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# Long-term decrease in Baltic Sea blue mussel shell length

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## ABSTRACT

Multi-decadal monitoring data and archived biological samples make the rapidly changing Baltic Sea an ideal system for quantifying alterations in ecosystem function. The Baltic Sea blue mussel (*Mytilus edulis trossulus*) acts as a keystone species by providing food and habitat for other species, and through its filtering activity clearing the water and promoting organic matter and nutrient cycling between benthic and pelagic ecosystems. A decrease in biomass of blue mussels along with altered environmental conditions has been observed in the northern Baltic Sea over a 24-year period (1993–2016), but the size distribution of the mussels was unknown. The present study focuses on retrospective measurements of the individual shell lengths of these archived blue mussels. The mean shell length was found to be significantly lower at the end of the time series than in the beginning (11.1–11.5 mm for the years 1993–1996 compared to 10.3–10.9 mm during 2012–2015), with the proportion of larger mussels decreasing in the population. This 6% decrease in shell length translated into a significantly lower (16%) mean filtration capacity at the end of the time series compared to the beginning, influencing the ecosystem services blue mussels provide.

## 1. Introduction

The well-studied Baltic Sea is a system undergoing rapid environmental changes and thanks to long time series of monitoring data and archived biological samples it is an ideal system for quantifying changes in ecosystem function over time (Reusch et al., 2018). The blue mussel is a marine suspension feeding bivalve that in the brackish Baltic Sea forms the species complex *Mytilus edulis trossulus* (Stuckas et al., 2009; hereafter referred to as blue mussel). In the northern Baltic Proper the biomass of blue mussels generally increased at all depths from 1974 to 1990 (Kautsky et al., 1992), probably due to favourable salinity conditions and high phytoplankton concentrations from eutrophication (Prof. Nils Kautsky, Stockholm University, Sweden, pers. comm.). A recent study in the same area demonstrates a decrease in biomass of blue mussels at several stations from the early 1990s to mid-2010s (Liénart et al., 2020). Decreases in blue mussel coverage have also been reported in the southern Baltic Sea during the last decades (Franz et al., 2019). Reasons for these decreasing trends in Baltic Sea blue mussel populations seem to be a combination of changes in salinity and food

resources and higher temperature during winters (Öst and Kilpi, 1997; Waldeck and Larsson, 2013; Franz et al., 2019; Liénart et al., 2020; Westerbom et al., 2021). Increased predation pressure from fish such as roach (*Rutilus rutilus*) or the invasive round goby (*Neogobius melanostomus*) has been reported to locally reduce blue mussel abundance (Lappalainen et al., 2001; Skabeikis et al., 2019; Nöomaa et al., 2022). Bird predation is however unlikely to be responsible for the declining blue mussel population, considering the declines in sea bird population, e.g. the common eider (*Somateria mollissima*) since the 1980s (Hario et al., 2009; Öst et al., 2016) or the long-tailed duck (*Clangula hyemalis*) since the 1990s (Bellebaum et al., 2014).

The biocalcification rate of the blue mussel shell is depressed at low salinity (Almada-Villela, 1984), restricting the growth of blue mussels in the Baltic Sea (Tedengren and Kautsky, 1986; Westerbom et al., 2002). In the northern Baltic Proper with a salinity rarely exceeding 6.6 (Liénart et al., 2020), blue mussels reach a maximum length of 55 mm (Remane, 1958 in Snoeijs-Leijonmalm et al., 2017). Although being dwarfed in the Baltic Sea, the blue mussel is a dominant species on hard substrates (generally down to 35 m; Kautsky, 1981; Attard et al., 2020)

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where it can constitute more than 80% of the animal biomass (Jansson and Kautsky, 1977). This keystone species provides habitat for other invertebrates (Norling and Kautsky, 2008) and is an important part of the diet of many predators, including sea birds (Waldeck and Larsson, 2013). The filter feeding of the blue mussels promotes organic matter and nutrient cycling between benthic and pelagic ecosystems (Kautsky and Wallentinus, 1980; Kautsky and Evans, 1987) and may locally control the plankton concentration (see e.g. Kotta et al., 2020), hence increasing water transparency (Nielsen et al., 2016; Schröder et al., 2014), which enhances the recreational and economic value of the Baltic Sea (Soutukorva, 2005).

