Journal of Sea Research 185 (2022) 102218

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Handling the heat: Changes in the heart rate of two congeneric blue mussel species and their hybrids in response to water temperature

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ARTICLE INFO

Keywords:
Cardiac activity
Mytilus edulis
Mytilus trossulus
Temperature
In situ
Bioinvasions
Hybridization

ABSTRACT

In this study we compared some aspects of the physiology of the invasive blue mussel species *Mytilus trossulus* and the native *Mytilus edulis* in the White Sea. We registered the heart activity of *M. edulis, M. trossulus* and the hybrids *in situ* for two years and tested their thermal tolerance in a laboratory experiment. *In situ* monitoring showed that the heart rate, as well as its variability, was greater in the invasive species and the hybrids than in the native mussel species. At the same time, the native species showed a higher thermal tolerance in the laboratory experiment. Our results suggest that, when it comes to adaptation to increased temperature, *M. edulis* has a greater physiological potential than *M. trossulus*. In a warming climate, the invasive species may lose in competition with the native one due to a higher level of metabolism.

1. Introduction

The Arctic is attracting increasingly more scientific attention because of the profound transformations ongoing in this region. Climate changes in the Arctic are faster and more extensive than elsewhere on the Earth (Jansen et al., 2020 and references therein). Decreased ice thickness, greater river input, increasing sea surface temperatures and increased inflow of Atlantic water mass have already been documented (Richter-Menge, 2009). These changes may affect ecological parameters such as distribution of plants and animals, structure of food chains, carbon cycles and borealization (Jin et al., 2021; Wojczulanis-Jakubas et al., 2022). As a result, habitat and biogeographic borders are broken, disrupting reproductive isolation between closely related species, which have previously been separated spatially (Laakkonen et al., 2021).

These factors may be the reason behind the arrival of the bivalve mollusc *Mytilus trossulus* in the White Sea, and the emergence of its hybrids with the native *M. edulis* (Katolikova et al., 2016; Khaitov et al., 2018). The basically Pacific *M. trossulus* have post-glacially invaded North Atlantic and neighboring Arctic coasts (Laakkonen et al., 2021). Among geographic populations of *M. trossulus* in the Atlantic, populations of the Kola Peninsula (White Sea, Barents Sea) are genetically very similar to the populations in the Western Atlantic (Canada, USA) and differ markedly from the Baltic *M. trossulus* (Väinölä and Strelkov, 2011; Simon et al., 2021). Väinölä and Strelkov (2011) suggested that *M. trossulus* entered the waters of the Kola Peninsula from the Western Atlantic with sea transport in the 20th century. Research in the Atlantic has shown that *M. trossulus* is more cold-tolerant than *M. edulis* (Braby and Somero, 2006; Brooks and Farmen, 2013; Yund and McCartney, 2016) but no such information is available for the White Sea intertidal zone, where macrobenthic species have to tolerate negative water temperature (Filatov et al., 2005) in winter. At the same time, physiological adaptations play an important role in the distribution potential of a species (Hochachka and Somero, 2002; Mardones et al., 2022). The knowledge of physiological determinants of actively spreading species may help explain the observed distribution patterns and predict their further incursion into new habitats (Parmesan et al., 1999; Roemmich and McGowan, 1995). It is especially important for the *Mytilus spp.* with their huge phenotypic plasticity to the temperature range from -1.5 (North Atlantic and the White Sea) to +35 °C (Mediterranean Sea) and salinity range from 5-6 (the Baltic Sea) to 35 PSU. In our case we dealt with local adaptation to the unique characteristics (winter temperature as low as −1.5°C and 25 PSU salinity). Another problem is that the comparative analyses of the responses of the native and the invasive species are often based on short-term observations lasting not more than a month (Gardner and Thompson, 2001; Rayssac et al., 2010; Thyrring et al., 2017).

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https://doi.org/10.1016/j.seares.2022.102218
Received 17 September 2021; Received in revised form 30 April 2022; Accepted 9 May 2022
Available online 14 May 2022

In this study we assessed the relative metabolic rates of the *M. trossulus*, *M. edulis* and their hybrids in the White Sea using non-invasive registration of the heart activity. We hypothesized that physiological differences between these groups of mussels should gradually disappear if the molluscs are kept under the same conditions for a long time, in other words, in locally adapted mussels. No such studies have been made so far, though it has long been understood that gradual changes in ambient characteristics may increase the limits of pejus temperatures (Zippay and Helmuth, 2012).

