

# The blue mussel color polymorphisms and growth rates in the Archipelago Sea, northern Baltic Sea

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The blue mussel (*Mytilus trossulus* × *edulis*) is one of the most abundant benthic animals in the Archipelago Sea in the northern Baltic. The mussel is considered a key species, because it participates in the biomass and nutrient cycles by filtering water, serves as a growth platform and is a food source for many organisms. The mussel exhibits a genetic polymorphism in its shell color, in which a recessive allele causes a dark blue color, whereas the dominant allele causes brown. Earlier studies have hypothesised about a relation between mussel color forms and growth rates. In this study, we examined the occurrence of the mussel's color forms in the Finnish Archipelago Sea and investigated the differences in mussel growth rates between the color forms. We analysed 524 individuals from regional mussel populations representing four sampling sites with varying environmental conditions. The study revealed that presently the distribution of both color forms is relatively even. The dark blue color form indicated only a slight dominance in abundance at the study sites. We did not detect differences in growth rates among mussels of the color forms. This was likely due to a large variation in the individual growth rates of mussels. Instead, differences in the average growth rates among the sampling sites were observed. This indicated that other factors that limit the survival of mussels in the Archipelago Sea habitats, such as salinity and temperature, play an important role in the growth rates of the color forms. In the future, the dark blue form can likely be expected to be proportionally more common in the Archipelago Sea, if the global climate warming and seawater temperature together with turbidity increase continues as expected. Numerically the brown color form will be preserved because it can tolerate higher temperatures.

## Introduction

The blue mussel (*Mytilus trossulus* × *edulis*) is one of the most important benthic animals in the Baltic Sea. It constitutes a major proportion of the biomass in the hard seabed areas of the Baltic Sea (Jansson & Kautsky 1977). The mussel is considered as a key species in the Baltic Sea region, as it participates in the biomass and nutrient cycles by filtering water (Kautsky & Evans 1987), serves as a food source for many fish and bird species

and acts as a breeding ground and growth platform for many other seabed organisms (Koivisto 2011). The blue mussel in the Baltic Sea has been defined to be a hybrid between two species of the *Mytilus* family being the Atlantic mussel (*M. edulis*) and the Pacific mussel (*M. trossulus*) (Varvio et al. 1988, Väinölä & Strelkov 2011).

The blue mussel is a polymorphic species in terms of its shell color, because it has separate color forms occurring simultaneously in the same population. In the Archipelago Sea, the mussels



Figure 1. Left: Dark blue- and brown color forms of *Mytilus* from a sample taken at the Bodö site. The dark blue shell is partially covered by barnacles (*Balanus improvisus*). Right: the growth ring and grooves in the shell of brown *Mytilus* form (photos: A. Lauerma).

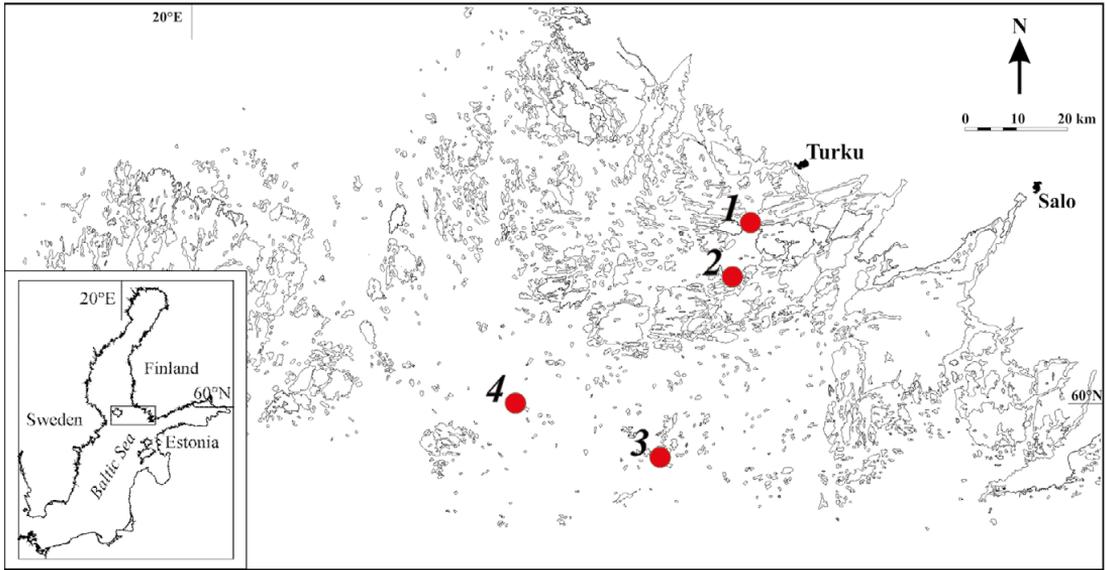
can roughly be divided into dark blue- and brown color forms (Figure 1).

