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Blue mussels in western Norway have vanished where in reach of crawling predators

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ABSTRACT: Blue mussels (*Mytilus* spp.) are declining around the world. In western Norway, they have widely disappeared from rocky shores but still thrive on floating structures. Other refugia are cracks in rocks, exposed sites, and low-salinity habitats. Climate change, pollution, disease, parasites, hybridization, and failed recruitment might not alone be able to create such distribution patterns. We hypothesized that crawling predators that are unable to reach floating structures may drive the present decline in western Norway. A known crawling predator without a pelagic stage and sensitive to low salinity and high wave action is the dogwhelk *Nucella lapillus*. Tributyltin (TBT) contained in anti-fouling paint rendered this snail sterile, but TBT is now banned, and populations are recovering rapidly. We first surveyed floating structures together with nearby rocky shores for blue mussels and dogwhelks. Blue mussels were present on all surveyed floating docks (65% area covered), but only on 18% of rocky shores (≤5% area covered). Similarly, blue mussels were found on 83% of tree branches suspended in water without bottom contact, but only on 1% when branches touched the seafloor. We then conducted a predator exclusion experiment with caged blue mussels (40–80 mm). In cages, mortality due to factors other than dogwhelks was extremely low (<1%) and confirmed that blue mussels continue to thrive when out of reach of predators. If dogwhelks or other crawling predators such as crabs or sea stars created the observed distribution pattern, then environmentally friendly mariculture with blue mussels growing on rafts and longlines might still have high potential in Norway.

KEY WORDS: *Mytilus* · Dogwhelk · *Nucella lapillus* · Foundation species · Invertebrate predators · Population decline · Predator recovery · Woody debris · Coarse woody habitat

1. 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 algae 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 Norway and sometimes interbreed (Brooks & Farmen 2013). *M. edulis* typically dominates in our study area on Norway's west coast around Bergen, and when we use the term 'blue mussels' we do not distinguish between these 3 species.

Blue mussels have declined across much of their distributional range. Over the last decade, they 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 4 marine regions (Baltic Sea, North-East Atlantic, Mediterranean

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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 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 may have suffered due to harvesting (Beukema & Dekker 2007), failed recruitment (Beukema & Dekker 2007, Petraitis & Dudgeon 2015), or predation by fishes (Šegvić-Bubić et al. 2011). Additionally, competition with invasive Pacific oysters (Troost et al. 2008, Joyce et al. 2019), ocean acidification (Sadler et al. 2018), hybridization of blue mussel species (Benabdelmouna & Ledu 2016), and parasites (Mortensen & Skår 2020) may negatively affect the persistence of blue mussel populations. In addition, harmful algal blooms, unfavourable weather conditions, competitors, and predators have been identified as threats to the European Union's blue mussel aquaculture (Avdelas et al. 2021).

A striking peculiarity with the decline in Norway is that blue mussels have disappeared from rocky shores while they continue to thrive a few metres away on buoys, floating docks, and hanging ropes (Fig. 1A,B) (Andersen et al. 2017, Christie et al. 2020). The same observations were made on the west coast of Sweden (Baden et al. 2021) and have been reported anecdotally from California, USA (Suchanek 1978). Our first aim was to document this pattern by pairwise comparisons of blue mussels on floating docks and nearby rocky shores.

A question that immediately emerges is to what degree floating structures could relieve mussels of negative impacts from the suggested mechanisms of decline. We evaluate each of the potential mechanisms as they pertain to western Norway in Section 4, but note here that one key difference for a mussel living on a floating structure is that it is always submerged. In contrast, during low tide, mussels in the rocky intertidal will be exposed to air, which in-

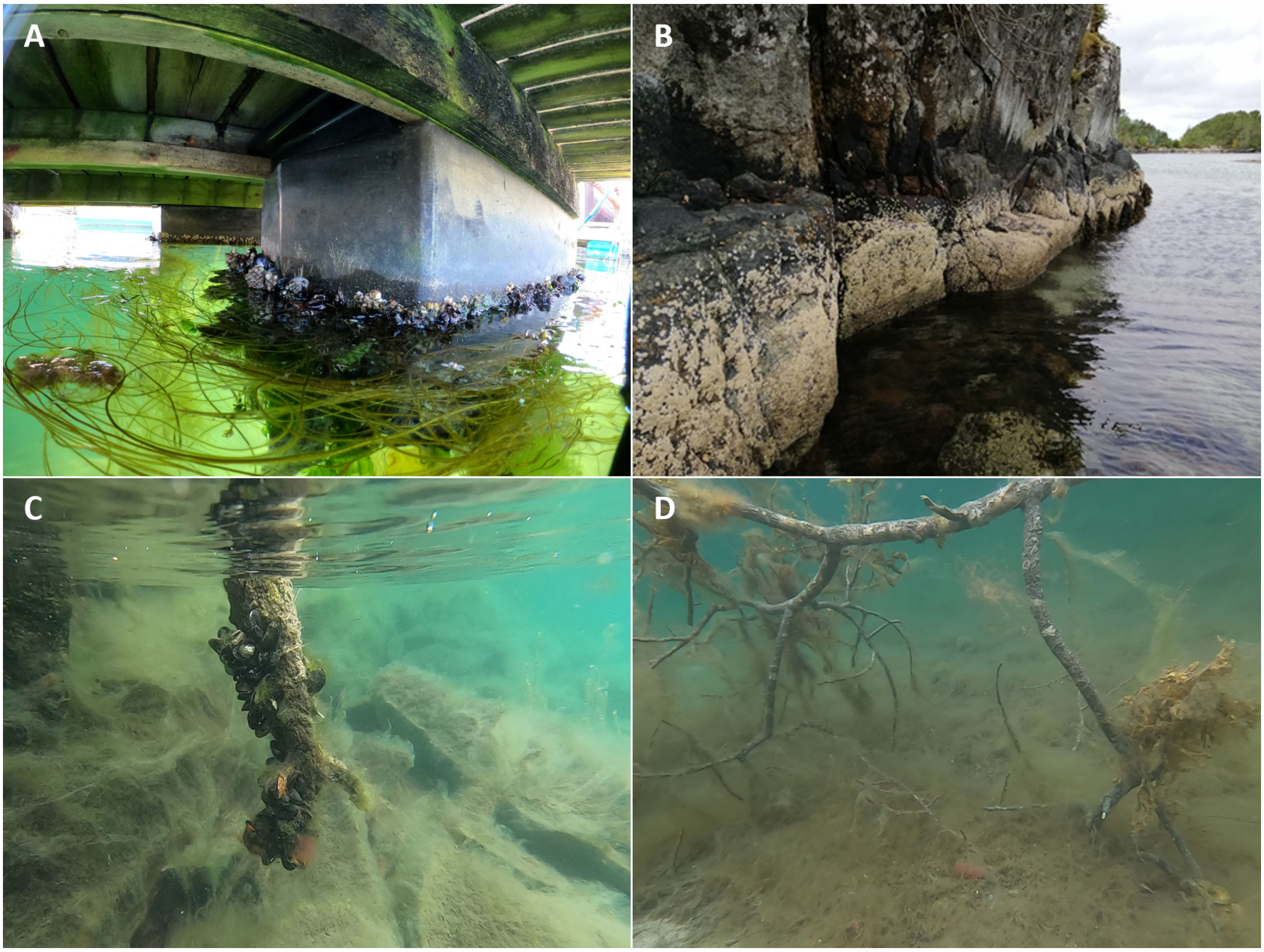

Fig. 1. (A) Floating dock with blue mussels, (B) rocky shore without blue mussels, (C) tree branch hanging freely with blue mussels, (D) tree branch touching bottom without blue mussels