This study presents new data from retrospective measurements of blue mussel shell length on archived samples from a 1993–2016 time series. Studies performed on the same time series found a considerable decrease by, on average, 50% in total biomass and a decrease in mean blue mussel size in the population estimated from the biomass to abundance ratio (Liénart et al., 2020). Here, we expect a decrease in blue mussel shell length in recent years compared to the early 1990s, and that such a decrease in shell length will translate into a reduced filtration capacity of the entire population. We specifically investigate whether a potential change in shell length is due to a change in the abundance of any specific size class of blue mussels.

## 2. Materials and methods

The study was performed on archived samples from the northern Baltic Proper collected within the Swedish Marine Monitoring Program at Iskären, a small island with, for the Baltic Sea, good conditions for *Mytilus edulis trossulus*, located close to the Askö Laboratory Research Station (58° 49'N, 17° 31'E) in the southern Stockholm archipelago (see Liénart et al., 2020 for details). Blue mussels were sampled every year between 1993 and 2016 in late August or early September by SCUBA divers. Samples were collected at a depth of approximately 5 m using three 20 × 20 cm sampling frames. Since 2017, samples at 5 m depth are no longer collected by the monitoring program. The mussels were sorted out and were oven dried at 60 °C (meat still inside shell). The dry samples were wrapped together in aluminium foil, placed inside plastic bags, and stored in cardboard boxes in dark and dry conditions.

For the present study, blue mussel samples from the four earliest years (1993, 1994, 1995, 1996) and four recent years (2012, 2013, 2014, 2015) were measured. One of the three sampling frames from each year was randomly selected for shell length analysis of all mussels; the other two frames were used to assess variability in total biomass and abundance between these years (details later). The shell length (from umbo to the most posterior point) of all blue mussels with a length of at least 5 mm were measured. Valves that had separated at the hinge, but were otherwise in a sufficiently intact condition, were paired using the following steps: (i) valves that differed no more than 0.1 mm in length were paired, (ii) if more than two valves differed no more than 0.1 mm in length, pairs were created with the smallest difference possible within each pair, (iii) valves unable to be paired according to rules (i) and (ii) remained unpaired. The mean length of valves paired according to rules (i) and (ii) was calculated. For unpaired valves the length of the single valve was used. Paired valves contributed 6–46% and unpaired valves 6–18% to the total abundance of any particular year. Data on total biomass and abundance for the three frames each year was extracted from the monitoring program database and upscaled to 1 m<sup>2</sup>.

The length distributions of blue mussels for the early and late years were visualized in a histogram and a Kolmogorov-Smirnov test was performed on the blue mussel length distribution to determine if the distribution changed over time. Additionally, a Wilcoxon rank sum test with continuity correction and Benjamini-Hochberg p-value adjustment (hereafter referred to as Wilcoxon test) was performed to test for differences in median length among the early and late years. Using the individual years as replicates in the early vs late comparison (n = 4; 1993-96 and 2012-15 periods), t-tests were performed on the mean blue

mussel shell length. To explore whether the abundance of specific size groups is driving the observed patterns, the mussels were divided into the size classes used within the Monitoring Program: large (≥10 mm) and medium (≥5 mm, < 10 mm), and t-tests (n = 4; 1993-96 and 2012-15 periods) were performed on the proportion (arcsine square root transformation) of blue mussels in these size classes. To test the robustness of this result, the same test was also performed with additional size class divisions: large (≥15 mm or ≥ 20 mm) and medium (≥5 mm, < 15 mm or ≥ 5 mm, < 20 mm).

Finally, t-tests were performed on the total biomass (dry weight including shell, including mussels with a shell length <5 mm but excluding juveniles, scaled to 1 m<sup>2</sup>) and the abundance of (i) the blue mussels from the one randomly selected frame within each year used for shell length analysis, and (ii) all blue mussels from all three sampling frames summed within each year.