The color of blue mussels is determined genetically. Based on cross breeding experiments, the color of the shell is determined by a single locus with two alleles. The recessive allele produces a dark blue color and the dominant allele causes a brown phenotype (Innes & Haley 1977). Moreover, the intensity of the brown color within the brown forms can vary considerably, and there also exists striped individuals. Therefore, an influence of discrete loci on the mussel color formation is considered to be likely, as well (Newkirk 1980).

The blue mussel is a unisexual species, which in the Archipelago Sea, reproduces in late spring. At that time, males and females release their eggs and sperm into the seawater. Depending on the mussel size, females can release a few million eggs at a time. The fertilized eggs go through a larval phase within a few weeks during which they float in the water. After the larval stage, the mussel settles to a hard-bottom substrate and begins to build up a shell for itself (Antsulevich et al. 1999). The mussel attaches to the substrate

with its filamentous byssus fibers but is still able to move to a limited extent (Seed & Suchanek 1992). The growth rate of the mussel varies seasonally. During winter, its growth decreases when the temperature drops causing the formation of winter grooves into the shell, which are more easily noticeable in comparison to the broader but more indiscernible summer growth rings (Vuorinen et al. 2002).

Experiments performed on the Atlantic coast have suggested that the dark blue form of the mussel grows more rapidly than the lighter brown form (Newkirk 1980). This has been estimated to be an adaptation to the variable environment. The color of the shell affects the thermoregulation of the mussel, as the lighter brown color absorbs less energy from sunlight resulting in lower heat stress-related mortality during sunny and warm summers (Mitton 1977), especially in bright waters. In the dark and cold conditions, the dark blue form can absorb less intensive solar energy more efficiently without the risk of overheating. These properties can cause selective pressures on mussel color forms. Since the 1960's, darker environmental conditions have become a reality on coast-



**Figure 2.** The Archipelago Sea and sampling sites from the middle to the outer archipelago: 1 = Grangrundet, 2 = Saunasaari, 3 = Bodö and 4 = Pattonskär.

al areas of Finland due to an accelerated eutrophication process resulting in increased turbidity of the seawater and favoring the dark blue mussel form. Although, at the same time, the seawater temperature has increased 1.5°C and salinity decreased by 0.5 PSU (Mäkinen et al. 2017), the Baltic Sea is still a cold, arctic sea with a great variation in temperature during the seasons with cold winters and mild summers. These conditions are expected to continue in the future as well (BACC 2008).

A basis for the present study stemmed from inquiries from local people living permanently in the archipelago area. Many people presented a question to the researchers at the research station about whether the researchers knew about the reasons behind the recent spread of the brown mussel color form that was seen rarely only couple years earlier. In principle, this study was driven by proactive crowdsourcing. As there were no historical data or sample available for detecting the manifested spread of brown mussel, a focus was only on the present situation of the mussel color polymorphism distributed over a larger geographical area in the Archipelago Sea of the northern Baltic Sea. Especially the differences in the occurrence of the brown color form between the more turbid and low-salinity waters of

the middle archipelago and the brighter and saltier waters of the outer archipelago were examined. The work was carried out by a sampling survey and by lab analysis, which aimed to elucidate the possible physiological and genetic differences between the color forms.