volves intermittent feeding, higher and lower ambient temperatures, as well as access for other predators such as gulls (*Larus* spp.) and the Eurasian oystercatcher *Haematopus ostralegus* (Hilgerloh 1997). Our second aim was therefore to document the occurrence of mussels on habitat that is disconnected from rocky shores but still subject to tidal cycles. We found such a habitat in branches and fallen trees where some branches hang freely into the water while others touch the bottom, also known as aquatic coarse woody debris or coarse woody habitat (Sass 2009). Again, a striking contrast appeared: branches that touched bottom, were free from blue mussels (Fig. 1C,D).

Competitors and predators stand out particularly among biotic factors that may affect blue mussels on rocks and floating structures unequally. We therefore hypothesized that crawling predators, which are unable to reach floating and free-hanging structures, may play a fundamental role in the recent decline of the blue mussel populations on rocky bottoms in western Norway. The known crawling predators of blue mussels in Scandinavian waters include common sea stars *Asterias rubens*, green crabs *Carcinus maenas*, edible crabs (also called brown crabs) *Cancer pagurus*, and predatory snails, namely dogwhelk *Nucella lapillus* and netted dogwhelk *Tritia reticulata* (Andersen et al. 2017, Christie et al. 2020, Baden et al. 2021). These species are common on rocky bottom, except for the netted dogwhelk, which prefers soft bottom and lives within the sediment (Colton 1916). However, we currently lack sufficient data or evidence to definitively exclude any of these species.

We became particularly interested in the dogwhelk *N. lapillus*, as populations all over the globe were decimated because the antifouling compound tributyltin (TBT) that was used on ship hulls from the 1960s (IMO 2002) made this snail sterile (Bryan et al. 1987, Gibbs et al. 1987). TBT was gradually phased out beginning in the 1980s (IMO 2002), and dogwhelk populations have been recovering since (Morton 2011). A survey in 2017 was the first time sterility was no longer found among dogwhelks along the Norwegian coast (Schøyen et al. 2019). Except for freshwater-influenced inner parts of fjords (Brattegard 1966), dogwhelks are distributed all along the Norwegian coast (GBIF 2022b, OBIS 2022a), and they mainly prey on blue mussels and barnacles (Colton 1916). Dogwhelks consume mussels by secreting 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 that was not immediately accessible (Carriker 1981).

We have observed that dogwhelks successfully drill blue mussels as large as 131 mm, so our third aim was to investigate the feeding potential of dogwhelks on blue mussels. We did this with cages placed on rocky bottoms with dogwhelk predators included or excluded to quantify feeding rates and potentially other causes of mortality on mussels beyond dogwhelk predation. Although the general lack of data on other predators means we cannot single out dogwhelks as the culprit behind the blue mussel decline in western Norway, we do conclude that the decline can be logically explained by a crawling predator and that the dogwhelk is capable of rapid consumption of mussel populations at the scale observed.

2. MATERIALS AND METHODS

2.1. 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 4 d long sailing trip from 9 to 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 (Fig. 2). We chose a paired sample design to look at floating docks together with rocky sites several metres away, with a focus on blue mussels and dogwhelks.

While we aimed to randomize our approach in selected areas, we did apply opportunistic sampling within some 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. The coastline exhibited variations in slope angle and substrate type across different sites. These variations ranged from near-vertical rock faces to gently sloping rocky shores composed of gravel and boulders, as well as man-made structures made of rock or concrete. For a more detailed description of the sites, see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m721p085_supp/.

