Identification of marine heatwaves in the Archipelago Sea and experimental testing of their impacts on the non-indigenous Harris mud crab

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Abstract

Seawater temperature is an important variable affecting both the distribution and performance of marine organisms. In conjunction with climate change, marine heatwaves are expected to become more frequent and increase in their intensity and duration, mainly driven by a warming trend in sea surface temperature (SST). The effects of warming on marine organisms are diverse, and arguably the Baltic Sea can be considered particularly prone to marine heatwaves, as it is a comparable shallow enclosed water body. Additionally, the Baltic Sea has low functional redundancy and species diversity, which may further increase the potential impacts of extreme events. Despite the rapid warming rates of SST observed in and projected for the Baltic Sea compared to other large marine waterbodies, not many experimental studies have been conducted on the impact of heatwaves on its coastal marine communities. This is particularly true for the northern parts of the Baltic, such as the northern Baltic Proper and the Finnish Archipelago Sea.

This study consists of a modelling and an experimental part. In the modelling part, the frequency, intensity, and duration of marine heatwaves in the Finnish Archipelago Sea were identified by applying the available software package "heatwaveR", on two SST datasets from the region (a long-term dataset spanning 52 years and a shorter dataset of high-resolution spanning 12 years). Subsequently, trends in these characteristics of marine heatwaves were examined. For the experimental part of this thesis, the impact of simulated marine heatwaves was tested on the non-indigenous Harris mud crab, *Rhithropanopeus harrisii.* Experimental treatments were designed based on metrics retrieved from the climatological SST data assessed in the modelling part. The treatments represented three scenarios for SST: a present average marine heatwave in the Archipelago Sea (*Present*), an event of increased amplitude (*Amplitude*) and a future heatwave scenario of a high amplitude (*Intensified*). The study species, *R. harrisii* recently entered the Finnish Archipelago Sea with an expanding distribution range, which may be driven by its relatively high tolerance to environmental stress in comparison to the corresponding tolerances of many native species. Thus, I hypothesized that *R. harrisii* would tolerate benign heatwave treatments of present-day intensity but may suffer from intense heat stress experienced in the applied future heatwave scenarios. Measured response variables were feeding on mussel prey and growth of the crab (wet weight and carapace width).

The long-term dataset showed that mean SST (both summer and annual) in the Archipelago Sea has increased over the last 52 years (0.4 and 0.5 °C per decade, respectively), and so has the frequency of marine heatwave events, partly driven by this increase in mean SST in the region. No significant trends were detected over the 12-year high-resolution dataset. There was no significant difference in crab feeding rates between the heatwave treatments over the 36-day long experimental period, although crabs showed a tendency to feed more with increasing temperatures (non-significant trends). There was, however, a significant time effect on feeding, but this effect was only present when no treatments were taken into consideration. No significant differences in crab growth between the three heatwave treatments could be detected.

Mean SST in the Baltic Sea is increasing and so are the extremes. Since rising SST is one of the main drivers of marine heatwaves worldwide, these are likely to become more common in the future. *R. harrisii* might benefit in a warmer Baltic Sea as it is indicated from this study: individuals showed intensified feeding with increasing SST and tolerated well the extreme temperatures associated with the applied marine heatwaves. Due to its recent introduction, the role of *R. harrisii* in the Archipelago Sea food web is still not fully understood. Yet, the combined effects of the temperature tolerance of this introduced secondary consumer and marine heatwaves may have possible consequences for the entire ecosystem, primarily by changing the interaction among species.

Keywords: Simulated marine heatwaves, heatwave identification/modelling, climate extremes, *Rhithropanopeus harrisii,* non-indigenous invasive species, tolerance

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1. Introduction

1.1. Changes in baselines and extremes of climate variables

Climate change models project shifts in baseline levels of numerous marine abiotic variables such as sea surface temperature (SST), water level, pH and salinity (Bindoff et al. 2019). In addition, as a worldwide phenomenon, an increase in the frequency and duration of extreme events is expected (Rahmstorf and Coumou 2011; Bates et al. 2018). Predicted extremes and changes for the Baltic Sea region are, among other things, increase in SST, the occurrence of more pronounced marine heatwaves during summer months, decreased salinity, increased precipitation during winter and hypoxic upwellings (Lehmann et al. 2012; Neumann et al. 2012; HELCOM 2013; Meier and Saraiva 2020). Over the past few decades, ocean temperature has also increased significantly in most regions due to human activities (Bindoff et al. 2019). Much of past climate change research focused on the effects of changing baseline values, while increased variation, such as an increase in the magnitude and frequency of extremes, may be a greater threat to species or communities, or may amplify the effect of a changing baseline (Helmuth et al. 2014; Vasseur et al. 2014). Generally, terrestrial extreme events are better understood and more extensively studied than marine extremes (Smale et al. 2015), yet marine extreme events are having large-scale impacts on biological systems (Wernberg et al. 2013; Smale et al. 2019). Marine heatwaves are already identified to be among the most detrimental environmental threats to marine life that reoccur periodically (Bindoff et al. 2019; Smale et al. 2019).

1.2. Marine heatwaves

A marine heatwave (MHW) is a prolonged event with discrete anomalously warm water conditions that can be described by its duration, intensity, and spatial extent (Hobday et al. 2016). More specifically, an event is considered a marine heatwave if it lasts for five or more consecutive days at temperatures warmer than the 90th percentile (threshold value) based on a 30-year historical baseline period (Hobday et al. 2016). This definition applies to oceanic regions as well as to estuaries and semienclosed seas, such as the Baltic and the Mediterranean Sea (Hobday et al. 2016). Marine heatwaves can be caused by a variety of factors, but at a local scale, ocean-atmosphere heat fluxes contribute largely and that result in either excessive heat entering the ocean or a supressed amount of heat being able to escape the surface waters (Holbrook et al. 2019). Clear skies, warm air and reduced wind speeds associated with high-pressure systems make rapid SST warming possible and increase the thermal stratification, which reduces vertical mixing (Gupta et al. 2020; Holbrook et al. 2020). Large-scale atmospheric pressure anomalies and anthropogenic warming also act as drivers of marine heatwaves on a global scale (Holbrook et al. 2020). Marine heatwaves and other extreme events are likely to become more frequent and increase in duration and intensity in conjunction with climate change (Hobday et al. 2018; Oliver et al. 2018, 2019).