To test our hypothesis, we performed an *in situ* experiment, keeping the mussels in the same biotope for two years and registering their heart rate and local environmental parameters. In addition, we tested the impact of abrupt temperature changes on the heart activity of the mussels in a laboratory experiment, taking into account the known thermal preferences of these two species (Qiu et al., 2002; Riginos and Cunningham, 2005; Hayhurst and Rawson, 2009; Fly and Hilbish, 2013) and the fact that the cardiac performance is a sensitive parameter for the estimation of the critical thermal limits of a species (Portner et al., 2006; Portner and Knust, 2007). The latter assumption is based on a recent hypothesis of oxygen- and capacity-limited thermal tolerance, which suggests that at both low and high extremes of temperature respiratory and cardiovascular functions are suboptimal and may result in systemic hypoxemia, which reduces aerobic scope of the animal and thereby compromises its over-all fitness (Hassinen et al., 2014).

2. Materials and methods

2.1. Experimental site and collection of mussels

Mussels for the experiment were collected in two locations: a freshened area in the head of the Chupa Inlet (average salinity 20 PSU; 66.25°N, 33.05°E) from fucoids at the lower horizon of the intertidal zone, where *M. trossulus* has been shown to dominate (Katolikova et al., 2016), and from artificial substrates (pontoons) near the White Sea Biological Station "Kartesh" of the Zoological Institute of the Russian Academy of Sciences (average salinity of the surface layer 25 PSU, 66.33°N, 33.65°E, Fig. 1), where only *M. edulis* was expected to be present (Strelkov, personal communication). Twenty-five mussels were selected from each location.

The mussels collected from the two locations (50 individuals) were kept in containers with seawater at 10°C and constant salinity at 25 PSU with aeration for 3 days. Their shells were measured with vernier caliper (these values were treated as initial shell length) and marked with the help of a ProxxonMicromot 50/E drill for later identification. Linear shell size of the mussels was, on the average, 25.9 ± 2 mm (Mean ± SD). After the experiments, all the mussels were measured again and the measurement data were used for growth analysis. Then the mussels were dissected to check their parasitological status because infection with metacercariae of the trematode *Himasthla elongata* has been shown to affect the heart activity of mussels (Bakhmet et al., 2019a). After these manipulations, the mussels were frozen at −80 °C for genotyping (see below).

2.2. In situ registration of mussel heart rate

The experiment was conducted in the Krivozerskaya Inlet near the White Sea Biological Station from May 2017 to March 2019 (Fig. 1). The heart activity of mussels (50 collected individuals) was measured after Depledge and Andersen (1990) with improvements. For this, a plethysmograph for continuous registration of the heart rhythm was conducted. Waterproof sensors CNY70 (Vishnay Semiconductors, PA, USA) were glued to mussel shells. After that, the mussels were randomly placed into cages. The cages were submerged in the Krivozerskaya Bay at a depth of about 3 m to avoid the impact of water mixing by waves and freshening. The cardiac functions of each individual mussel were recorded seven times over the course of 2017 and 2018. At each test point, three heart rate recordings were obtained for 5 min from each animal. The heart rhythm was registered as the number of heart beats per minute (beats min^{-1}). Water temperature was recorded at the same time by means of U22–001 and U24–002-C data loggers (Onset HOBO Data Loggers, USA), which were placed in the cages with the experimental mussels.

2.3. Laboratory-based temperature experiment

In March 2019, 25 randomly selected mussels from the cages were placed in an aquarium. The water in it was heated, at a rate of 2°C per hour, from 1.8°C to 28.8°C. The latter value is thought to be the upper border of thermal tolerance of *Mytilus spp.* (Pickens, 1965; Widdows, 1973). Then the water was cooled down at the same rate. The heart rate was registered throughout the experiment.

2.4. Genotyping

DNA was isolated from the foot tissues of the mussels with the help of GeneJET Genomic DNA Purification Kit (Thermo Scientific). Hepatopancreas tissues were used for allozyme analysis.

The mussels were genotyped at five nuclear markers traditionally employed for distinguishing *M. edulis* and *M. trossulus*—PCR-markers ME15/16 (Inoue et al., 1995) and ITS (Heath et al., 1995) and allozymes Est—D, Gpi, Pgm (Väinölä and Hvilsom, 1991) with the use of protocols from the original publications.