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

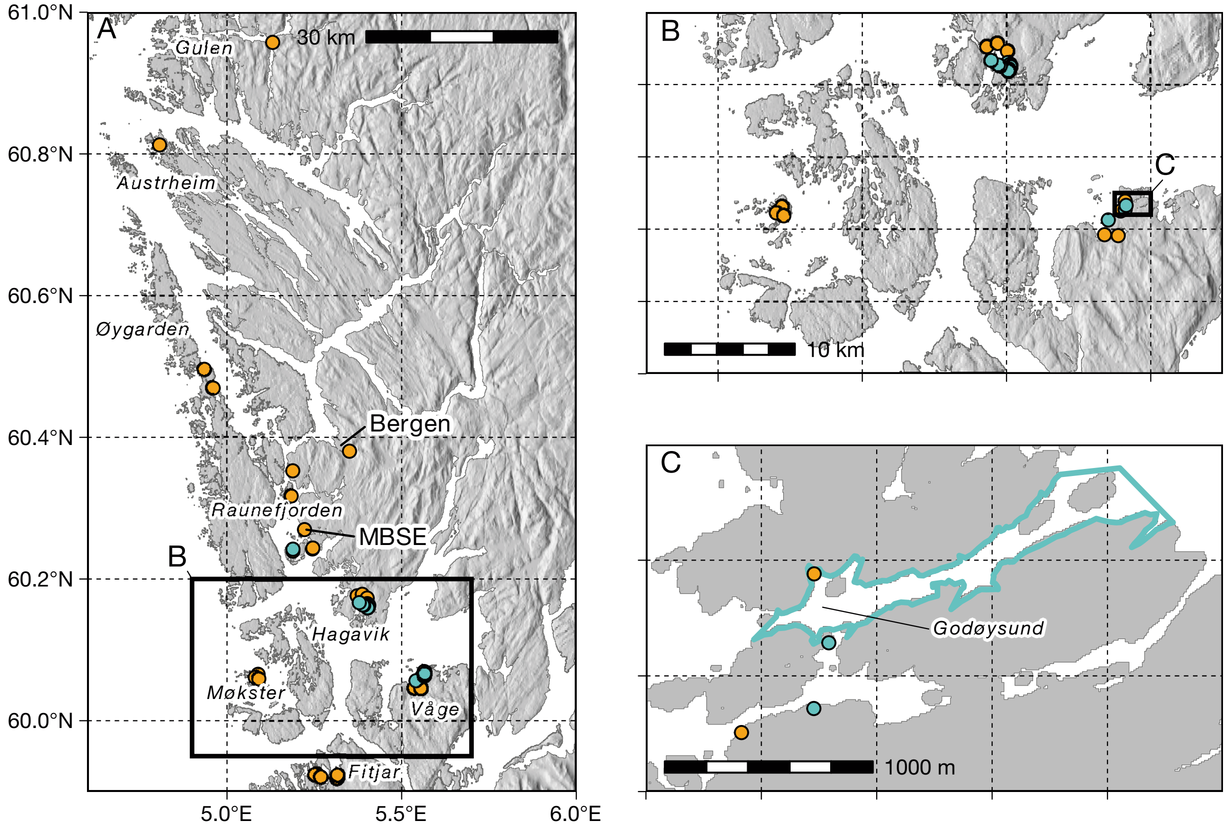

Fig. 2. (A) Sampling sites along Norway's west coast around Bergen and the Marine Biological Station Espegrend (MBSE). (B) Close-up of the more densely sampled area (black frame in panel A), and (C) further magnification of the tree transect in Godøysund (black frame in panel B). Floating docks together with nearby rocks are denoted by orange 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

frames randomly 3 times on submerged sides and/or undersides of the floats. On nearby rocks, we placed frames randomly in the mid-intertidal zone. The aim was to get an overview of the percent area covered by blue mussels as a proxy of local abundance and the average number of dogwhelks on floating docks and rocky shores (including man-made structures such as wharfs, piers, and breakwaters) a few metres away for direct comparison. Additionally, we recorded length distribution of blue mussels within 5 different size classes (0–20, 20–40, 40–60, 60–80, and ≥80 mm, always measured from anterior to posterior end) 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. Water depth around these trees was similar, usually around 2 m. We 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 (n = 81) trees within a predefined transect (Fig. 2C) and analysed them separately. A detailed description of the tree sites can be found in Table S2 in Supplement 1. Additionally, we took pictures and videos (see Videos S1 & S2) under and above water using GoPros 7 and 8. We sampled 17 floating docks together with nearby rocks and 119 trees during the sailing trip. We added another 11 floating docks together with nearby rocks and 2 trees from fieldwork in Øygarden, Raunefjorden, Austrheim, Gulen, and Bergen during summer 2021. We covered those locations snorkelling from shore and motorboats using the same procedures as described above.

2.2. Caging experiment

In June 2021, we constructed 40 stainless steel cages with an edge length of 0.33 m, half with 8 × 8 mm and half with 28 × 28 mm mesh size. The smaller mesh size prevented adult dogwhelks from moving in and out of the cages while still allowing unobstructed water flow so mussels could feed. The larger mesh size allowed the passage of even the largest dogwhelks while preventing other potential predators (crabs, sea stars, fishes, seabirds) large enough to feed on blue mussels. Prior to the experiment, we hung all cages from the dock at the Marine Biological Station Espegrend (MBSE) into seawater for 3 wk to remove 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 divided 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 d prior to the experiment to get them attached to the rope and minimize possible shell loss from large-meshed cages. We added 2 concrete bricks on the bottom of each cage to make them heavier and keep them in place. We 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; always measured from apex to siphon canal) 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 2 by 2 design: small- and large-meshed cages, with or without dogwhelks added. The number of dogwhelks added per cage corresponds to the approximate density of dogwhelk aggregations observed in the area. Adult-sized dogwhelks could not pass through the small mesh, but they fitted through the mesh of the large-meshed cages. Therefore, small-meshed cages without dogwhelks served as a control to measure blue mussel mortality due to factors other than predation, and large-meshed cages provided insight into natural blue mussel mortality rates due to predation by only dogwhelks.

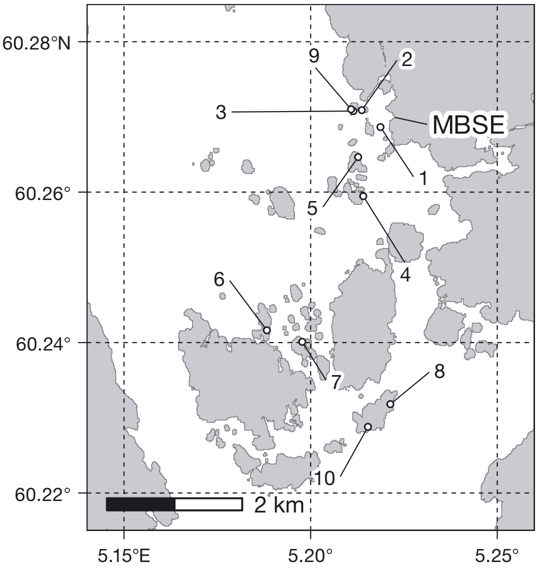

Fig. 3. Cage locations in Raunefjorden, Norway, within ca. 5 km from the Marine Biological Station Espegrend (MBSE)

We set the cages up at 10 locations around 8 small uninhabited islands in Raunefjorden within ~4.5 km from the MBSE on 19 August 2021 (locations 1–5) and 14 September 2021 (locations 6–10) (Fig. 3). In the study area, mean tidal amplitude is usually about 1 m. We placed the cages within the mid-intertidal zone of gently sloping rocky shores with low to intermediate wave exposure, where macroalgae of the genus *Fucus* dominated and dogwhelks were present. We avoided locations where cages would be completely covered by macroalgae, as dense macroalgal coverage could limit dogwhelk access to the cages. At each location, 4 cages (1 of each category) were placed in a random order, all within the same water depth and similar 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 wk, we recovered the remaining cages and recorded if blue mussels were open, closed, or lost. We did not observe any biofouling on either the small-meshed or large-meshed cages that could have prevented dogwhelks from reaching the cages. Shells were analysed by recording the 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; otherwise, 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.