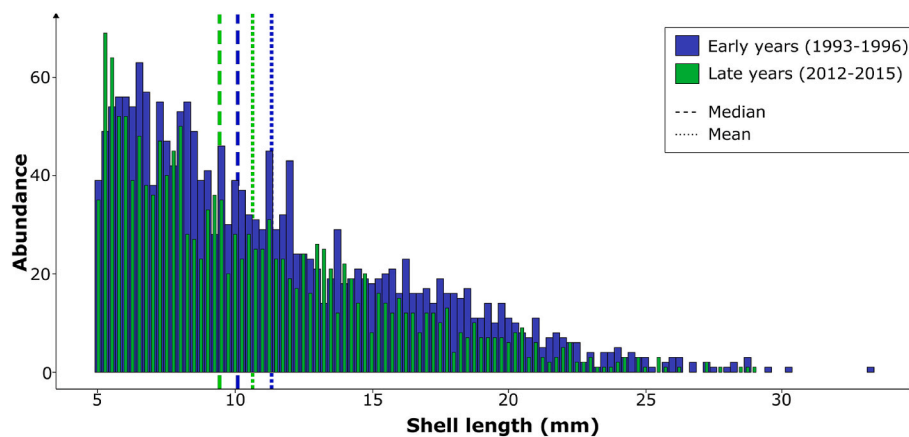
The filtration capacity of the measured blue mussels was calculated to measure the effect changes in shell length have on the capacity of blue mussels to filter the water at a set temperature and salinity, which is relevant for interpreting the impact changes in shell length has on phytoplankton control. There exist several equations that give the relationship between the shell length of blue mussels and their filtration rate (see review by Riisgård et al., 2014). We used the equation presented by Riisgård et al. (2013) who found the relationship  $F = 0.003L^{2.71}$ , where  $F$  is filtration rate in ml min<sup>-1</sup> individual<sup>-1</sup> and  $L$  is the shell length in mm, at a water temperature of 8 °C for dwarfed (≤ 24 mm) Baltic Sea blue mussels sampled outside Askö. Thereafter t-tests (n = 4; 1993-96 and 2012-15 periods) were used to test for a shift in the mean (per mussel) and total (sum of all measured mussels) filtration rates.

All statistical analyses were performed using the statistical computing programming language R and its integrated development environment RStudio (R Core Team, 2020; R version 4.0.3).

## 3. Results and discussion

The length distribution during the early and late years of the time series was significantly different with the median shell length of *Mytilus edulis trossulus* being significantly lower in the late period based on all individuals measured (Fig. 1, Kolmogorov-Smirnov test,  $D = 0.623$ ,  $p < 0.003$ , Wilcoxon test,  $p < 0.00006$ ). Using the calculated mean value for each year, the mean blue mussel shell length decreased significantly from 1993-96 to 2012-15 (t-test,  $t = 4.436$ ,  $p < 0.005$ ; Table 1). When the blue mussels were divided into size classes, the proportion of blue mussels in the large size class was always significantly higher in the 1993-96 period compared to the 2012-15 period. Blue mussels ≥10 mm contributed to the abundance with a mean of 51% in the early years and 46% in the later years in the time series (t-test,  $t = 3.106$ ,  $p < 0.040$ ), mussels ≥15 mm contributed with a mean of 23% and 18% (t-test,  $t = 3.545$ ,  $p < 0.021$ ), and mussels ≥20 mm contributed with a mean of 7% and 5% (t-test,  $t = 3.427$ ,  $p < 0.034$ ), for early and late years, respectively. These complementary analyses indicate that the decrease in shell length is due to a smaller proportion of large individuals.

In contrast to time trends shown in Liénart et al. (2020), the present study did not find an increase in abundance between the early and recent years (t-test,  $t = 0.5832$ ,  $p < 0.59$ ; Table 1) nor a decrease in the biomass between the two time periods, based on the sampling frame randomly selected for shell length analysis (t-test,  $t = 1.2204$ ,  $p < 0.269$ ; Table 1). We did neither find a significant decrease in total biomass of all three sampling frames summed for each year (t-test,  $t = 1.3133$ ,  $p < 0.239$ ; Table 1) and hence the random selection of sampling frames was representative of the biomass each year. The discrepancies between our results and those of Liénart et al. (2020) are most likely caused by different statistical approaches (time trends based on 20 years in Liénart et al. (2020) vs t-test for the four earliest and four recent years here). However, our results indicate that the decrease in mean blue mussel body mass reported by Liénart et al. (2020) is at least partly due to a