2.5. Data analysis

The amplitude of the plethysmograms was calculated by

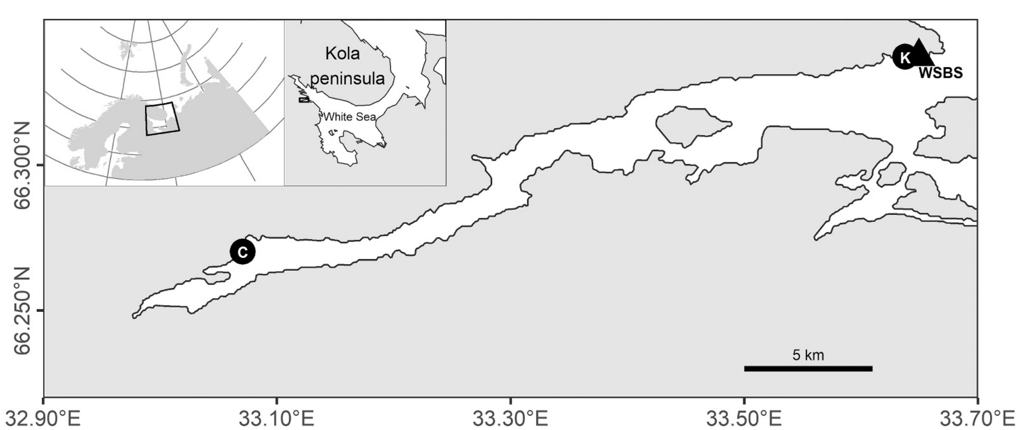

Fig. 1. Study area. C – head of the Chupa Inlet, K – artificial substrates near Kartesh White Sea Biological Station (WSBS) (map based on: Wessel & Smith, 1995).

normalizing: the maximum value in the amplitude series of each mollusc was selected and then each value was divided by the maximum.

Multilocus data were analysed in Structure software (Pritchard et al. 2000) under the two-population admixture model using default parameters. 50,000 MCMC replicates were conducted after discarding the first 30,000 replicates as burn-in. The program assessed the contribution of genes of parent species into the genotypes of individuals. Based on the contribution of *M. trossulus* (q-values) and *M. edulis* (1-q) genes, the mussels were separated into three categories: genotypes with predominance of *M. edulis* genes ($q \leq 0.1$, hereafter *M. edulis*), genotypes with predominance of *M. trossulus* genes ($q \geq 0.9$, *M. trossulus*) and intermediate genotypes ($0.1 < q < 0.9$, hybrids). The category of hybrids included individuals of mixed ancestry, mostly probably early generation hybrids. The threshold values chosen for classifying the mussels into purebreds and hybrids were proven in Katolikova et al. (2016).

The growth rate of *M. trossulus*, *M. edulis* and hybrids during long-term observations *in situ* was assessed as the increase of the shell length between the start and the end of field-based experiment with the help of a linear Mixed-Effects odel (LMM): $L = L_{init} + Date + Genotype + Genotype \times Species$, where L denoted the length of a mussel, L_{init} was the initial mussel length, *Date* was two-level factor (in the beginning of the survey and after it), *Genotype* had three levels (*M. trossulus*, *M. edulis* and hybrids), × means interaction term and random effect associated with the mussel specimen. The model was fitted using lme4 R-package (Bates et al., 2015). The influence of predictors was accessed using type-III ANOVA (Zar, 2010), and all assumptions for the use of parametric analysis were met.

To reveal correlations between the heart rate, the temperature and the mussel genotype, we constructed two linear models. In the first model, the heart rate of individual mussels was used as a response, the predictors being water temperature (T), mussel genotype (G) and their interaction. The heterogeneity of residuals was successfully removed by transforming the initial data (response) by Box-Cox transformation (Fox and Weisberg, 2019). After that, visual analysis did not reveal any violations of applicability (Zuur et al., 2009).

In the second model, the dispersion of the heart rate of individual mussels on certain observation days was used as a response, while the predictors were the same. Visual analysis of the residuals did not reveal any violations of applicability (Zuur et al., 2009). The statistical significance of the coefficients was analysed with the help of ANOVA dispersion analysis; the null hypothesis was rejected at 5% significance level.