2.3. 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), ‘sf’ (Pebesma 2018), ‘terra’ (Hijmans 2022), and ‘tidyterra’ (Hernangómez 2023). For all other figures, we used ‘ggplot2’ (Wickham 2016) and combined them using ‘patchwork’ (Pedersen 2020). We bootstrapped (50 000 resamples) our data on blue mussel and dogwhelk occurrence (presence/absence) on floating docks, rocky shores, and fallen trees with ‘rsample’ (Silge et al. 2022) to obtain the 95 % confidence intervals of the mean occurrence probabilities (see bars in Fig. 4). To test for differences in blue mussel and dogwhelk occurrence on floating docks versus nearby rocks, we used McNemar's test, which is a specific type of chi-squared test for paired binary data, with continuity correction for small sample sizes. To test for differences in blue mussel occurrence on trees touching bottom versus trees suspended in the water, we used a chi-squared test for independence. To compare blue mussel coverages within frames on floating docks and nearby rocks, we used a Wilcoxon signed rank test for clustered data from the package ‘clusrank’ (Jiang et al. 2020). 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 occurrence using Firth's logistic regression, a penalized likelihood model that can deal with quasi-complete separation of the response variable, from the package ‘logistf’ (Heinze et al. 2022). We compared blue mussel mortalities between the 4 cage categories using a logistic regression with proportions. We corrected this model for overdispersion with a quasibinomial term and *F*-test, and then applied Tukey's pairwise comparison. To test for the effect of cage category on the numbers of dogwhelks feeding/drilling per cage and visit, we used Poisson regression for clustered data from the package ‘lme4’ (Bates et al. 2015). Therefore, we first compared the model with cage category as predictor variable to a null model that included only an intercept and random factor using the function ‘anova’. In a second step, we applied Tukey's pairwise comparison to the better model, i.e. the model that included cage category as a predictor variable. For Tukey's pairwise comparisons, we used the function ‘glht’ within the package ‘multcomp’ (Hothorn et al. 2008). To study relationships between dogwhelk abundance and blue mussel mortality within cages, we chose a second-order polynomial regression model, which had a lower value of Akaike's information criterion (AIC = 285) than a linear regression (AIC = 292). A complete overview of test statistics can be found in Tables S3–S6 in Supplement 2.

3. RESULTS

3.1. Floating docks, rocky shores, and trees

We found that blue mussels were present on all (100 %; bootstrapped mean μ = 100 %, 95 % CI [100 %, 100 %]) visited floating docks but only on a few (18 %; bootstrapped mean μ = 18 %, 95 % CI [4.3 %, 33 %]) rocky shores (McNemar's chi-squared test, $\chi^2 = 21.04$, df = 1, p < 0.001; Fig. 4A). At one of

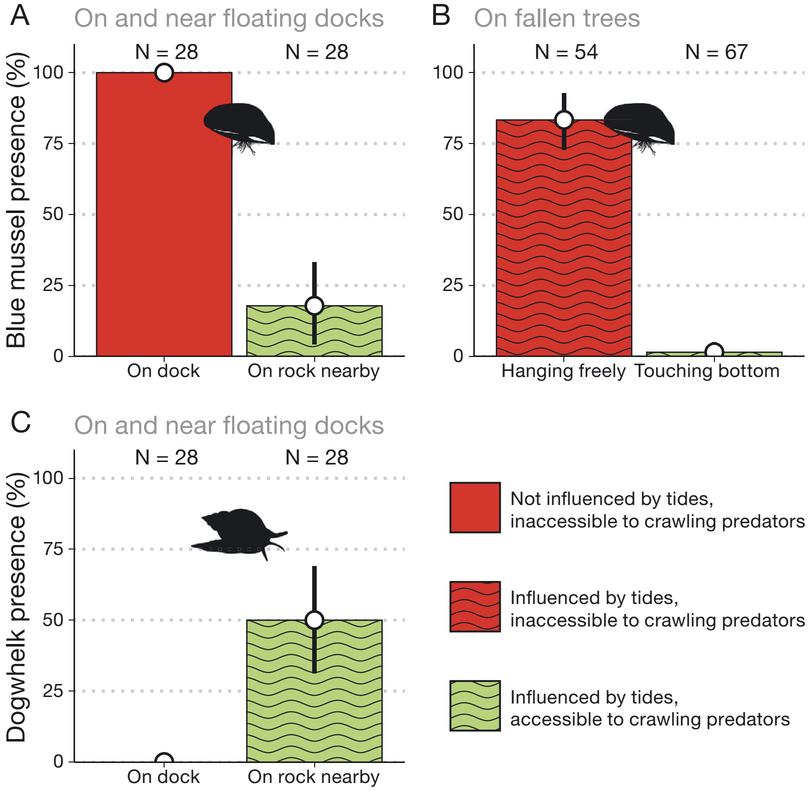

Fig. 4. (A) Differences in the presence–absence of blue mussels on floating docks and nearby rocks, and (B) on fallen trees hanging freely or touching bottom. (C) Differences in the presence–absence of dogwhelks on floating docks and nearby rocks. Colours indicate whether habitats are influenced by tides or not and whether they are accessible to crawling predators or not. Dots indicate the bootstrapped mean and bars the bootstrapped 95 % confidence intervals

the 5 rocky sites with blue mussels, blue mussels (≤100 mm) were patchily distributed below a freshwater surface layer, and at the other 4 sites, blue mussels (≤60 mm) were scattered within cracks in the rocks. Large blue mussels (60–120 mm) were present on all floating docks. We found that floating docks and nearby rocky shores also significantly differed in terms of the area covered by blue mussels (Wilcoxon test, $p < 0.001$). On floating docks, the area covered by mussels was often high, on average 65 ± 35% (SD), and ranged from 5 to 100%. On rocks, blue mussels appeared only sparsely, and the area covered was around 1 ± 1% and always ≤5%.

Trees 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; bootstrapped mean μ = 83%, 95% CI [73%, 93%]) inhabited by blue mussels. In contrast, blue mussels virtually never (only 1% of cases; bootstrapped mean μ = 1.5%, 95% CI [0%, 5%]) occurred on trunks and branches that were in contact with the bottom (chi-squared test of independence, $\chi^2 = 81.55$, df = 1, $p < 0.001$; Fig. 4B). Three out of a total of 9 trees not touching the bottom but with no mussels were barely submerged at high tide. In one other case, the tree was free of any biofouling, suggesting that it had only 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 blue 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 trees without bottom contact and 2% of the cases with bottom contact; chi-squared test of independence, $\chi^2 = 49.32$, df = 1, $p < 0.001$) aligned with observations elsewhere, we pooled all observations of trees across sites (Fig. 4B). It is important to note that no apparent difference in the size of blue mussels was observed between the floating structures and trees.

Pooling presence/absence data from floating docks, rocky shores, and trees together, we found that both the accessibility to crawling predators (Firth's logistic regression, $p < 0.001$; Table S3) and tidal exposure ($p < 0.02$) significantly influenced blue mussel occurrence. Our data suggest that finding blue mussels was 66 times more likely on structures out of reach from crawling predators (floating docks and trees hanging freely) than on structures accessible to crawling predators (rocky shores and trees touching bottom; reciprocal value of the odds ratio 0.015 from Firth's logistic regression; Table S3). It was only 12 times more likely that blue mussels were on structures constantly submerged (floating docks) than on structures exposed to the tidal cycle (rocky shores and trees with and without bottom contact; reciprocal value of the odds ratio 0.084 from Firth's logistic regression; Table S3). The probability of blue mussels being present differed between all 3 habitats (Fisher's exact test, p-values < 0.025): accessible to crawling predators and with tidal exposure (i.e. rocky shores and bottom-touching trees; bootstrapped mean μ = 6.3%, 95% CI [2%, 12%]), inaccessible to crawling predators but with tidal exposure (i.e. free-hanging trees; bootstrapped mean μ = 83%, 95% CI [73%, 93%]), and inaccessible to crawling predators and constantly submerged (i.e. floating docks; bootstrapped mean μ = 100%, 95% CI [100%, 100%]).