**Fig. 1.** Shell length distributions of blue mussels with a shell length  $\geq 5$  mm at 5 m depth from Isskären in northern Baltic Proper during two time periods more than 15 years apart. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 1**

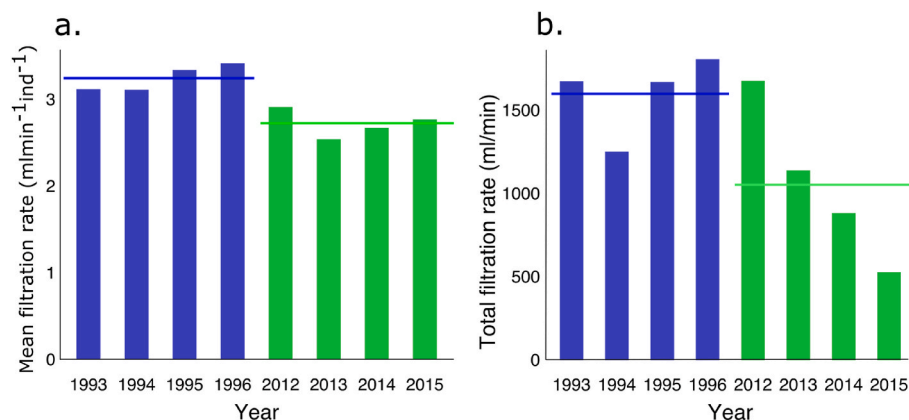
Abundance, biomass (total dry weight including shells), measured shell length and calculated filtration rates from blue mussels from Isskären in the Askö area, northern Baltic Proper. Measured blue mussels exclude mussels with a shell length  $< 5$  mm and are based on one randomly selected sampling frame each year. Values in parentheses refer to the standard deviation of the three frames sampled each year. ind = individuals.

Year	1993	1994	1995	1996	2012	2013	2014	2015
Mean abundance (ind $m^{-2}$ )	25 658 ( $\pm 5650$ )	11 658 ( $\pm 5481$ )	21 983 ( $\pm 2810$ )	12 908 ( $\pm 1880$ )	16 291 ( $\pm 11$ ) 250	22 883 ( $\pm 5459$ )	10 533 ( $\pm 4635$ )	12 267 ( $\pm 4791$ )
Mean biomass (g $m^{-2}$ )	1143 ( $\pm 220$ )	462 ( $\pm 202$ )	930 ( $\pm 92$ )	849 ( $\pm 49$ )	723 ( $\pm 468$ )	881 ( $\pm 229$ )	355 ( $\pm 85$ )	439 ( $\pm 120$ )
Biomass in the randomly selected frame (g $m^{-2}$ )	981	673	889	895	1046	768	453	302
Sample size of measured blue mussels (n = nr individuals)	536	401	499	528	575	447	329	189
Abundance of measured blue mussels (ind $m^{-2}$ )	13 400	10 025	12 475	13 200	14 375	11 175	8225	4725
Mean shell length (mm)	11.2	11.1	11.5	11.5	10.8	10.3	10.8	10.6
Mean filtration rate (mL $min^{-1}$ ind $^{-1}$ )	3.11	3.11	3.34	3.41	2.91	2.54	2.67	2.77
Total filtration rate (mL $min^{-1}$ )	1669	1246	1665	1802	1672	1135	878	523

decrease in length.

In addition to Liénart et al. (2020), our data on how the size structure has changed, i.e., a decrease in abundance of the large individuals, can give additional insights into the population status of blue mussels in this region of the Baltic Sea. Small individuals dominate in blue mussel populations (Kautsky, 1982) and a potential decline of the largest individuals may negatively affect the ecological value and ecosystem services provided by this keystone species, e.g. by decreasing the filtration capacity of the blue mussel population.