All calculations and transformation of the data were made in R with the help of car (Fox and Weisberg, 2019) and tidyr (Wickham, 2020) packages. The data were visualized with the help of ggplot2 package (Wickham, 2016).

3. Results

All three mussel genotypes were present in our sample: *M. trossulus* (19 individuals), *M. edulis* (11 individuals) and their hybrids (14 individuals) (Fig. S1 in Supplementary). Six mussels died during the observation period (23 months). The sizes of *M. trossulus*, *M. edulis* and hybrids did not differ either at the start or at the end of the field-based experiment (initial (M ± SD): *M. trossulus*24.7 ± 2.5, *M. edulis* 26.1 ± 2.6, hybrids 25.0 ± 2.6; final (M ± SD): *M. trossulus* 43.5 ± 6.6, *M. edulis* 45.4 ± 3.2, hybrids 47.6 ± 5.5; $F_{Date \times Genotype} = 2.07$, df = 2, $p = 0.13$). No parasitic infection was recorded in the mussels.

During the two-year-long field-based experiment the heart rate of the mussels varied, on average, from 4.3 to 37.9 beats min^{-1}. The temperature varied from −0.7 (March) to +19.8°C (July) (Fig. 2).

We hypothesized that the variation of the mussel heart rate was associated with the water temperature changes. To test this hypothesis, we constructed a model taking into account the correlation of the heart rate of *M. edulis*, *M. trossulus* and hybrids with the temperature (see Materials and Methods). The results of the dispersion analysis of coefficients in this regression model showed a statistically significant influence of predictors “Temperature” and “Genotype” as well as their interactions ($F_T = 3302.1$, df = 1, $p < 0.0001$; $F_G = 12.5$, df = 2, $p < 0.0001$; $F_{T \times G} = 7.2$, df = 2, $p = 0.0009$; Fig. 2). At the same time, statistically significant differences between mussels of different genotypes were expressed at temperatures higher than 16°C. Starting from this point, the intensity of heart activity was statistically significantly greater in *M. trossulus* and the hybrids than in *M. edulis* (Fig. 3).

Dispersion of heart rate values was different among the three genotype groups. This parameter was also affected by all the predictors of the model ($F_T = 127.2$, df = 1, $p < 0.0001$; $F_G = 5.6$, df = 2, $p = 0.008$; $F_{T \times G} = 5.2$, df = 2, $p = 0.01$; Fig. 4). Apparently, the variation of the heart rate increased with the increasing temperature in all mussels, but in *M. trossulus* and the hybrids the increase was more pronounced after the water temperature reached 10°C.

During the laboratory experiment with increasing water temperature, the heart rate of all mussels increased in a linear fashion, decreasing at +8.8°C and + 11.2°C in *M. edulis* and the hybrids, respectively. In contrast, the heart activity of *M. trossulus* achieved a plateau at +12.8°C (Fig. 5)

An abrupt decrease of the heart rate (critical break point temperatures) was registered in *M. trossulus*, the hybrids and *M. edulis* at 15.0, 15.8 and 18.3°C, respectively, while the only abrupt increase was registered at 14.8, 18.3 and 20.7°C, respectively. After further increase of the temperature, the heart activity of the mussels reached plateaux at 23.2, 24.6 and 22.9°C in *M. trossulus*, *M. edulis* and the hybrids, respectively (Fig. 5). After the temperature started to decrease, the heart