We found dogwhelks only on rocky shores (bootstrapped mean μ = 50%, 95% CI [31%, 69%]), a habitat accessible to crawling predators and with tidal exposure, and never on any floating structures, a habitat inaccessible to crawling predators and constantly submerged (bootstrapped mean μ = 0%, 95% CI [0%, 0%]; McNemar's chi-squared test, $\chi^2 = 12.07$, df = 1, $p < 0.001$; Fig. 4C). Dogwhelks were present on half of the rocky sites, and in more than a third, we found them in at least 1 of the 3 frames. The distribution of dogwhelks was very patchy and abundances within frames varied greatly, from 0 to 15 individuals (mean $\mu = 1.4$, standard deviation $\sigma = 3.1$). We found both blue mussels and dogwhelks at only 1 rocky site, 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 observed on floating docks, but in low densities (maximum 1 per frame).

3.2. Caging experiment

The caging experiment showed that dogwhelks predated on average about half of the blue mussels within 8 wk, unless large dogwhelks were excluded from the cages (Fig. 5). In small-meshed cages with 10 added dogwhelks, blue mussel mortality varied little among locations (μ = 51%, σ = 16%), and on average, every dogwhelk preyed on 1.11 blue mussels during the experiment. In large-meshed cages, regardless of dogwhelks being added (μ = 49%, σ = 32%) at the beginning of the experiment or not (μ =

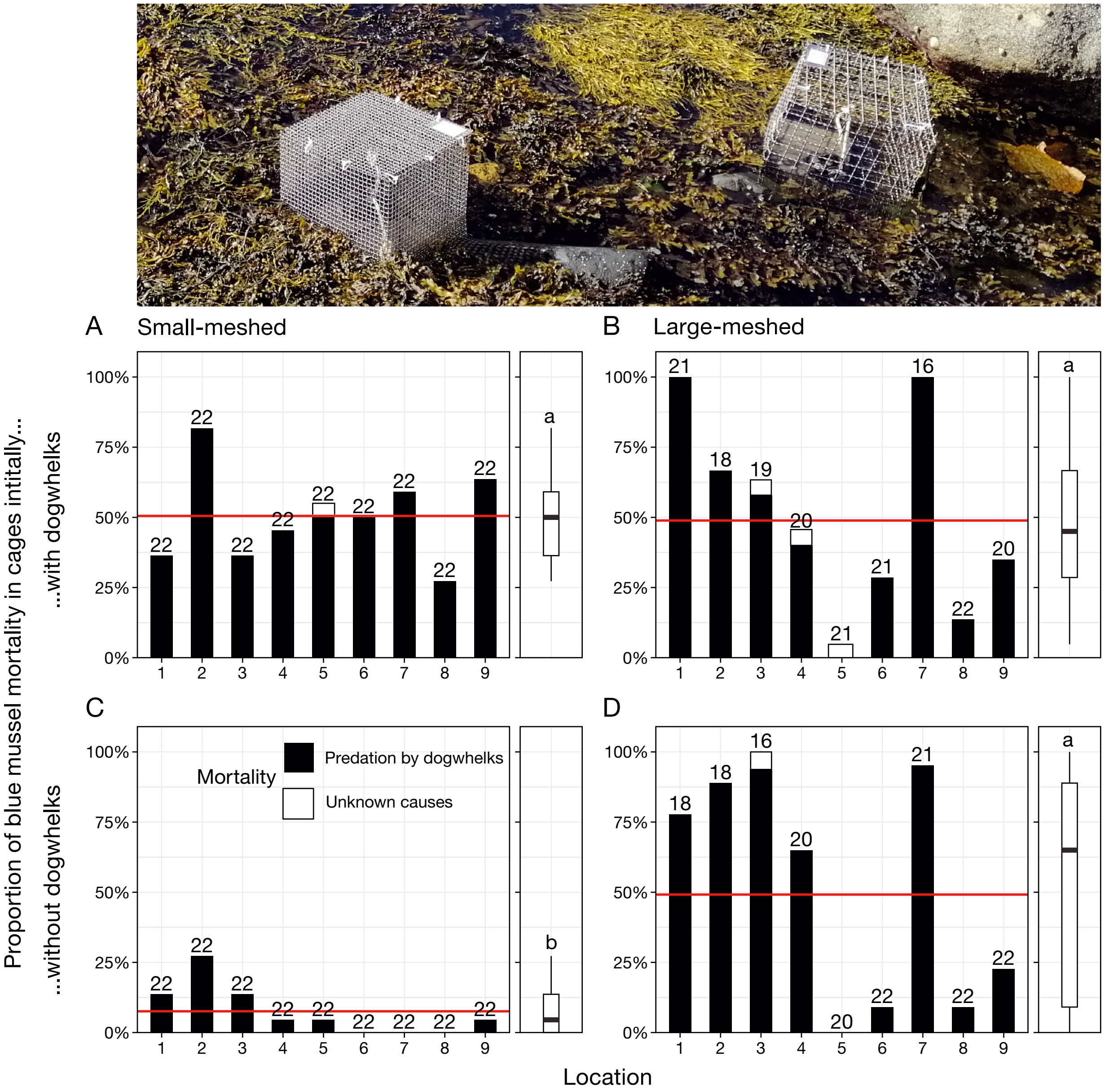

Fig. 5. Blue mussel mortality (in %) in the 4 categories: (A,C) small- and (B,D) large-meshed cages, with or without 10 dogwhelks added per cage, after 8 wk. Locations are comparable among categories. Mortality is divided into predation by dogwhelks and unknown causes. The number of blue mussels that remained in each cage and contributed towards the analysis is noted above each bar; if no blue mussels were lost, n = 22. Red horizontal lines indicate mean mortalities within categories. Boxplots summarize data within categories. Boxplots marked with the letter 'a' are not significantly different from each other, but they are significantly different from the category marked with 'b'. Boxes indicate 25, 50, and 75% quartiles. Whiskers end on the smallest value within 1.5 times the interquartile range (IQR) below the 25th percentile and on the largest value within 1.5 times the IQR above the 75th percentile. There were no outliers (observations >1.5 times the IQR) beyond either end of the box

49%, σ = 39%), blue mussel mortality varied more among sites. 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, 39 blue mussels were lost through the openings in the mesh, 20 and 19 from large-meshed cages with and without dogwhelks added, respectively. Blue mussels disappeared predominantly from cages with high predation. Noting that it is easier for 2 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 ($\mu = 8\%$, $\sigma = 9\%$). 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 (10–20 mm length) entering the cages to feed. We also made these observations in 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) did not significantly differ from each other (logistic regression with proportions and Tukey's pairwise comparison, p-values > 0.99; Table S4), but they all differed significantly from the proportion of blue mussels that died in cages where large dogwhelks were excluded (small-meshed cages without dogwhelks added; p-values < 0.02; see boxplots in Fig. 5). In total, only 5 blue mussels, <1%, died without being predated by dogwhelks during the 8 wk. 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 that looked as if it had been crushed by the concrete bricks, presumably during wave action. Only 2 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 1, up to 7, completed drilling holes. Drilling attempts were also found on 6% of live blue mussels.