Our understanding of the impacts of marine heatwaves is largely based on a few well-studied and documented individual and natural events (Frölicher and Laufkötter 2018; Holbrook et al. 2019). Examples of such are the 2003, 2012 and 2015 Mediterranean Sea heatwave events (Garrabou et al. 2009; Darmaraki et al. 2019) and the 2011 event in Western Australia (Pearce and Feng 2013; Wernberg et al. 2013). Additionally, there was until recently no way of consistently comparing marine heatwave events, which could potentially lead to difficulties when spreading scientific findings to the public and when implementing mitigation measures. Hobday et al. (2016) defined, analysed, and documented past marine heatwaves and Hobday et al. (2018) then categorised and named these events according to their intensity. This type of approach allows for a comparison of marine heatwaves across regions and events. By applying this approach, Oliver et al. (2018) found a significant increase in both duration (34%) and frequency (17%) of marine heatwaves worldwide over the last century (1925–2016), with the annual number of registered marine heatwave days increasing by more than 50%. These trends can largely be explained by the increase in mean ocean temperature (Oliver 2019), meaning that a further increase in marine heatwave days is to be expected with intensified climate change (Oliver et al. 2018, 2019).

1.3. SST trends and variability in the Baltic Sea

Coastal habitats are especially prone to experience fluctuations in abiotic conditions, both spatially and temporally. The Baltic Sea is a shallow, temperate system with an occasionally highly stratified water column, both with regard to salinity and temperature, and these properties make the influence of various abiotic variables especially strong (HELCOM 2018; Reusch et al. 2018). During spring towards summer, the upper water column heats up, which creates a seasonal thermocline, often at depths of about 15–20 metres, restricting the vertical mixing of water bodies during summer months (Kautsky and Kautsky 2000; HELCOM 2013).

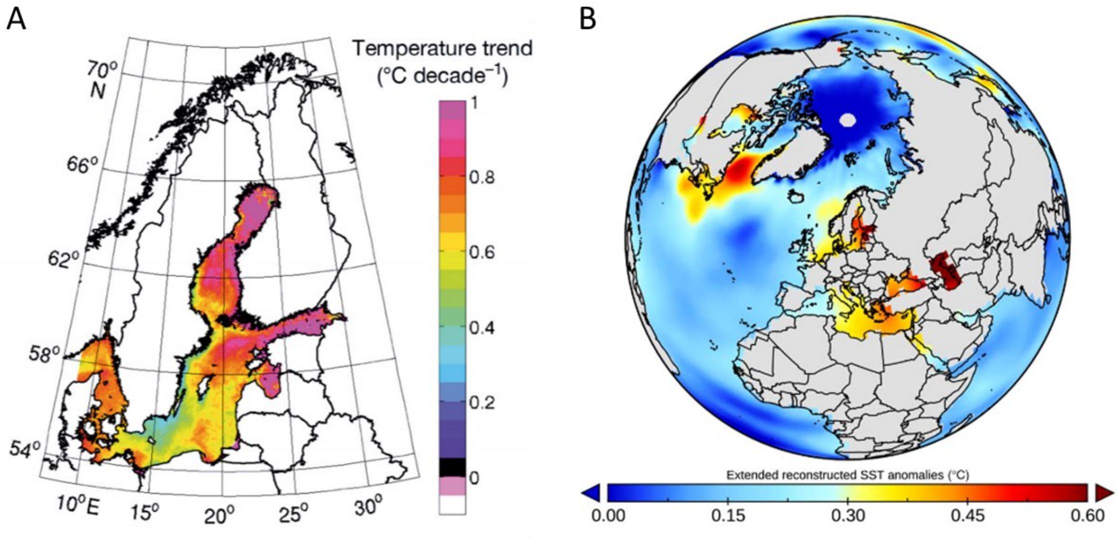


Figure 1. A) Linear trend of annual mean SST based on infrared satellite data between 1990 and 2008. Data by the Federal Maritime and Hydrographic Agency, Hamburg. Figure from Lehmann et al. (2011). **B)** SST change per decade since 1980. The rate of change in marginal seas such as the Baltic Sea and the Mediterranean Sea has been higher than in the oceans. Figure from Reusch et al. (2018).

The surface water temperature in the Baltic Sea reaches its maximum in August (Kautsky and Kautsky 2000) and surface waters have warmed in all seasons since 1985, with the largest increase during the summer season (HELCOM 2013). The areas with the steepest warming trends in recent decades have occurred in the Gulf of Finland, the Gulf of Riga and the Bothnian Bay (Figure 1; Lehmann et al. 2011; HELCOM 2013). The strongest changes in SST are also projected to occur in the Bothnian Bay and Bothnian Sea during summer and in the Gulf of Finland during spring (HELCOM 2013; BACC II Author Team 2015). As a rise in mean SST is found to be the main driver of the increasing frequency (and duration and amplitude) of marine heatwaves (Oliver 2019), these events will likely impact the Baltic Sea in the near future.

During individual heatwaves, SST in the Western Baltic Sea can rise by up to 1.2 °C per day and a temperature increase of 3–6 °C can be reached during a single marine heatwave event (Pansch et al. 2018). Similarly, in the Gulf of Finland, surface water temperature can increase or decrease by several degrees in a single day in conjunction with down-welling and upwelling events, respectively (Suursaar 2020). The thermal variability in shallow areas of the Baltic Sea can also be large on shorter temporal scales, but does not always imply a marine heatwave. In the Kiel Fjord, Western Baltic Sea, in spring and summer, for instance, temperature increases of up to 4 or 6.5 ° C in two or five days have been recorded, and a day-night variability of 6 °C can occur in the shallowest areas (Pansch and Hiebenthal 2019). In the Gulf of Finland, surface water temperature has been reported to increase with as much as 11 °C in four days (Suursaar 2020).

The baseline summer SST in the northern parts of the Baltic Sea is predicted to increase as much as 4 °C by the end of the century (Meier et al. 2012; HELCOM 2013; BACC II Author Team 2015), a rate much higher than in most oceans worldwide (Belkin 2009; Reusch et al. 2018; Figure 1). Studies have also shown that the amplitude and duration of the heatwaves of today will increase in the future (Oliver et al. 2019), yet no specific forecasts have been made for marine heatwaves in the Archipelago Sea. The consequences for the coastal ecosystems of the Baltic Sea are, thus, of immediate concern, although they are currently unknown.

1.4. Implications of marine heatwaves for marine life

Temperature is an important driver for many processes in marine organisms, such as primary and secondary production, metabolism, growth, reproduction and survival, and higher baseline temperatures can lead to a shift in species distributions and range extensions or even to the local extinction of species (Doney et al. 2012). The responses of individual species and communities to marine heatwaves can be diverse. Thus, marine heatwaves can have major impacts on marine biodiversity, species interactions, community composition and ecosystem functioning (Garrabou et al. 2009; Wernberg et al. 2013; Smale et al. 2019). Mass mortality of sessile species has been reported in the Mediterranean Sea after a marine heatwave event in 2003 (Garrabou et al. 2009), while extreme temperature events on the west coast of Australia have caused harm to and loss of foundation habitats such as seagrass meadows (Thomson et al. 2015) and kelp forests (Wernberg et al. 2013, 2016). At the species level, increased temperature has been shown to affect physiological processes of marine organisms, such as growth (Sareyka et al. 2011), immunocompetence (Roth et al. 2010), metabolism (Hegele-Drywa and Normant 2014) and feeding (Leung et al. 2017), all of which may lead to decreased survival. Sessile and low-mobility species in coastal waters are most vulnerable to thermal stress, especially if these species are adapted to cold conditions (Wernberg et al. 2013).