### The study area

The Archipelago Sea is a semi-enclosed archipelago at the southwest coast of Finland between the Baltic proper and the Bothnian Sea (59°45'–60°45'N and 21°00'–23°00'E) in the northern Baltic Sea (Figure 2). Depending on the definition of an island, the area is estimated to contain up to 60 000 islands, of which some 41 000 are named in regional charts (Väänänen et al. 2020). In this respect, it is the biggest archipelago in the world that has a complex and variable topography and mainly wind-driven water mass movement patterns. The total area of this brackish water sea is 9 436 km<sup>2</sup> with a water volume of 213 km<sup>3</sup> and salinity content of 4 to 6 PSU (Voipio 1981). The total catchment area of the Archipelago Sea is approximately 8 900 km<sup>2</sup> with a lake area of less than 2% and arable land 28% (Hänninen et al. 2000). The average water depth is only 23 meters, as the deepest hollows reach 140 meters.

The wind-caused sea level variation is generally low with mostly a plus or minus 0.5-meter variation compared to the theoretical mean level with insignificant tidal fluctuation (BACC 2008). The sea is characterized by strong seasonality with the summer temperature of seawater reaching 20°C and with 0–60 days of ice cover during the winter (Leppäranta & Myrberg 2009).

Locations with variable water quality from the middle archipelago to the outer archipelago were selected as sampling sites. The four selected sites were named after the nearest island (Figure 2). Background variables, such as site depth (m), seawater transparency or Secchi depth (m), seawater salinity (PSU) and temperature (°C) were also measured as complementary information taken from the surface water (above the thermocline of 0–3 m) in the vicinity of each sampling site covering only one sampling with different dates at various sites (Table 1).

## Materials and methods

### Sampling

Sampling at selected sites was conducted with an epibenthic dredge, which was operated from a boat. The rope was lowered into the sea for at least the depth of the site, after which, the dredge was pulled by a boat along the bottom surface to collect any detaching material. After lifting the dredge, the material was washed in a 1-mm screen, which allows all impurities to be flushed out of the sample. Finally, the mussels were pooled as a composite sample in a bucket filled with seawater. The procedure was repeated for a sufficient sample size, which was estimated to more than 100 individuals. No advanced information was available about the mussel populations

at any sites. For this reason, the sampling was to determine whether populations existed at the sites, therefore the number of dredges per sites varied. Moreover, the sampling was not conducted only in one location at sites, but more sampling was performed all along the whole island coastline from prone rocky bottoms that made the accurate depth estimation difficult. The procedure fulfilled the assumptions of random sampling at each site in later statistical analyses. However, one sampling had to be done by diving in order to reach the mussels, as they lived in rocky bays and were attached to the lower surface of the boulders. The mussel samples were transported to a lab and frozen (–20°C) for later analysis.

### Treatment in the lab

Prior to analysis, the frozen mussel shells were cleaned by scraping away all the organisms that use the shells as culture media. The age of the collected mussels was determined by counting the winter grooves from the shell structure. Age determination and identification of the innermost winter groove were performed according to Vuorinen et al. 2002. They showed that the mussels in the Archipelago Sea grow to 0.6–4.8 mm in length before the first winter of their life, and this innermost groove in the mussel shell was considered to be the starting point for the age determination, i.e., the year starting at 0+. This procedure was followed systemically with all individuals in mussel samples. A stereo microscope (Zeiss Stemi 508) was used to determine the mussel age. A few decrepit individuals were found unsuitable for a reliable age determination, and those were excluded from the data. The mussels were sorted by color under the light of a stereo microscope. An individual was categorized into a color form cat-

**Table 1.** Sampling sites and measured environmental background variables taken once from the surface water (0–3 m) in the vicinity of sampling sites in the moment of sampling.