Weekly visits revealed high densities of active predators 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 (Fig. S1 in Supplement 2). In small-meshed cages with dogwhelks added, we observed a maximum of 8 dogwhelks simultaneously handling blue mussels, and in small-meshed cages without dogwhelks added, a maximum of 7 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 ($\mu = 3.3$–3.6) for the other 3 categories. For the latter, the number of active predators per visit was most stable for small-meshed cages with dogwhelks added ($3 = 3.3$, $\sigma = 2.1$), 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) did not significantly differ from each other (Poisson regression with Tukey's pairwise comparison, p-values > 0.89; Table S5), but they all differed significantly from the number of dogwhelks per visit in cages where large dogwhelks were excluded (small-meshed cages without dogwhelks added; p-values < 0.001). 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, $p < 0.001$; Fig. 6, Table S6). We did not observe any predators other than dogwhelks inside the cages, but we noticed a green crab just next to a large-meshed cage during one visit.

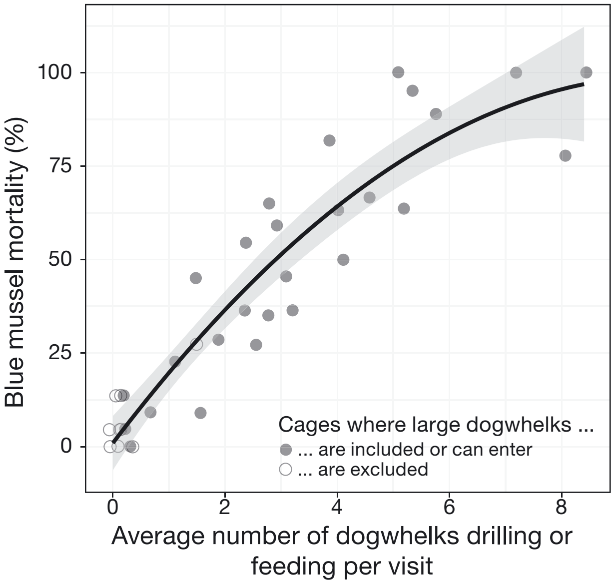

Fig. 6. Correlation between average number of dogwhelks drilling or feeding per visit and blue mussel mortality (in %) in cages where large dogwhelks were included or could enter and in cages where they were excluded. The black line is a second-order polynomial regression ($p < 0.001$) with a 95% confidence interval (shaded area)

4. DISCUSSION

We compared floating docks with nearby rocky shores, and trees that hang freely in the water with those that touch bottom, and showed that blue mussels were almost always absent when the substrate was connected to the bottom. Although this circumstantial evidence suggests that a crawling predator that is unable or unlikely to reach floating and free-hanging structures may have caused the population decline in western Norway, blue mussels have a complex ecology intimately intertwined with the dynamic environment of the intertidal. Blue mussel declines have occurred in many places, and there is a range of reported explanations, plus potentially others that may apply in western Norway. Some of these explanations could operate in parallel with or sequentially to predation. In the following, we evaluate the situation in western Norway by considering potential mechanisms, we assess the role the dogwhelk may have played in particular, and we conclude that the mechanisms that can potentially explain the patterns observed in western Norway can be narrowed down to crawling predators but that a definite answer of which species is the culprit requires further data.

4.1. Potential effects of water characteristics

One class of mechanisms with great impact on blue mussel biology pertains to water characteristics or waterborne substances that act diffusively in the water column, for example climate warming, ocean acidification, pollution, or pathogens. Generally, water temperatures exceeding 25°C begin to negatively affect blue mussel physiology and survival (Dowd & Somero 2013, Gazeau et al. 2014). Norwegian summers are relatively cool, with water temperatures rarely and only locally becoming this warm, and it is not only in the warmest regions mussels have declined (Andersen et al. 2017). Cold water temperature in winter is no problem for blue mussels, but the formation of sea ice in calm bays or inlets can cause anoxic conditions below and thus lower survival or recruitment (Andersen et al. 2017). During the last 2 decades, coastal water temperatures in winter have been increasing in Norway (Albretsen et al. 2012, Aksnes et al. 2019), with sea ice only occurring locally over small scales; low temperatures have therefore been evaluated as an unlikely driver of the widespread decline (Andersen et al. 2017). Another diffuse factor is ocean acidification, which may lead to thinner-shelled and slower-growing blue mussels that are more vulnerable to predation, but these effects are only observed for projected future and higher levels of acidification (Sadler et al. 2018). Finally, blue mussels are susceptible to a range of pathogens in the form of viruses, bacteria, and endoparasites. For example, the newly discovered parasitic protozoan *Marteilia pararefringens* was recently found on blue mussels in England, Sweden, and Norway (Mortensen & Skår 2020), but its impact remains unclear (Mortensen et al. 2021). Common to this and other known pathogens of mussels is that they spread through water. Because blue mussels in western Norway still thrive on suspended and free-hanging structures fully exposed to the same water, it is hard to envisage how pathogens, ocean warming, acidification, pollution, or other such factors that act through local water quality could explain the observed decline.

4.2. Potential effects of tide

A second class of mechanisms relates to tidal cycles, as mussels in the intertidal are intermittently exposed to water and air, which poses challenges to their physiology and ecology. The upper range limit of blue mussel in the intertidal is controlled by thermal stress while air-exposed (Harley 2011) and limited duration of submergence to permit sufficient feeding. Blue mussels exposed to air temperatures >31°C during low tide suffered increased mortality on both sides of the Atlantic, and survival was lower when exposure was longer or occurred for several consecutive days (Jones et al. 2010, Seuront et al. 2019). In western Norway and farther north, the persistence of blue mussels is affected by low air temperatures and ice scouring during winter (Clark et al. 2021). A harsh Alaskan 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 coastline where they previously dominated (Carroll & Highsmith 1996). At the MBSE, we observed many dead, large mussels hanging underneath the concrete dock in the spring of 2021. This part of the construction is only submerged for a short while every high tide, and the blue mussels had likely died from freezing. We saw no sign of similar freezing elsewhere, and particularly not at the tree branches we studied. It is likely that constantly submerged blue mussels on floating docks are sheltered from temperature extremes and can feed continuously. Effects of climate change such as extreme weather conditions, in particular increased precipitation leading to hyposaline surface water or longer-lasting atmospheric high pressures leading to locally decreased sea level, might affect blue mussels on rocky shores more negatively than the constantly submerged ones. Some predators, notably oystercatchers and gulls, have easier access to mussels when the tide is low. Still, we found that mussels were abundant on tree branches that were out of water on each low tide, but only as long as the branch had no access route for crawling predators from the sea bottom. Pooling floating docks, rocky shores, and trees together, both the accessibility to crawling predators and tidal exposure significantly influenced blue mussel occurrence. The lower occurrence of blue mussels on trunks and branches without bottom contact (83 ± 5%) compared to floating docks (occurrence of 100 ± 0%) may be caused by an influence of tide. Because most branches were 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 compared to that of connectedness.

