (Bourdeau & Padilla 2019, Hughes & Elner 1979, Morton 2011, Quinn et al. 2012), which also take over dogwhelks' abandoned and only partly consumed blue mussel prey (Morton 2011). An ocean recovering from TBT pollution might not only have led to growing dogwhelk populations but might also have caused cascading effects on their blue mussel prey and other species in the community. After the TBT ban, Morton (2011) observed that green crabs increased together with dogwhelks. Additionally, changing environmental conditions can cause shifts in the dominance of intertidal predator species (Menge 1983). Dogwhelks have the capacity to withstand drastic environmental changes and high flexibility to adapt to new conditions (Morgan 1972a), and might be less affected by worsening environmental conditions than sea stars and crabs (Menge 1983). In the end, it might be the cumulative change in several crawling predators that in concert causes a broad blue mussel decline, as the one observed in Norway.

General discussion

The aim of these pilot experiments was to determine i) dogwhelks' feeding potential on blue mussels to evaluate if dogwhelks can cause a country-wide decline of blue mussels in Norway, ii) their crawling potential to evaluate if the refugia, where we still observe blue mussels thriving in Norway, are out of reach from dogwhelks, and iii) which other crawling predators have high impacts on blue mussels.

In the pilot experiments, dogwhelks fed effectively on blue mussels and increased their prey handling time with the size of their blue mussel prey, which they usually accessed with their first drilling attempt but could not consume completely (pilot experiment 1). They had more difficulties crawling up chains and ropes than branches and concrete bricks (pilot experiment 2). They were able to cross short distances of soft bottoms, but mud slowed down their progress (pilot experiment 3). Juvenile dogwhelks managed to successfully drill medium-sized blue mussels, but they used more time than adult dogwhelks (pilot experiment 4). Growing large did not protect blue mussels from dogwhelks, as dogwhelks managed to drill and feed even on the largest (131 mm) blue mussel (pilot experiment 5). Dogwhelks showed flexibility to switch to feed on other bivalve species (pilot experiment 6). Furthermore, other crawling species such as small common sea stars had limited impact on blue mussels (pilot experiment 7). All these findings help to understand predator-prey dynamics in the intertidal and suggest that dogwhelks might have the capacity to play an important role in the Norwegian blue mussel decline. However, the pilot experiments with their small sample sizes only suggested trends and did not allow to draw conclusions about dogwhelks' feeding and crawling potential to cause a country-wide decline with the blue mussel occurrence pattern observed in Norway.

While running and analysing the pilot experiments, we found some points that could be improved: i) the experiments should be monitored more frequently i.e., daily or multiple times per day, to allow for more accurate time measurements; ii) the inclusion of tidal cycles, waves, and currents could result in more realistic predation rates; iii) larger sample sizes would allow to statistically analyse the data and draw clearer conclusions. The latter could be achieved by increasing the duration of the experiments and in case of the predation rate experiment (pilot experiment 1) by lowering the number of blue mussels within each replicate from four to three.

At the beginning of the predation rate experiment (pilot experiment 1), we planned to record exact blue mussel sizes and determine in which order they are consumed to identify possible prey size preferences of dogwhelks within prey size classes. This analysis was not possible because blue mussels, primarily small ones that were not immediately consumed, grew during the experiment, and recognition became impossible. In future studies, we should consider marking blue mussel shells to ensure recognition and track their growth.

In the walkway experiment (pilot experiment 2), we would need to increase the length of the walkways to test if dogwhelks can sense prey cues over longer distances and are still motivated to crawl up. The longer distance could also increase dislodgement of dogwhelks, especially on flexible walkways under hydrodynamic forces. Therefore, with the results obtained from this experiment it was not possible to predict if dogwhelks can reach floating docks held in place by ropes and chains.

Similarly, to draw clear conclusions about dogwhelks' ability to cross soft bottoms and to evaluate if blue mussels thrive on soft bottoms because they provide refuge from dogwhelks, we should consider repeating the substrate experiment (pilot experiment 3) with longer crawling distances and give dogwhelks the option to choose the substrate they crawl on. In the experiment, dogwhelks had to crawl on soft bottoms to avoid starvation. This might have triggered responses that we would not have observed if dogwhelks had the choice to stay on solid surfaces.

The set-ups of the small dogwhelk experiment (pilot experiment 4) and the large blue mussel experiment (pilot experiment 5) were successful, but inference would be stronger with more replicates. Nevertheless, we were able to monitor the efficiency of juvenile dogwhelks to drill blue mussels and discovered that even the largest (131 mm) blue mussel was not safe from dogwhelks.

With the alternative prey experiment (pilot experiment 6) we explored dogwhelks' abilities to feed on other bivalve species than blue mussels. In future studies, we should consider determining their feeding potential on a wider size range of each bivalve species. Additionally, to understand the consequences of the blue mussel decline on dogwhelk populations, we would need to identify which other mollusc species that are abundant in Norway serve as prey for dogwhelks.

The alternative predator experiment (pilot experiment 7) was the least structured. Nevertheless, it showed that dogwhelks might have greater potential in eradicating blue mussels than many other crawling predators such as small common sea stars. For future studies, we should consider including various sea star species of all sizes, as well as crabs, such as edible crabs and green crabs. Additionally, we should standardize the study design for all potential predators to facilitate comparison.

In a further step, we could analyse the positions of the drilling holes and their microstructure, as well as measure thickness of the collected blue mussel shells to study the relationships between length and thickness and between thickness and prey handling time. In short, the pilot experiments delivered insights into feeding and crawling behaviours of dogwhelks and allowed us to determine improvements to the experimental set-ups to address remaining knowledge gaps in future studies.

Conclusions

Pilot experiments suggested that dogwhelks have the potential to be efficient predators on blue mussels of any sizes. Dogwhelks not only managed to drill small blue mussels within less than a day, but they also successfully drilled blue mussels as large as 131 mm. Even juvenile dogwhelks accessed the flesh of medium-sized blue mussels. All this confirms that dogwhelks have high impact on blue mussels and might have the capacity to drive the Norwegian blue mussel decline. The fact that dogwhelks had difficulties to crawl up flexible structures such as ropes and chains might be the reason why blue mussels continue to thrive on floating structures held in place by ropes and chains. Similarly, dogwhelks needed more time to approach blue mussels on mud than on sand, which might explain why muddy bays are another refugium for blue mussels in Norway. Together, these results lend some support to our hypothesis that dogwhelks are behind the Norwegian blue mussel decline, but repeating these experiments with larger sample sizes would be necessary to reach firm conclusions. Furthermore, pilot experiments suggested that dogwhelks might have higher impacts on blue mussels than many other crawling species that feed on them. We are aware that also these results lack statistical power and that further studies are required.

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