Site	Date	Depth (m)	Secchi depth (m)	Salinity (PSU)	Temperature (°C)
Grangrundet	11/06/2020	2–2.5	2.5	5.6	12.4
Saunasaari	27/05/2020	8–10	5.0	5.6	11.0
Saunasaari	04/06/2020	8–10	5.0	5.6	13.2
Bodö	17/06/2020	10–11	4.5	6.2	13.9
Pattonskär	20/07/2020	9–11	3.2	5.8	20.0

**Table 2. Total catches, frequencies and annual growth rates (GR; mm/a) of blue- and brown color forms per sites (\*= combined samples).**

Site	Tot. (n)	Blue (n)	Brown (n)	GR (mm/a)	SD <sub>GR</sub>	GR-blue (mm/a)	GR-brown (mm/a)
1. Grangrundet	152	92	60	2.97	0.67	2.98	2.95
2. Saunasaari*	113	61	52	3.40	0.67	3.49	3.28
3. Bodö	118	64	54	4.06	0.69	4.02	4.11
4. Pattonškär	141	74	67	3.61	0.81	3.67	3.53
Mean	131.00	72.75	58.25	3.54	0.73	3.56	3.53

**Table 3. T-test results of means of growth rates of color forms.**

Method	Variances	DF	t-value	Pr >  t
Pooled	Equal	513	0.420	0.671
Satterthwhite	Unequal	474.11	0.420	0.674
Equality of Variances				
Method	Num DF	Den DF	F-value	Pr > F
Folded F	228	285	1.140	0.305

egory only if it had a clearly detectable shade of blue/brown color. Dimensions (i.e., length, width, height) and wet weight (g) were also determined for each mussel. Dimension measures were taken with a caliper, and weighing was conducted with a precision scale. The growth rates were calculated by dividing the length of the mussel (mm) by its specified age in years (a).

### Statistical analysis

Considering the potential variables measured from mussels, we eventually decided to use mussel length and age as the only parameters in the statistical analysis. Statistical analysis of the data was performed with SAS Enterprise Guide 9.1 (SAS 2009). Two-way ANOVA was used to investigate the possible interactions of color form and growth location on mussel growth rate. Microsoft Office Excel (MS Office 2008) was used for the treatment of the data as well as for the calculations of the mussel growth rates.

## Results

A total of 524 mussel individuals were collected from the four sampling sites, and, of which, 291 were dark blue and 233 were brown. The frequencies of the mussel color forms were fairly even-

ly distributed among the different sampling sites, but the dark blue form indicated a slight dominance (Figure 2; Table 2).

No significant difference in the average growth rates of the dark blue- and brown color forms was observed by the t-test (Table 3). Due to the size of the standard deviation of the data, the measured growth rate differences would have to be significantly larger ( $p < 0.05$ ) in order to be considered statistically significant.

As a two-way ANOVA did not show significance in the data, no interaction effect between the sampling site and the mussel growth rate was revealed. However, ANOVA's F-test revealed a statistically significant difference in the average growth rates of mussels among the sampling sites (Table 4). However, no increasing or decreasing patterns or trends in growth rates from the middle to the outer archipelago could be detected (Figure 3, Table 1). The model explained some 24% of all variation observed in mussel growth rates at study sites.

## Discussion

We found that there was no large variation in the local abundance of mussel color forms, only the dark blue color form indicated a slight dominance in abundance at each sample site. In-