4.3. Recruitment and early life stages

A third class of mechanisms focuses on recruitment and the particular challenges of early life stages of blue mussels. Blue mussels begin their life in the pelagic, and invasive Pacific oysters are known to filter-feed on their larvae (Troost et al. 2008). Although spreading in Norway, Pacific oyster distribution is largely limited to the southern coast (IMR 2020), and there are too few oysters to cause a mussel decline in our study area. Jellyfish also prey on bivalve larvae, and their blooms might cause recruitment failures (Schroeder et al. 2023). At the time the blue mussel larvae settle, biofilm can differ between substrates and might lead to unequal settlement rates on floating structures and rocky shores, and thus cause differences in recruitment success on those structures (Baden et al. 2021). Biofilm is likely not different between branches only metres apart where one touches bottom and the other does not. If differences in biofilm were contributing to a decline in blue mussels in western Norway, it would logically require that the biofilm on natural rocks was hostile to recruitment while that on plastic floating docks and other man-made structures was not. Recruitment failure during the pelagic stage has been suggested as central to the mussel decline in the Northwest Atlantic (Petraitis & Dudgeon 2020). Both in Sweden and Norway, continually high densities of settlers in mussel farms and on floating structures (Andersen et al. 2017, Baden et al. 2021) further corroborate that the cause of the decline acts later than settlement.

A range of mobile subtidal predators are known to have high impacts on intertidal invertebrates and feed efficiently on newly settled blue mussels, particularly during high tide (Rilov & Schiel 2006). In the Wadden Sea, warmer winters have resulted in higher populations of epibenthic predators like crabs and shrimps (Beukema & Dekker 2007), with large impacts on the mortality of juvenile blue mussels (Beukema & Dekker 2005). On the east coast of North America, low recruitment was linked to years with hot summers (Petraitis & Dudgeon 2020) and potentially to high densities of benthic predators such as sea stars and crabs (Bologna et al. 2005). Common sea stars and green crabs feed effectively on small blue mussels in Norway (Christie 1983, Bodvin 1984, Christie et al. 2020). Green crabs have increased in Scandinavia (Eriksson et al. 2011), probably due to overfishing of top predators such as cod *Gadus morhua* (Christie et al. 2020). In particular, green crabs showed the potential to diminish blue mussel recruits drastically within a few hours in mesocosms and could therefore contribute to blue mussel declines in Norway (Christie et al. 2020). *Asterias 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 (with blue mussels). Predatory snails, particularly dogwhelks, are also known predators on juvenile and adult blue mussels and are well researched in North America (Menge 1976, 1978, Lubchenco & Menge 1978) and Britain (Burrows & Hughes 1990, 1991, Morton 2011), but we have found no detailed studies on their effects in Scandinavia. Crabs, sea stars, and predatory snails are all crawling predators and could be among the predators that negatively affect blue mussel abundance during their early life stages.

4.4. Survival and growth of adult blue mussels

Reports collected from the public showed that well-established blue mussel beds in Norway, where collection had been ongoing for decades, disappeared over 1–2 yr, starting from 2015 (Andersen et al. 2017). This suggests that large adult mussels also died in considerable numbers, and quickly at each location. Focus must therefore extend beyond the juvenile life stage, and the fourth type of mechanism focuses on factors that affect growth or survival of adult blue mussels. Harmful algal blooms or changes in food abundance at scales that could explain regional declines have to our knowledge not been reported from Norway. *Mytilus edulis* and *M. galloprovincialis* frequently interbreed, and their hybrid offspring show reduced fitness and recruitment, which can negatively impact population persistence (Benabdelmouna & Ledu 2016), but it is not clear how hybridization could have different effects on floating structures versus rocky bottom. In Europe, harvesting of wild blue mussels peaked at ca. 184 000 t in 1993 and triggered local declines in wild populations (FAO 2021). After harvesting had removed most intertidal blue mussel beds in the Wadden Sea by 1990, regulations from 1995 onwards have resulted in recovery, albeit slow, of blue mussel beds (Beukema & Dekker 2007, 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 has been restricted to a few locations near packaging plants in central Norway. In Norway as well as in Sweden (Baden et al. 2021), biomass harvested and geographic scale are and have been too small to cause the observed declines in wild mussel stocks.

At several rocky bottom locations, we observed a few adult mussels protected in cracks but not elsewhere, pointing to limited access of predators as influencing small-scale distribution patterns. Although a variety of predators may feed on adult mussels, fishes and diving birds can generally reach blue mussels on floating structures and feed on them, so while blue mussels may be part of their regular diet, consumption by these predators is unlikely to have had an impact at the scale that can produce the distribution patterns we observed. It can be argued that common eiders *Somateria mollissima*, a known voracious predator (Hilgerloh 1997) that we repeatedly observed feeding on blue mussels, might struggle to feed from the underside of floating structures, but we did not observe any floating structures with mussels below but not on the vertical and accessible sides. If we restrict focus to crawling predators, then sea stars, crabs, and predatory snails remain as foragers on adult blue mussels. The common sea star opens small blue mussels with short force impulses that increase rapidly in strength, and handles larger mussels through exhaustion of the posterior adductor muscle by applying force for an extended period (Norberg & Tedengren 1995). Sea stars generally seem to have a larger impact on mussel beds in Pacific North America (Paine 1974). In the Atlantic, *A. rubens* prefer smaller blue mussels as prey (Hummel et al. 2011), although they can handle larger mussels than green crabs (Dolmer 1998), and their consumption rate is much lower (Bodvin 1984, Kamermans et al. 2009). Green crabs are efficient predators on juvenile and small blue mussels (Christie et al. 2020), and the size of preferred prey correlates positively with crab size, mostly restricted to shells <40 mm (Elner & Hughes 1978). Juvenile edible crabs prefer blue mussels over other oyster species when given the choice (Mascaró & Seed 2001). As adults, edible crabs are able to crack or pry open blue mussels of any size (Ebling et al. 1964). It has been suggested that crabs avoid large hard-shelled prey because crushing them causes mechanical wear on the claws, and that they thus prefer smaller prey than predicted by purely energetic foraging considerations (Juanes 1992). Although it is generally assumed that the edible crab is a voracious predator on blue mussels, it has proven difficult to find literature on experimental predation rates of adult *Cancer pagurus* on blue mussels or of their foraging rates in the wild.