The brackish Baltic Sea is a generally species-poor system (Kautsky and Kautsky 2000) with low functional redundancy compared to fully marine ecosystems (Elmgren and Hill 1997), which, in turn may increase the vulnerability of this system to extreme events (Elmgren and Hill 1997). A mobile species can either avoid heat stress through physiological adaptations or acclimation, or by migrating towards more favourable living conditions (Pörtner and Farrell 2008). For temperate species, a common response would be poleward migration (Lenoir and Svenning 2015). This, however, is not possible for many species in the Archipelago Sea, partly because of the low saline almost freshwater conditions that subsist in the northern Baltic Sea (Kautsky and Kautsky 2000), which are likely too low for many species. Also, the largest increase in summer seawater temperature is projected to occur in the Bothnian Bay and the Bothnian Sea over the next decades (HELCOM 2013; BACC II Author Team 2015), which means that migration in the end could be futile.

To date, there are not many experimental studies in the Baltic Sea that specifically test species and community responses to marine heatwaves (but see Reusch et al. 2005; Ehlers et al. 2008; Roth et al. 2010; Takolander et al. 2017; Pansch et al. 2018; Saha et al. 2020). In the Western Baltic Sea, Pansch et al. (2018) studied the impact of repeated marine heatwaves on temperate benthic communities and Saha et al. (2020) the response of foundation macrophytes, both using the same near-natural mesocosm approach. These studies found that while some species can cope well with or are not affected at all by marine heatwaves, others suffered severely. These differences in responses of species to heatwaves may lead to a re-structuring of the ecosystem or even to functional shifts in communities (Pansch et al. 2018; Saha et al. 2020). Still, the number of investigations is remarkably low and there is an urgent need for more studies on the impacts of both present and future marine heatwaves on species and communities in order to better understand the potential responses.

1.5. Non-indigenous species and the Baltic Sea

The introduction of a species outside of their native range poses problems due to the unwanted or unexpected impacts they may induce on the recipient ecosystem (Gollasch and Leppäkoski 1999). A non-indigenous species (NIS) can be defined as a species that has intentionally or unintentionally been introduced outside of its native range or its natural dispersal potential, often as a result of human activities (Olenin and Minchin 2011). Non-indigenous species are often generalists (Weis 2010), with broad tolerances for various abiotic factors (Paavola et al. 2005), both characteristics that make survival and establishment more likely (Gollasch and Leppäkoski 1999).

Most non-indigenous species do not have a negative impact on the biological diversity or ecosystem functioning in the Baltic Sea, although for a large number of these, their long-term impacts are still unknown (Ojaveer and Kotta 2015). Both, species richness and diversity in the Baltic Sea is low (Paavola et al. 2005), partly because of its geologically young origin and because of the low-salinity brackish conditions (Elmgren and Hill 1997), and low-diversity communities have shown to be more susceptible to invasions than those with a high diversity (Paavola et al. 2005). In addition, there are numerous unoccupied niches in the Baltic Sea (Paavola et al. 2005) and also several vacant or new possible functional roles within which a non-indigenous species can perform (Olenin and Leppäkoski 1999; Paavola et al. 2005). In fact, a large part of species currently inhabiting the Baltic Sea can be considered invaders, of recent or less recent origin (Leppäkoski et al. 2002). Currently, 195 species are registered as non-indigenous or cryptogenic in the Baltic Sea (AquaNIS 2021), a number that is continuously increasing due to increased human activities. An added non-indigenous species increases the species richness, yet the invaded ecosystem loses its biogeographical peculiarities (Leppäkoski and Olenin 2001), contributing to the global biotic homogenization of ecosystems (Olden et al. 2004).

The study of non-indigenous species is important, as these may have a particularly strong impact on the ecosystems they are introduced to.

1.6. The study organism – *Rhithropanopeus harrisii*

The Harris mud crab, *Rhithropanopeus harrisii* (Gould 1841), is an estuarine crab native to the North American east coast (from Canada to the Gulf of Mexico) (Williams 1984) and it is considered among the most widely spread and successful brachyuran invaders globally (Roche and Torchin 2007). *R. harrisii* is small, up to 26 mm in carapace width, and omnivorous (Turoboyski 1973), which enables it to survive in various communities. *R. harrisii* feeds on both sessile and mobile invertebrates such as blue mussels (Figure 2), amphipods and gastropods (Turoboyski 1973; Hegele-Drywa and Normant 2009). The depth distribution for *R. harrisii* in the inner and middle Archipelago Sea is recorded as < 2 m (Fowler et al. 2013), but in their native habitat as well as in the southern Baltic Sea, crabs can be found down to 20 metres depth (Hegele-Drywa and Normant 2009). The optimum conditions of *R. harrisii* are found in brackish waters and it can survive at salinity concentrations as low as 1 ‰. *R. harrisii* has a broad thermal tolerance and tolerates rapid increases and decreases in temperature. In laboratory conditions, some individuals survived 37 °C for two days and some survived 35 °C for two weeks (Turoboyski 1973).

Figure 2. A male Harris mud crab (*Rhithropanopeus harrisii*) collected for this study consuming a blue mussel (*Mytilus trossulus*).

R. harrisii has been present in the southern Baltic Sea since the 1950s or earlier (Turoboyski 1973) but it has more recently expanded northwards and was first observed in the Archipelago Sea in 2009 (Karhilahti 2010). The northern parts of the Baltic Sea hosted no native crab species previously (Elmgren and Hill 1997; Bonsdorff 2006) and since its first observation in 2009, *R. harrisii* seems to have established and spread quickly (maps, see Fowler et al. 2013; Gagnon and Boström 2016) to several types of habitats (Gagnon and Boström 2016; Jormalainen et al. 2016; Riipinen et al. 2017). Yet, true densities of *R. harrisii* are not known since the crab has not been targeted in monitoring programs to date (Lokko et al. 2018). The lack of competition from native crab species in the northern parts of the Baltic Sea can potentially further facilitate its expansion and establishment (Gagnon and Boström 2016). *R. harrisii* is known to have changed native ecosystems around the world through altering species interactions. In the Baltic Sea, *R. harrisii* is reported to both act as an effective predator and to serve as prey to native species (Turoboyski 1973; Fowler et al. 2013). Thereby this species alters food webs and potentially affects the structure and functioning in coastal ecosystems (Forsström et al. 2015), possibly contributing in a positive way to the ecosystem functioning in the species poor Baltic Sea (Aarnio et al. 2015). The ability to effectively utilize Baltic Sea habitats and the broad tolerance to various abiotic factors might benefit *R. harrisii*, compared to native species in a future climate scenario. As a non-indigenous predator, *R. harrisii* may have a particularly strong impact on Baltic Sea communities (Jormalainen et al. 2016). Considering how influential *R. harrisii* is likely to be and the lack of experimental studies on the sensitivity and tolerance of this predator in its new range, it is very important to test its response to extreme events that are likely to occur in the Archipelago Sea.