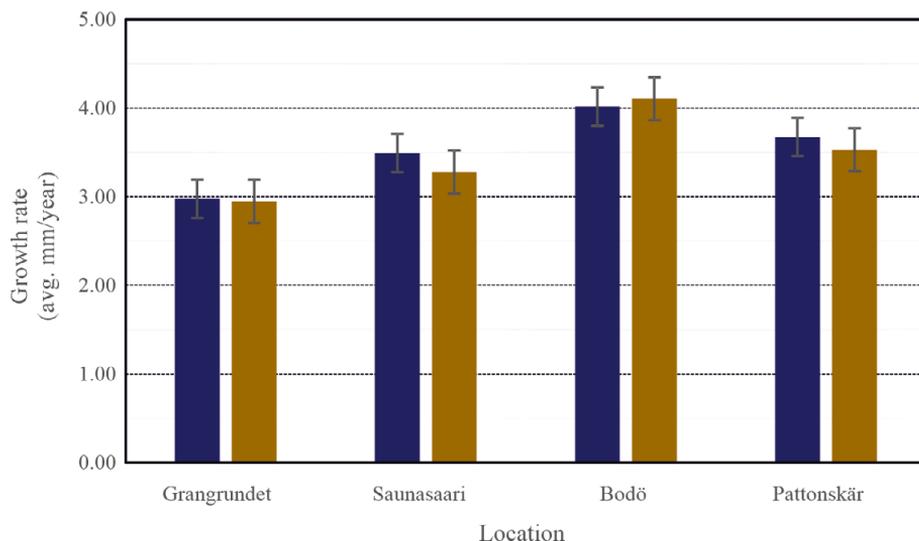


Figure 3. Average annual growth rates (GR; mm/a) of dark blue- and brown color forms per location (form colors as presented). The scatter bars indicate standard errors (SE) by sites.

Table 4. One-way ANOVA table of the mean growth rates and the effect of the site on the growth rate of blue mussels.

Source	DF	Sum of Squares	Mean Square	F-value	Pr > F
Model	3	81.275	27.092	52.74	< 0.0001
Error	511	262.509	0.514		
Corrected total	514	343.784			
R-Square	Coeff Var	Root MSE	Growth rate Mean		
0.236	20.623	0.717	3.476		

stead, the growth location was found to be important for the growth rate of the mussel regardless of color. Nevertheless, there were no areal trends in the growth rates among the archipelago zones. This indicates that other factors that limit the survival of mussels in the Archipelago Sea habitats, such as salinity and temperature, could also play an important role in the growth rates of the two color forms. We will discuss this in more detail. Our one-time measurements for the salinity match rather well with the latest conducted large-scale survey in 2007 by Suominen et al. 2010, who showed that the average salinity gradients in the Archipelago Sea increase southwards from the coastline. In this zonation, our innermost station in Grangrundet belongs to the zone where seawater salinity was typically less than or equal to 5.7 PSU, Saunasaari in the salinity zone between 5.7–5.8 PSU, Pattonskär in the salinity zone of 6.0–6.1 PSU and Bodö at greater than or equal to 6.1 PSU. In the long-term data since 1966, Mäkinen et al. 2017 showed that in the Ar-

chipelago Sea around Seili Island, the seawater salinity generally decreased by 0.5 PSU, while the seawater temperature has increased 1.5°C during the same period. However, in the Archipelago Sea, the temperature shows only vertical thermal stratification; horizontally gradual changes or trends in temperature do not exist between the archipelago zones.

Considering the trends, the interaction of the growth rates of the color forms among the sites could have been too small to show a difference in the present data. This could either be due to the large variation in the individual growth rates of mussels or the too small sample size to reveal a difference. However, as the variation between the average growth rates of color forms was low, and the p-values of the t-test comparisons of the growth rates of the color forms were non-significant, we have a reason to believe that the sample size was big enough to reveal a difference, and that our results can be considered true and valid. Therefore, we suggest that the large variation

in the individual growth rates of mussels could hide the possibly existing trends between archipelago zones.

In the present study, differences in average growth rates of mussels were true among sample sites. As there were no obvious trends in growth rates between the archipelago zones, the differences are probably due in part to variations in local environmental conditions, such as the seawater salinity and temperature. It has long been known that both temperature and salinity are environmental factors that have an important influence on many marine species, such as mussels, living in the cold and low-saline Baltic Sea, which limit their success and existence in available habitats (e.g., Segerstråle 1969, Leppäkoski et al. 1999, Westerbom et al. 2002, Vuorinen et al. 2015). Other possible influencing environmental factors could be sample depth and elements related to local eutrophication such as the nutrient concentrations of seawater. Earlier, it has been shown that depth together with the susceptibility to wave exposure could be crucial factors in the abundance and growth of blue mussels in the Baltic Sea (Westerbom & Janttu 2006). In the case of eutrophication, the findings are more contradictory. The effect of eutrophication on benthos is usually reported as negative (e.g., Grall & Chauvad 2002). However, in the Gulf of Gdansk, eutrophication increased the availability of food resources to filter feeders that affected positively their physiology and vertical distribution, which further allowed efficient colonization of mussels in a wider depth range (Wołowicz et al. 2006). Their location has a great impact on their success. However, for the latter case, there exists no data with the desired local resolution to evaluate its effect on the mussel growth rates. The growth rate of mussels in the Grangrundet area was slower than in other areas, which may, at least partly, be due to the shallowness of the sampling site. In that case, the bottom of the area may heat up enough during a warm summer to cause thermal stress on the mussels. The energy balance of mussels turns negative at a temperature of about 17°C, i.e., at higher temperatures, and the mussel growth rate declines (Fly & Hilbish 2013). This is supported by the fact that we did not find any individual large mussels from the Grangrundet. On the other hand, at times, especially during winters and