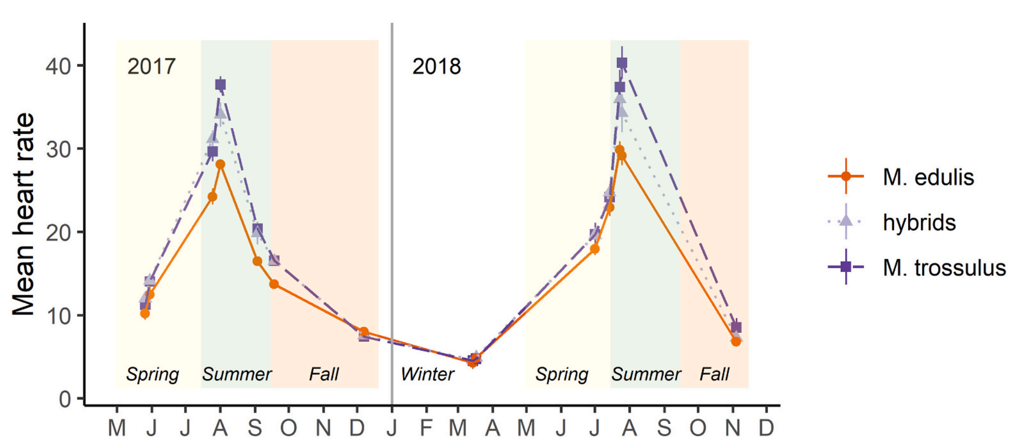

Fig. 2. Mean heart rate changes in mussels with different genotypes (*M. edulis*, hybrids and *M. trossulus*) throughout the period of *in situ* observations (May 2017–November 2018). *X*-axis – abbreviated sequential month names, Y-axis - mean heart rate (beats min-1). Rectangles show periods of hydrological seasons (after Naumov et al., 2003) in 0–10 m water layer at the White Sea.

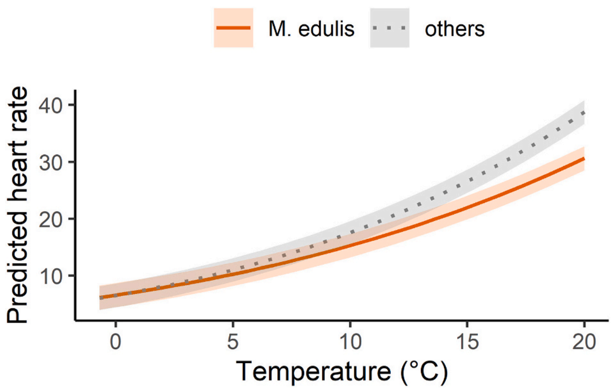

Fig. 3. Correlation between water temperature and predicted heart rate (beats min-1) in mussels with different genotypes (*M. edulis* and others, reverse Box-Cox transformation). Regression lines are shown (they are the same for *M. trossulus* and hybrids, so the united line is shown), shaded area – limits of 95%-confidence intervals.

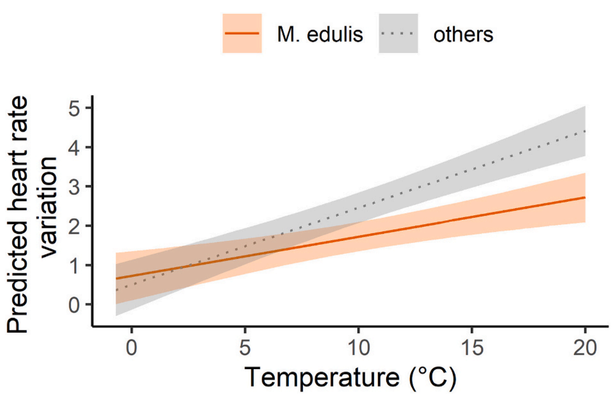

Fig. 4. Correlation between water temperature and predicted dispersion of heart rate in mussels with different genotypes (*M. edulis* and others). Regression lines are shown (they are the same for *M. trossulus* and hybrids, so the united line is shown), shaded area – limits of 95% confidence interval.

rate of the mussels increased fairly rapidly but it also occurred at a different temperature for each genotype: at 27.7, 21.6 and 26.4°C for, respectively, *M. trossulus*, the hybrids and *M. edulis*. After that, a linear correlation between temperature changes and the heart rate of all the mussels was observed (Fig. 5). Noteworthy, the heart rate values registered at the time points of the heart activity changes differed among the genotypes. The heart stopped beating at high temperatures only in one *M. edulis* individual, while there were three such cases among the hybrids and four such cases among *M. trossulus* individuals. When the temperature dropped again, the hearts of these eight individuals started beating again.

4. Discussion

Molluscs are typical ectotherms, and temperature is a key factor determining their metabolic rate and thus the heart activity (Hassinen et al., 2014; Xing et al., 2016). Findings from invertebrate ectotherms suggest that the cardiac function, and the heart rate particular, is a limiting factor for the cardiac output and therefore for the aerobic performance of the animal (Hassinen et al., 2014). It may be said that it is the cardiac function that is a weak link in case of critical high temperatures. This phenomenon was fully confirmed in our study.