1.7. Aims, research questions and hypotheses

This thesis used (*i*) a long-term (52 years) temperature dataset to retrieve natural thermal variability in the Archipelago Sea and (*ii*) a shorter high-resolution temperature dataset was utilised to identify past marine heatwaves based on climatological data. Finally, the impacts of simulated marine heatwaves modelled on the climatological data from the Archipelago Sea data were tested on the recent invader, *R. harrisii.*

This thesis addresses the following more specific research questions and hypotheses:

Q1a: What characterises a common marine heatwave in the Archipelago Sea, regarding its duration and amplitude?

Q1b: Has the mean SST and the frequency of marine heatwaves in the Archipelago Sea increased over the recent past?

Q2a: Does the impact of marine heatwaves in the Archipelago Sea on the recent invader, the Harris mud crab *R. harrisii*, increase with increasing heat intensity?

> **H2a:** A simulated future marine heatwave (*Amplitude*) will have a negative impact on the overall performance (energy uptake) of *R. harrisii,* compared to a simulated marine heatwave with an amplitude representative of an average heatwave that occurred between 2008 and 2019 (*Present*).
>
> **H2b:** A future marine heatwave simulated onto an increased baseline temperature (*Intensified*) will have the largest, yet sublethal, negative impact on the performance of *R. harrisii* compared to the other two treatments.

Q2b: Is *R. harrisii* able to recover after the different heatwave events, and does this capability depend on the intensity of the simulated event?

> **H2c:** Recovery for *R. harrisii* is greater in the *Present* heatwave treatment than in the future (*Amplitude* and *Intensified*) heatwave treatments.

2. Materials and Methods

This thesis is divided into two parts: (*i*) the identification and modelling of past marine heatwaves in the Archipelago Sea based on two SST datasets from Seili and (*ii*) an experimental approach to test the sensitivity of *Rhithropanopeus harrisii* to simulated marine heatwaves with amplitudes of today and those representative of the future (identified from part *i*).

2.1. Temperature modelling

Temperature data were provided by the Turku University of Applied Sciences in collaboration with the Archipelago Research Institute of the University of Turku, the Finnish Meterological Institute (FMI) and other FINMARI partners. Two time series datasets from the University of Turku's marine station (Archipelago Research Institute), at the island of Seili in the Finnish Archipelago Sea (Figure 3) were used to detect past marine heatwave events and to identify their frequency, intensity, and duration. Cold spells were also detected, but will not be analysed further in this thesis, although these may also be relevant for marine ecosystems. To identify marine heatwaves and their characteristics from these datasets, the R package "heatwaveR" (Schlegel and Smit 2018) was used. The simulated marine heatwave treatments for the experimental part (*ii*) were determined based on the results from this modelling approach.

The first dataset is a long-term dataset and covers the period 1966–2019 (54 years) with 27 to 36 snapshot measurements taken per year from a research vessel (hereafter: long-term dataset). The second dataset covers a shorter period 2006–2019 (14 years) but with very frequent measurements along a depth gradient by means of an automated buoy (hereafter: high-resolution dataset).

Figure 3. Map showing an overview of the Archipelago Sea with the Seili marine station (blue), where the temperature measurements for the long-term and the high-resolution datasets were conducted, and the location of the Husö Biological Station (red) in the Åland Sea, where the experimental work was conducted. The map is retrieved from https://maanmittauslaitos.fi/karttapaikka.

2.1.1. 54-year long-term dataset: 1966–2019

The sampling point for the long-term dataset is situated north of the Seili island at the Päiväluoto intensive monitoring station (*N° 60.255278; E° 21.951028*; Figure 3). The long-term dataset consists of 1,796 observations of SST beginning on September 11th, 1966 and concludes with a measurement on October 31st, 2019. (Figure 4A). Data were collected using a Limnos water sampler between 1966 and 2017. As of August 2nd, 2017, an RBR CTD-sonde was used. Measurements were scheduled every ten days, on the 1st, 11th and 21st of each month (±2–3 days) along a depth gradient down to 40 metres with measurements taken every 5 metres. In my thesis, I will focus on the upper water column, and only examine the measurements taken at 5 metres depth, which roughly represents the typical depth horizon of my study species.

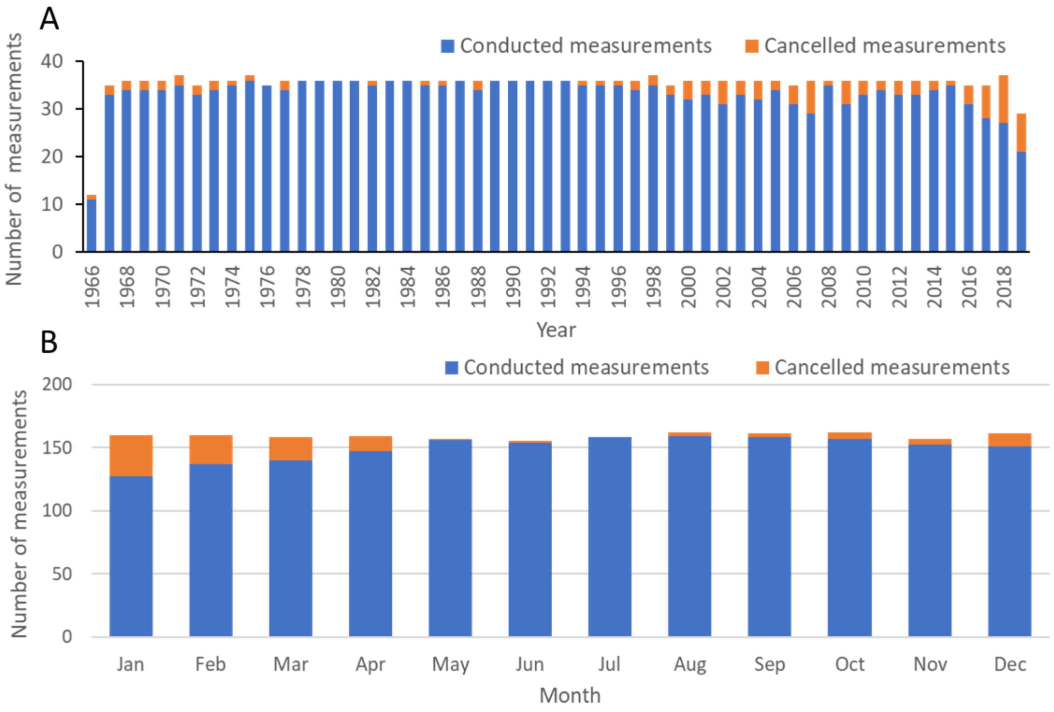


Figure 4. ***Long-term dataset:*** **A)** Measurements have been conducted every ten days (±2–3 days), which adds up to a total of 36–37 measurements per year and a total of 1,796 measurements over the period 1966–2019. 71% of the scheduled measurements that were not conducted (cancelled measurements) occurred between 2000 and 2019 and are displayed in orange. **B)** Between 127 and 159 measurements in total were conducted each month over the period 1966–2019. Most cancelled measurements occurred during late winter and early spring and, all in all, only 7% of the cancelled measurements occurred between May and September.