Predatory snails are particularly interesting candidates for the recent changes in blue mussel abundance because their populations have rebounded from the detrimental effects of TBT pollution (Bryan et al. 1987, Gibbs et al. 1987). TBT is an organotin compound that triggers imposex, the imposition of male organs on females in many marine gastropods (Bryan et al. 1987, Gibbs et al. 1987). At a later stage of imposex, it causes sterilization of adult females through blockage of the oviduct by vas deferens formation (Bryan et al. 1987, Gibbs et al. 1987). Both the netted dogwhelk *Tritia reticulata* and dogwhelk *Nucella lapillus* were affected by TBT and may drill blue mussels. *T. reticulata* is found along most of Norway's coastline (GBIF 2022a, OBIS 2022b), and although this species is common around rocky shores, it prefers patches of soft sediment (Tallmark 1980). Further, *T. reticulata* is more often described as a scavenger than as a carnivore, as it lies buried in the sediment until triggered by the scent of carrion (Crisp 1978, Tallmark 1980, Davenport & Moore 2002). All of this suggests that *T. reticulata* is not a likely culprit for the observed large-scale decline of blue mussels in Norway.

The dogwhelk is very sensitive to TBT, and a small amount (a few ng l^{-1}) is enough to induce significant levels of imposex, leading to population declines (Bryan et al. 1987). *N. lapillus* populations in Norway were severely affected (Følsvik et al. 1999, Schøyen et al. 2019). 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 and its use was banned globally in 2008 (IMO 2002). TBT levels are now low in the environment, and 2017 was the first year imposex was not found in *N. lapillus* along the Norwegian coast (Schøyen et al. 2019). In southern England, dogwhelk populations increased 50-fold from 2004 to 2010 (Morton 2011, Bray et al. 2012). Many sites became recolonized (Birchenough et al. 2002), and juveniles again dominated the population structure (Evans et al. 1996). The situation in the Northwest Atlantic is different, where dogwhelks, as well as blue mussels, have declined by ca. 50% over the period 1997–2018 (Petraitis & Dudgeon 2020). To our knowledge, similar data are not available from Norway, but it seems plausible that the recovery of a predator on the scale observed in England, just across the North Sea, could have large effects on its prey.

A role for predation in Norway is further corroborated by the observation from western Norway that blue mussels were more common in low-salinity habitats such as bays and inner parts of fjords (IMR 2022). This distribution pattern points to predation, since both sea stars (Binyon 1961) and dogwhelks (Stickle et al. 1985) have low tolerance for freshwater and are found at lower abundance or not at all in the inner parts of Hardangerfjord, where summer salinity falls below 15–20 PSU (Brattegard 1966). A similar salinity threshold, 17 PSU, has been reported for the edible crab (Wanson et al. 1983).

Our caging experiment showed that dogwhelks fed 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 might 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 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.

4.5. More indirect ecosystem effects

Predator–prey interactions are complex, and indirect effects of multiple predators can further influence outcomes. Blue mussels have a high phenotypic plasticity and respond to waterborne predator cues. If dogwhelks are in the vicinity, mussels grow thicker shells (Sherker et al. 2017); if mussels sense sea stars, they invest in a stronger adductor muscle (Reimer & Tedengren 1996, Freeman 2007); and if crabs are present, mussels 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, leaving them immobilized (Petraitis 1987, Farrell & Crowe 2007). Predators also interact with each other; for example, predation can attract other scavengers, such as the polychaete worm *Eulalia viridis* (Morton 2011) and the common whelk *Buccinum undatum* (Christie 1983), and co-consumption by 2 species can more efficiently reduce blue mussel abundance (Christie et al. 2020). Edible crabs feed on dogwhelks smaller than ca. 20 mm but are not successful on larger individuals (Lawton & Hughes 1985). Green crabs also prey on dogwhelks (Hughes & Elner 1979) as large as 30 mm (Ebling et al. 1964) and may suppress feeding activity of dogwhelks through non-consumptive effects (Quinn et al. 2012, Bourdeau & Padilla 2019), similar to those induced by sea stars (Gosnell & Gaines 2012). Dogwhelks differ substantially in the thickness of their shells, and the size range available to predators may depend on shell thickness (Ebling et al. 1964).

Dogwhelks are not a new species in European waters, so even though dogwhelks may exert a large impact on blue mussels now, there have been times where these 2 species coexisted. Within species, there may be geographic structuring of the gene pool, so that some traits are more common in specific areas. When this plays out across species linked by e.g. predator–prey interactions, this can lead to rich outcomes as theorized by the geographic mosaic of coevolution (Thompson 2019). For species temporarily released from predation, as blue mussels may have been when dogwhelk populations were at a minimum, a reduction in defensive traits such as shell thickness is expected. As the predator population bounces back, rapid predation may ensue, until selection for thicker shells once again increases mussel survival. Similar dynamics have been described among freshwater snails and their fish predator across lakes in Mexico (Chaves-Campos et al. 2011). Phenotypic plasticity, causing within-life variation in shell thickness in response to olfactory cues from dogwhelks (Sherker et al. 2017), may speed up such processes. Changing environmental conditions can cause rapid shifts in the dominance of intertidal predators (Menge 1983), although mechanisms cannot always be identified. Changes in species abundance can further drive cascading community shifts (Paine 1966, Sorte et al. 2017), so that dogwhelk populations recovering from pollution-induced sterility might be responsible for a new ecosystem state with few blue mussels.

4.6. Conclusions

To summarize, we compared blue mussel occurrence on floating docks and nearby rocks, as well as on fallen trees hanging from the coastline into the water where some touched bottom while others were suspended freely. The review of potential mechanisms above concludes that crawling predators, which are unable to reach floating and free-hanging structures, are the most likely explanation for the present Norwegian blue mussel decline on rocky shores. Many of the observed patterns, our cage experiments, and reports from other regions suggest that the dogwhelk *N. lapillus* has the capacity to inflict large impacts on blue mussel populations. We did not study the edible crab, and it too remains a candidate predator we cannot rule out as impacting blue mussel populations in western Norway. Based on what is known about green crabs and common sea stars, we are inclined to conclude that these are continually active predators on blue mussels; while they may exert considerable predation pressure particularly on juvenile life stages of blue mussels, they did likely not cause the observed broad declines of adult blue mussels. Identifying the cause(s) driving blue mussel declines is crucial and, in the case of a crawling predator with no pelagic stage, could give the green light for future investments in the development of one of the most environmentally friendly and nutritious food productions, blue mussel mariculture with blue mussels growing on rafts and longlines.

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