For the *in situ* experiment, the fact that the differences in the heart rate of mussels of different genotypes were noted only after the water temperature rose above 10°C confirms our previous assumption that there is some baseline metabolic level characteristic of *M. edulis* at lower temperatures (Bakhmet et al., 2019b). In contrast, at elevated temperatures species-specific features can be expressed, as shown in our study. We emphasize that the differences in the heart rate of mussels of different genotypes were observed only when the water temperature exceeded 16°C, in other words, only under temperature conditions that are very rarely observed in the White Sea (Usov et al., 2013). On the other hand, we may suppose that the invasive species spend more energy under high temperatures than the native ones and that, consequently, *M. trossulus* is less adapted to such conditions. We suppose that this extra energy is spent on coping with stress. Besides, the higher rate of cardiac activity suggests that the invasive species is more cold-adapted (cold-compensated) (Braby and Somero, 2006). At the same time, a sharper increase in the heart rate variability at temperatures above 10 °C was recorded in *M. trossulus* and the hybrids (Fig. 4). It is well-known that the increase in variance of physiological indices may be regarded as a sign of animal stress (Leung and Forbes, 1996; Sukhotin et al., 2003). Therefore, we may conclude that high temperature is a particular stressor for mussels of these genotypes.

Though the upper temperature was rather high (+28.8°C), no mussel mortality was observed in our experiments, in contrast to previous studies (Fly and Hilbish, 2013) This experiment showed that *M. trossulus* had a reduced ability to temperature acclimation, because its heart rate became stable already at 12.3°C and then decreased further. This pattern of changes in the physiological parameters in response to temperature change, referred to as "tissue compensation for temperature" (Bullock, 1955) or "capacity adaptation" (Jankowsky, 1973), indicates that the animal's heart can no longer cope with temperature acclimation. In this light, it is striking that the upper critical temperature in *M. edulis* is +21.5°C. A reduced ability of *M. trossulus* to temperature acclimation agrees with the experimental results showing that the spat of *M. trossulus* has a higher mortality at 20 °C compared to the spat of *M. edulis* (Hayhurst and Rawson, 2009). In addition, larval thermal preferences determined in another study were 10-17°C for *M. trossulus* and 17-24°C for *M. edulis* (Rayssac et al., 2010). To note, 50% mortality of *M. edulis* and *M. trossulus* occurred at 25.1 and 23.7 °C, respectively (Fly and Hilbish, 2013). On the other hand, the invasive species may detect pejus and consequently initiate the anaerobic metabolism as a life-saving response. Additional experiments with the use of other methods are necessary to clarify this issue.

Changes in the heart rate of hybrids deserve special mention. It is known that hybrids between congeneric *Mytilus* species can exhibit both intermediate phenotypes for different physiological traits (*e.g.*, Braby and Somero, 2006) and phenotypes similar to one of the parental species (Michalek et al., 2021; Boutet et al., 2022 and references therein). In our study, the heart rate of hybrids was similar to *M. trossulus* in all the experiments. The dominance of the physiological phenotype of *M. trossulus* in hybrids between *M. edulis* and *M. trossulus* is interesting and deserves further study.

Our study showed that, when it comes to adaptation to increased temperature, *M. edulis* has a greater physiological potential than *M. trossulus* and hybrids. At the same time, we observe the obvious invasive success of *M. trossulus* in the White Sea (Katolikova et al., 2016). Poor physiological performance of *M. trossulus* at high temperatures in summer seems to be counterbalanced by some other adaptations, which are yet to be discovered. With further warming and an increase in the period with temperatures above 16 °C, at which the heartbeat of *M. trossulus* is depressed, the survival of the species will be threatened. However, according to the data on the dynamics of SST in the White Sea near White Sea Biological Station "Kartesh" (increase in mean annual temperature roughly by 0,04° per year; Usov et al., 2021), this is unlikely to happen any time soon.