The long-term dataset contains 114 missing values, which is due to either faulty or broken equipment, winter storms or staff holidays. Most of the missing data points occurred after 2000 (Figure 4A). The largest time gap in between two measurements until the year 2000 is three data points in a row (i.e., no measurements were taken in February 2000). Other, more recent significant time gaps in measurements occurred in the winter months of 2016–2019, between January and March. Overall, the missing data points normally occur in the months between December and April (Figure 4B). All in all, only eight missing values (NA) are recorded in the months between May and September, which are the months most relevant to this thesis. The data from years with incomplete time series (1966 and 2019) were excluded from mean and trend analyses, since they consist of fewer measurements (Figure 4A) and would therefore influence the annual means.

2.1.2. *14-year high-resolution dataset: 2006–2019*

The high-resolution dataset has been collected by a YSI 6952 automated buoy with a multiparameter YSI 6000 sonde. In addition to water temperature, the sonde measures salinity, dissolved oxygen, turbidity, chlorophyll-α, and blue-green algae content. The analysed high-resolution dataset consists of SST measurements taken between October 5th, 2006 and November 20th, 2019. The buoy is installed (*N° 60.255278; E° 21.951028;* Figure 3) to operate in spring as soon as the ice melts and is removed in early winter before ice forms. The buoy takes four depth-measuring profiles from the entire water column per day and a winch moves the measuring device vertically in the water column, with measurements taken at depth intervals of one meter (2–40 metre depth). This dataset contains multiple daily measurements, between four and eight per day for each specific depth. The heatwaveR package used to retrieve climatology only accepts one value of water temperature per day. Therefore, the mean seawater temperature for each day was calculated before further analyses.

As previously stated, the buoy did not collect data year-round, and start or end dates of measurements varied between years, depending on when the buoy was placed into the water and removed for overwintering. Consequently, the number of days with measurements taken each year (Figure 5A) and month (Figure 5B) over the entire period varies strongly.

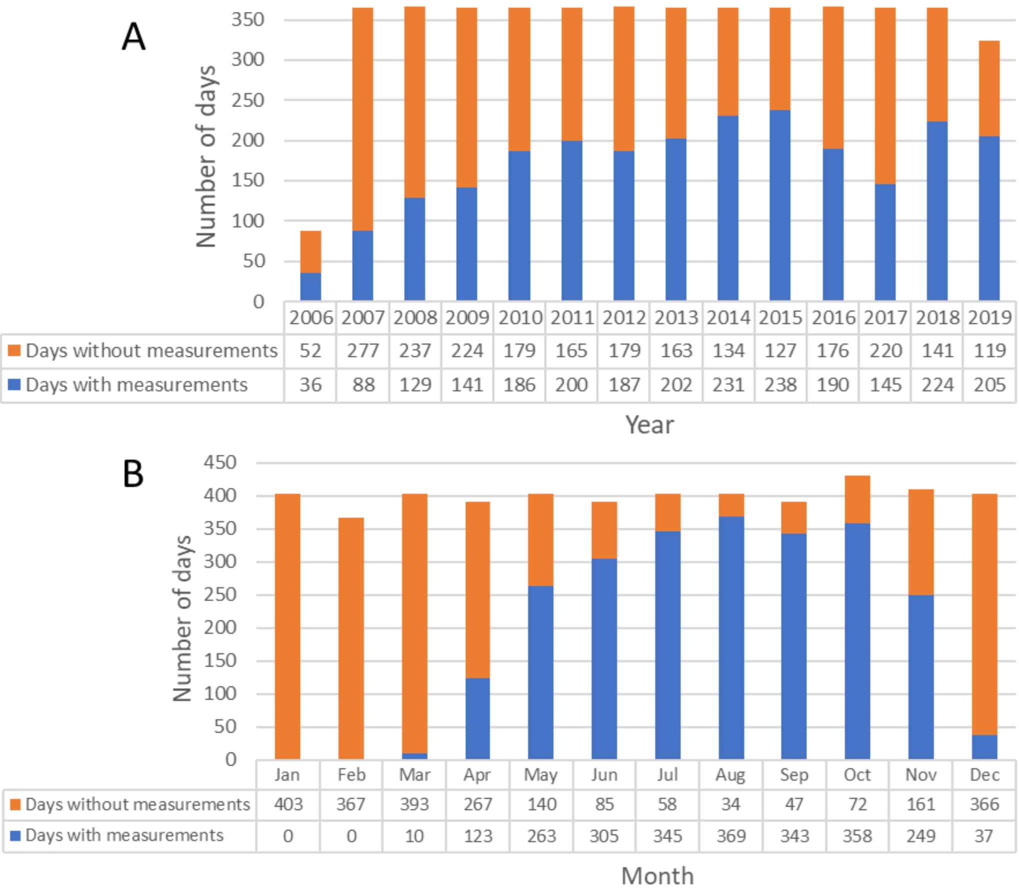


Figure 5. ***High-resolution dataset:*** **A)** Multiple measurements have been conducted every day, but not year-round. The number of days with (blue) or without (orange) observations each year varies. **B)** Between 249 and 369 days with measurements are recorded between May – November from 2006 to 2019.

The buoy has collected complete seawater temperature data from approximately May-November 2010 onwards, since the observations started slightly later in the season during 2008 and 2009 (Figure 6). The data collected during the years 2006 and 2007 are incomplete, with the measurements taken in 2006 (although frequent) only containing observations during October and November and, unlike all other years, has no collected data from 5 m depth. The data from 2007 have missing values between the 5th of May to the 4th of August and from the 27th of August to the 16th of October. For further analysis of the high-resolution dataset, it is crucial that a year includes most measurements in July and August, since this is the experimental period, and also the time when marine summer heatwaves normally occur. The years 2006 and 2007 were, therefore, not included in any further analyses. The months between December and April were also excluded, since some lacked measurements while others only included very few data from specific years (Figure 6). The analysed data include 2,137 days of measurements collected between May and November, from 2008 to 2019 (start date July 16th, 2008, end date November 20th, 2019).