A decreasing filtration rate can reduce phytoplankton control and hence diminish the positive effect of blue mussels on decreasing the water nutrient concentrations and increasing water transparency. According to our calculations, the mean filtration rate of blue mussels significantly decreased by 16% between 1993-96 and 2012-15 ( $t$ -test,  $t = 4.751$ ,  $p < 0.004$ ; Table 1, Fig. 2), highlighting the effect a decrease in shell length has on the filtration rate. Decreases in total filtration rate (34%) were however not significant ( $t$ -test,  $t = 2.012$ ,  $p < 0.109$ ; Table 1, Fig. 2), likely due to the high value in 2012 compared to



**Fig. 2.** Mean (a) and total (b) filtration rates of Baltic Sea blue mussels with shell length  $\geq 5$  mm sampled outside Askö in northern Baltic Proper, filtration equation:  $F = 0.003L^{2.71}$ ,  $F$  = filtration rate,  $L$  = shell length, ind = individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2013–2015. To enable upscaling of decreases in filtration rate to ecosystem level, however, blue mussel biomass and size distribution with spatial coverage over all depths needs to be considered. Such comprehensive data is unfortunately not available and hence the results found here reflects the current understanding of the impact a decrease in blue mussel shell length has on filtration rate.

A decrease in the size of blue mussels may have negative effects on predators. For example, blue mussels are a major part of the diet of sea ducks such as the common eider (*Somateria mollissima*) and the long-tailed duck (*Clangula hyemalis*) (Waldeck and Larsson, 2013). Both species have shown a decline in the Baltic over the last decades (Hario et al., 2009; Bellebaum et al., 2014; Öst et al., 2016). Although estimates from this area suggest that only around 2% of the annual blue mussel biomass is predated (Kautsky, 1981; Gilek et al., 1997), a lower meat content per mussel will decrease the amount of food intake per time spent foraging which in other areas has decreased the reproductive success of seabirds (Waldeck and Larsson, 2013).

It is beyond the scope of the present study to statistically explain the environmental reasons behind the decrease in blue mussel shell length since the study is restricted to a few selected years with detailed information from shell length measurements. It is unlikely that the decrease is explained by a natural resettling process where the oldest blue mussels are replaced by new juveniles since Liénart et al. (2020) found oceanographical and food quality changes such as plankton composition and amount of terrestrial particles to correlate with reduced mean and total biomass. It needs to be considered, however, that the shell length reductions we found are relative to the early 1990s, when blue mussel biomass was higher than the previous two decades (Kautsky et al., 1992). The mean biomass in the early 1970s tends to be lower than what is found in our study for both the 1990s and 2010s (Kautsky et al., 1992). A decrease in blue mussel size might therefore be an indication of the population returning to its pre-eutrophication size distribution.

To conclude, we found that the mean shell length of Baltic Sea blue mussels decreased with 6% from the 1990s to the 2010s, likely due to a shift in the length distribution towards a higher proportion of small mussels. This translated into a 16% reduction in the mean filtration capacity of the blue mussels at the study site highlighting the importance of large mussels in the population and stressing the need for continued monitoring of this keystone species.

### Ethics approval

This study was carried out in accordance with the current laws in Sweden. There are no legal or ethical restrictions for invertebrates.

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### Authors' contributions

Cedric Åkermark: Conceptualization, Investigation, Formal analysis, Writing – Original Draft, Camilla Liénart: Formal analysis, Writing – Review and Editing, Chiara D'Agata: Resources, Writing – Review and Editing, Agnes ML Karlson: Conceptualization, Formal analysis, Writing – Review and Editing.

### Availability of data and material

Phyto-benthic monitoring data are publicly available from the SHARK database at [www.smhi.se](http://www.smhi.se). The shell length datasets generated during the current study are available as supplementary material.

### Code availability

Not applicable.

### Consent to participate

All authors agreed on being co-authors of this manuscript.

### Consent for publication

All authors agree on publishing the paper.

### CRediT authorship contribution statement

**Cedric Åkermark:** Writing – original draft, Investigation, Formal analysis, Conceptualization. **Camilla Liénart:** Writing – review & editing, Formal analysis. **Chiara D'Agata:** Writing – review & editing, Resources. **Agnes ML Karlson:** Writing – review & editing, Formal analysis, Conceptualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data has been submitted as supplementary material

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2022.108029>.

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