At the same time, our hypothesis that the differences in the responses of the native and the invasive species kept in the same biotope should be levelled was not supported, even though the experiment was conducted for a long time (two years). Thus, *M. edulis* and *M. trossulus* are clearly

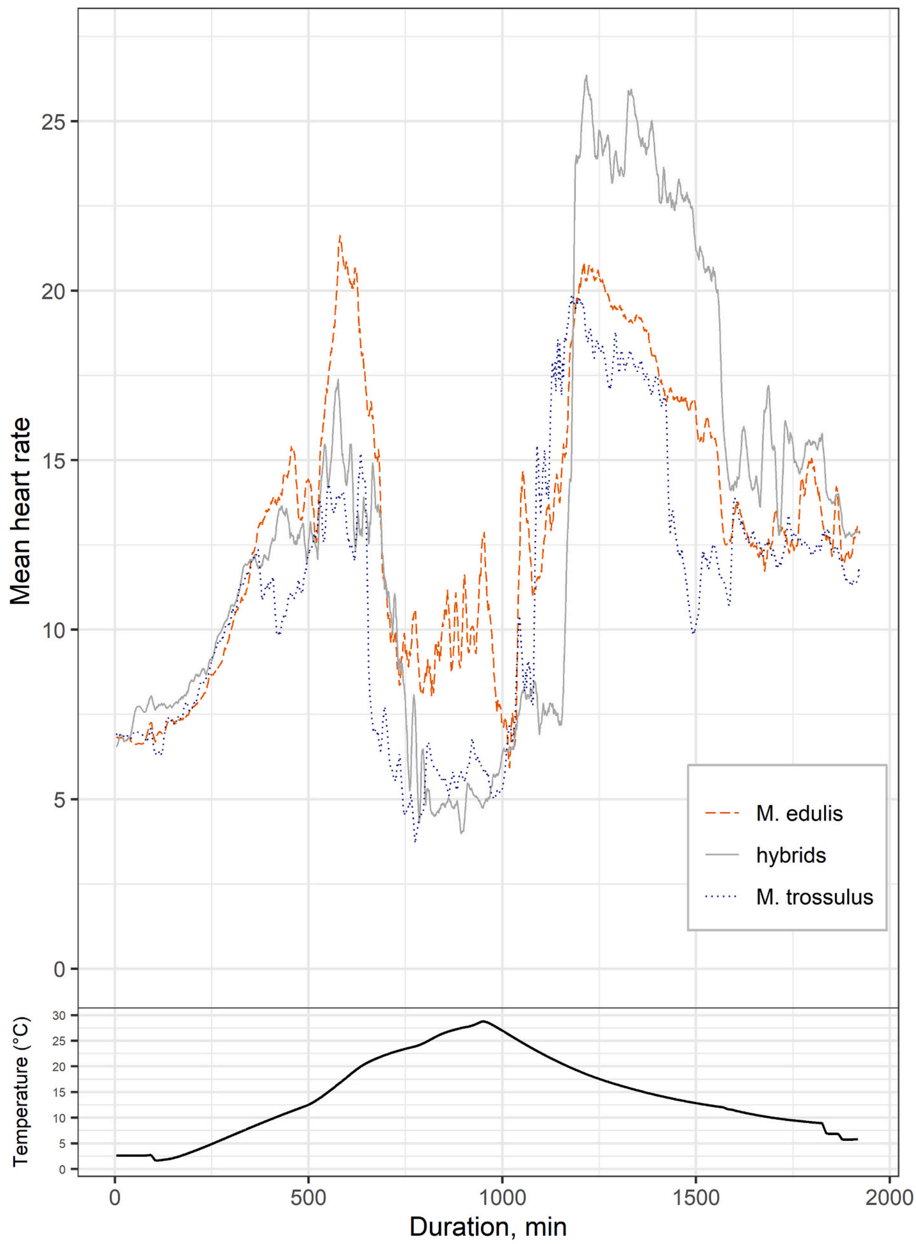

Fig. 5. Heart rate changes in mussels with different genotypes in the temperature experiment. Dark line shows changes of the temperature throughout the experiment.

distinguishable physiological entities in the White Sea.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2022.102218.

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.

Acknowledgements

We would like to thank the personnel of the Kartesh White Sea Biological Station (Zoological Institute, Russian Academy of Science) for their help in collecting and maintaining the organisms.We thank Dr. Petr Strelkov and Dr. Vadim Haitov (SPbSU) for their valuable comments and discussion as well as two anonymous reviewers who helped us to improve the text of the article. Our work was supported by a grant from the Russian Science Foundation (no. 19-74-20024), and federal funding for government-ordered project themes (nos. 122031100283-9 and AAAA-A19-119062490055-4).

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