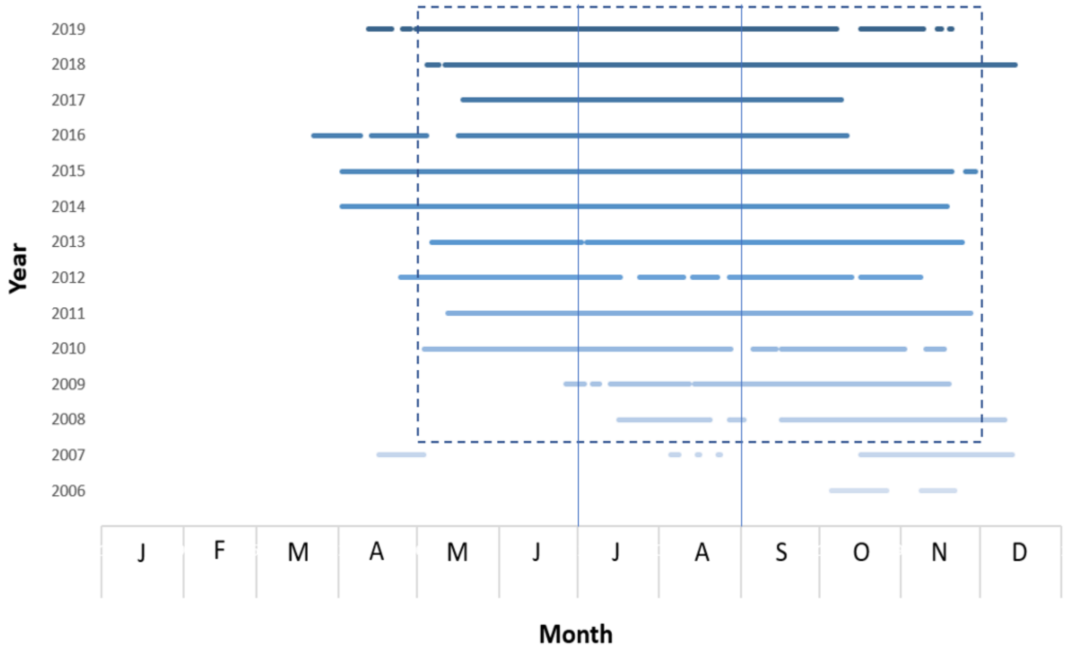


Figure 6. ***High-resolution dataset:*** *Variation* in length of the period that the Seili buoy has been operational from 2006 to 2019. July and August are the months most relevant to this thesis, since this is when marine summer marine heatwaves and annual maximum temperatures normally occur. As the months July and August were not monitored in 2006 and 2007, these years were excluded from further analyses. The months of May to November between the years of 2008 and 2019 were included in the heatwave mean and trend analyses and used as input when calculating climatology for this dataset.

2.1.3. Identification of marine heatwaves

The '*heatwaveR*' R package contains functions that calculate and display marine heatwaves according to the definition of Hobday et al. (2016). The output consists of a daily climatology, and a list of detected heatwave events with descriptive metrics (see Appendix; Figure A1, Table A1 and Table A2). Firstly, the daily climatology is generated for a chosen period of a time series, which is then used to calculate the seasonal cycle and threshold values (90th and 10th percentile for heatwaves and cold spells, respectively). Calculating climatology on a baseline period that is at least 30 years long is recommended, since this smoothens out decadal thermal periodicities that may exist in the dataset (Schlegel and Smit 2018) and, additionally, full years should be used as start and end dates for the climatology, to avoid unequal weighing of certain days within the data. Gaps in the data should preferably not last longer than three consecutive days and only one value per day is valid as input (Hobday et al. 2016; Schlegel and Smit 2018; Schlegel et al. 2019). Functions in the heatwaveR package can handle some missing days, but the longer and more frequent the gaps in the time series become, the lower the accuracy of the calculated climatology and threshold becomes (Schlegel and Smit 2018; Schlegel et al. 2019). This can change both the exactness of the event detection and the number of detected events. Both time series examined in this thesis can be considered sub-optimal for calculating and displaying marine heatwaves using this package, with the long-term dataset containing too few measurements per year to retrieve reliable climatology, and the high-resolution dataset covering a period shorter than 30 years, and only containing measurements frequent enough between May and November. Nevertheless, both datasets were examined, and their respective strengths and weaknesses and how these were taken into consideration when analysing are described in detail below.

For the long-term dataset, all temperature measurements from 1966 to 2019 were used as input in R, with the climatology baseline period set to January 1st 1967 to December 31st 2018. Since this dataset has 10 or more missing values (NA) in between every observation, these were interpolated. The results from the long-term dataset outputs might not detect all the anomalous thermal events due to its low coverage or may merge two or more separate events into one. An additional problem is that the heatwaveR package assumes the mean for the entire period as a reference, potentially representing a year from the middle of the dataset. This means that if one assumes that climate change has warmed the SST over this period, all early observations will underestimate while most recent observation will overestimate the occurrence of marine heatwaves (Schlegel et al. 2019). It is to be expected that most of the detected events using this baseline period will have occurred in the most recent decades. This dataset will not be optimal for determining treatments for the experimental part, since it is only at best indicative due to its low accuracy. Then, when examining and interpreting the detected events in the output, I will remain cautious, since part of the trend in heatwave occurrence is based on climate mean changes.

The high-resolution dataset only covers the months of May to November (Figure 6), since measurements outside that range were sporadic or non-existent and of less relevance to the thesis. The baseline period of 12 years (2008–2019) is considerably shorter than recommended, which means that decadal thermal periodicities cannot be registered, nor proper trends in duration, frequency, and intensity of marine heatwaves. A daily mean temperature for each day was calculated and used as input for the climatology, with the baseline period set to July 16th, 2008 to July 15th, 2019. The output displays climatology between May 11th and November 20th. This dataset is optimal for determining the treatments for the experimental part, since it gives an accurate picture of the events that have occurred over the last decade.

2.1.4. Statistical evaluation of the data

The data from the heatwave modelling were analysed in R (version 3.6.3, R Core Team 2020) using the package '*heatwaveR*'. This output derived heatwave statistics on the duration (start date, peak date and end date), mean maximum and cumulative intensity, rate of onset and rate of decline for each heatwave recorded in each of the two datasets (see Hobday et al. 2016; Schlegel and Smit 2018 for details on the procedure). The metrics duration and mean and maximum intensity were further analysed in this thesis (for an overview of the calculation of these, see Appendix; Figure A1).

The occurrence and trends of heatwaves over the long-term and the high-resolution datasets were tested using general linear models (regression), with time (year) being the predictor variable and the number of detected events per year being the response variable. Similarly, regression was applied for mean intensity and duration, with time (year) as the predictor variable and mean intensity and duration as the response variables, respectively. Regression was also applied for mean summer temperatures (means of the months July to August), with time (year) being the predictor variable and mean temperature being the response variable. Before running the parametric analyses, normality of residuals was verified using a Shapiro-Wilk normality test as well as graphical tools in R (qqplots and histograms), and homogeneity of variance was verified using Levene's Test for Homogeneity of Variance. Where assumptions for parametric analyses were not met, the non-parametric Kruskal-Wallis test was applied. A Pearson correlation analysis was applied to examine the relationship between the means (seasonality) and the 90th percentiles of the long-term and the high-resolution dataset. In addition to this, the correlation between the number of detected marine heatwaves per year in the two separate datasets was checked.