early springs, the Grangrundet belongs to an area of high runoffs by the Aurajoki river that brings lots of sediments from the catchment area and thus increases remarkably the sea's turbidity for weeks in the area. In the long run, this could have a great impact on nutrient availability and especially food quality and explain the slower mussel growth rates and the lack of larger mussels.

The growth rates between mussel populations have been previously studied in the Archipelago Sea (Antsulevich et al. 1999). However, that study did not concentrate on the growth rate differences between the mussel color forms. Under the Atlantic marine conditions, Newkirk (1980) found a clear 10–20% difference in the growth rates of dark blue- and brown color forms. The differences in growth rates between the Atlantic Ocean and the Archipelago Sea mussel populations can most likely be explained by environmental conditions. Mussels are marine organisms that are affected by low salinity, and this limits their growth due to osmotic stress. Due to low salinity, the cell organs of the *Mytilus* have to maintain their physiological state by excreting the excess water outside the cell membrane, which requires a lot of energy. This excess energy demand is then compensated for by the shift to other biological functions such as individual growth. Another potential explanation for the decreased mussel growth rates was provided by Sanders et al. 2021. They showed that mussels exhibit decreasing growth when salinity is less than 11 PSU, and the mechanisms behind this is reduced calcification rates in a low-saline environment due to the ionic composition of seawater, especially  $\text{HCO}_3^-$  and  $\text{Ca}_2^+$ , being lowered resulting in undersaturation of the main building material of  $\text{CaCO}_3$  to calcifying organisms leading to further decreased growth.

However, it has already been shown that the mussels in the Baltic Sea region live in a constant state of physiological stress due to the low salinity of the seawater (Tedengren & Kautsky 1986). The Atlantic mussel grows on average to 10 cm in length, while in the Baltic Sea, the mussels remain smaller than 4 cm. Therefore, there is an effect of adaptive energetic differences in the mussel forms due to the proportion of sunlight transformed into heat in the seawater, as presented by Mitton (1977). During the past decades, this may have a certain influence on mussel color forms

due to a eutrophication-driven increase in the turbid conditions of the Archipelago Sea. In the dark and cold conditions, the dark blue form can absorb less intensive solar energy more efficiently without the risk of overheating. These abilities have the potential to cause selective pressures favoring the dark blue color form and can explain their high proportion in the mussel population despite having a recessive allele. In the future, the dark blue form can be expected to be still proportionally more common in the Archipelago Sea, if the global climate warming, seawater temperature increase and eutrophication together with accelerated turbidity continues as expected. The brown color form with dominant allele will remain abundant, because it can tolerate higher temperatures. In that sense, as the development of the share of mussel color forms, in our opinion, has gone contradictory to the intuition of the local people, we were not able to give answer to their fundamental question.

The Archipelago Sea is the subject of several ongoing processes of large-scale changes (e.g., Hänninen 1999, Hänninen & Vuorinen 2011, Hänninen & Vuorinen 2015, Vuorinen et al. 2015) that threaten the mussel populations. Due to eutrophication, increased sedimentation in the seabed will reduce the number of habitats suitable for mussels in the future. In addition, a decrease in salinity increases the effect of osmotic stress (Vuorinen et al. 2015), while an increase in seawater temperature exposes the mussels to thermal stress. Elevated stress levels increase mortality and interfere in the growth and reproduction of mussels (Westerbom et al. 2019). Possible differences in the tolerance of these environmental changes between the color forms will probably also influence the development of the genetic structure of the mussel population.

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