2.2. Determining climatology for the experimental approach

Simulated marine heatwave treatments were determined for the experimental part based on the high-resolution dataset output from the modelling section. The seasonality and threshold values (90th percentile) for the experimental period (July 16th – August 21st) were extracted and used as a baseline for the treatments, since these temperatures are realistic to what *R. harrisii* may experience in their natural environment at present in the Archipelago Sea. The climatology extracted for the experimental period represents the baseline SST recorded for these dates between 2008 and 2019 and, therefore, gives a good starting point when determining the experimental treatments. From the high-resolution dataset, a common marine summer heatwave in the Archipelago Sea was identified, characterised by the parameters mean duration (13 days) and mean intensity (2.6 °C above seasonality) in the months of July to August. The mean intensity and duration when considering all marine heatwaves registered between May and November in the high-resolution dataset was 12.9 days and 2.4 °C. The treatments for the experimental part of this thesis are to represent a present average marine heatwave in the Archipelago Sea (*Present*), an event of increased amplitude (*Amplitude*) and a future high amplitude heatwave scenario (*Intensified*). For a detailed description of how treatments for the experimental approach were determined, see section 2.3.3.

2.3. Experimental approach

2.3.1. Study sites and species collection

The experimental work was conducted in the aquarium facilities of Husö Biological Station (Figure 7), Åbo Akademi University, between July 16th and August 21st, 2020.

Figure 7. Map showing the important localities for the experimental work, the mussel (red) and crab (yellow) collection sites and Husö Biological Station (blue). The map is retrieved from https://maanmittauslaitos.fi/karttapaikka.

R. harrisii individuals were collected in the Åland Archipelago from Godby's small boat port by Färjsundet (*N° 60.24067; E° 20.00799;* Figure 7), between June 30th and July 13th, 2020. Twelve traps (Figure 8) were distributed around the harbour area at a depth of 1–3 metres and checked for mud crabs daily. In total, 74 crabs with carapace widths between 9.0 and 21.5 mm were caught (See Appendix; Figure A7).

Blue mussels were collected every 3 to 6 days from the north-eastern side of the island Gomholm, Åland (*N°60.34459; E° 19.73068;* Figure 7) using a triangular benthic scraper (Swe.: Triangelskrapa) and by snorkelling. At the time of collection, seawater temperature, salinity and pH at Gomholm were measured and ranged between 17.8–18.2 °*C*, 5.7–6.0 PSU and pH 7.9–8.1 (NBS scale), respectively. The mussels were kept alive in a separate aquarium, provided with a flow through of sand-filtered seawater and aeration. This ensured that fresh and alive mussels could be provided to the crabs in each feeding event, with mussels not being in the lab for more than five days.

Figure 8. A crab trap, consisting of a basket filled with small rocks, bricks, PVC-tubing, and shards of terracotta pots, was used to collect *Rhithropanopeus harrisii* individuals for the aquarium experiment. Trap dimensions = 35 x 25 x 15 cm.

2.3.2. Experimental design and setup

Only male crabs were included in the experiment. This ensured that the mud crabs were not caring for eggs, which was shown to affect the crab's activity (Turoboyski 1973). Only individuals >12 mm carapace widths are carnivorous (Aarnio et al. 2015) and interested in the provided mussel prey. The chosen 27 crabs had a carapace width between 16 and 20 mm. Prior to the start of the experiment, all crabs were acclimatised to laboratory conditions in separate aquaria (22 x 22 x 29 cm: 14 L) for 1–2 weeks, depending on the date when the individual crab was caught. The aquaria were supplied with sand-filtered seawater from Husö Bay, aerated and provided with habitat complexity in form of half a terracotta pot and plastic shoots of artificial eelgrass (Figure 9C).

The aquaria were moved into the climate room five days before the experiment started, and randomly distributed into the three water baths (360 L; Figure 9A). The aquaria were placed on top of a wooden construction, so that the tops of the aquaria were raised slightly above the water level (Figure 9B). The aquaria had fresh seawater inflow from the Husö Bay of about 5–8 L/day. The aquarium temperature in the water baths was continually measured by a probe, and manually measured in all experimental units every second day. Three temperature loggers (HOBO Pendant Temperature 16K Data Logger, Onset Computer Corporation) were distributed to randomly chosen units of each treatment (Figure 11).

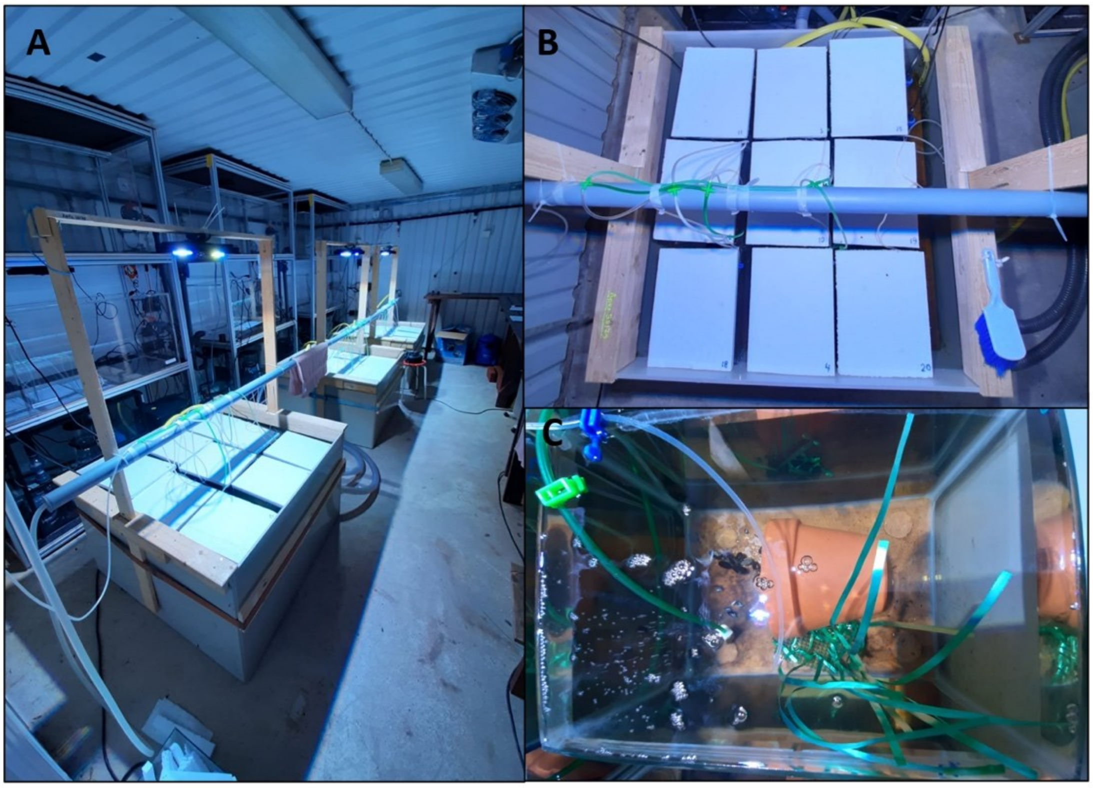


Figure 9. A) An overview of the experimental setup in the climate room, with the three water baths and the wooden construction where lights were attached. Seawater inflow came through the PVC tubing fastened above the water baths. **B)** One water bath, containing one treatment and nine replicates, and the aeration and water inflow tubing leading to the experimental units. **C)** The structures provided for the *Rhithropanopeus harrisii* in each experimental unit and the aeration stone and water inflow tubing.

To maintain the targeted temperatures in the treatments, the water baths were equipped with two 300 W heaters (EHEIM GmbH & Co., KG, Deizisau, Germany) and a cooling system (AB Aqua Medic GmbH, Bissendorf, Germany). To avoid stagnation or the formation of gradients in the water baths, these were supplied with water pumps (AquaBee Aquarientechnik, Zerbst, Germany). Probes continuously measured the water bath temperature, salinity and pH_{NBS}. Aquarium controllers (Neptune Systems, Morgan Hill, USA) operated heaters and chillers at a hysteresis of 0.1 °C.

Radion XR30w G4 PRO lights (EcoTech Marine, Allentown, USA) were programmed to mimic daylight, with the sun to rise at 5:07 AM and set at 10:26 PM, which equals the median sunrise/sunset time of the experimental period, and which provided radiation mimicking light conditions at water depth of ca 3 metres in the area (30 μmol m^{-2} s^{-1}). Lids were placed on top of all aquaria, as crabs usually shelter under natural structures.

2.3.3. Experimental treatments

The impact of three simulated marine heatwave treatments, each with nine replicates, was tested on *R. harrisii.* The experimental period can be divided into five phases; pre-heatwave (6 days), heatwave onset (5 days), maintained heatwave (13 days), heatwave decline (5 days) and post-heatwave (7 days). In total, the experiment was run for 36 days (July 16th – August 21st, 2020). The metrics duration and amplitude of the simulated marine heatwave for the ***Present*** treatment were modelled on the metrics mean duration (13 days) and amplitude (2.6 °C) retrieved from the summer marine heatwave events registered in the high-resolution dataset (see above). The first treatment, *Present*, had temperatures that followed the seasonality retrieved from the model, and then roughly rose to a marine heatwave of today's average amplitude (amplitude of +2.5 °C) and duration (13 days). The second treatment ***Amplitude*** followed the seasonality, but an additional 3 °C was added to the marine heatwave event (amplitude of +5.5 °C), which also prolonged the heatwave duration by six days (19 days in total). The third treatment ***Intensified*** represented an offset of the *Amplitude* treatment by +2 °C (amplitude of +7.5 °C).

The prolonged duration of the *Amplitude* treatment corresponds with future global predictions of increased duration (Oliver et al. 2018, 2019) while the temperature addition during the simulated heatwave exceeds the maximum mean amplitude of a marine heatwave recorded by the high-resolution dataset (maximum mean amplitude of +3.6 °C, maximum amplitude of +4.9 °C). Therefore, the *Amplitude* treatment can be considered to simulate a probable event of the future, but with a maximum temperature that is already registered at present. The temperature offset in the treatment *Intensified* was applied because of the likelihood that the mean baseline temperature in the Baltic Sea will be between 2–4 °C higher by the end of the century (BACC II Author Team 2015). Therefore, the applied treatments represented a common event of today, an event of increased amplitude and a future marine heatwave event of increased amplitude with a warmed baseline scenario, respectively (Figure 10).

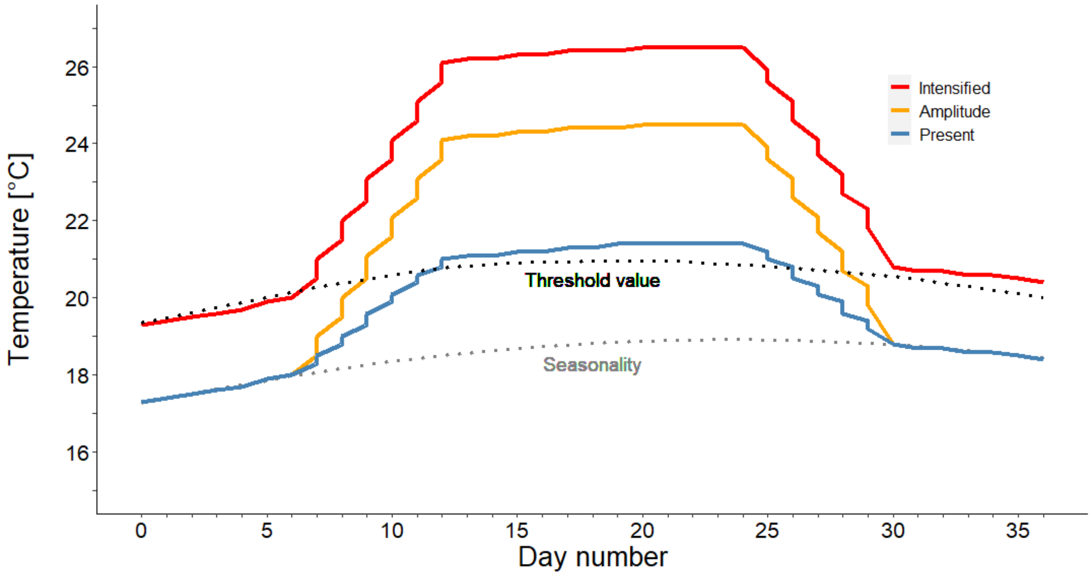


Figure 10. The simulated heatwave treatments and climatology (see Figure 18) for the experimental part are based on the high-resolution temperature dataset. The seasonality is the climatological mean extracted from the high-resolution dataset, showing the average historical temperature for a particular day during the experimental period, and the threshold is the seasonally changing temperature value above which events may be detected. The temperature in the different treatments crosses the threshold value at different times, hence, the duration of the marine heatwave event varies between treatments.

Three days prior to the beginning of the experiment, the temperature in the water baths was gradually adjusted from 18 °C to reach the target starting treatment temperatures of 17.4 °C and 19.4 °C (maximum rate of 0.5 °C per day). The daily changes in temperature during the experiment were achieved through discrete adjustments of the controlling units twice per day, at 9 AM and 9 PM.

Experimental units within each treatment were independent in water supply and aeration but shared the same location in the room and the same water bath. Yet, to avoid confounding room and water bath effects, treatments were shuffled once between water baths during the experiment. Therefore, the positioning of the treatments in the climate room was changed on August 4th, at the halfway mark of the experiment (Figure 11).

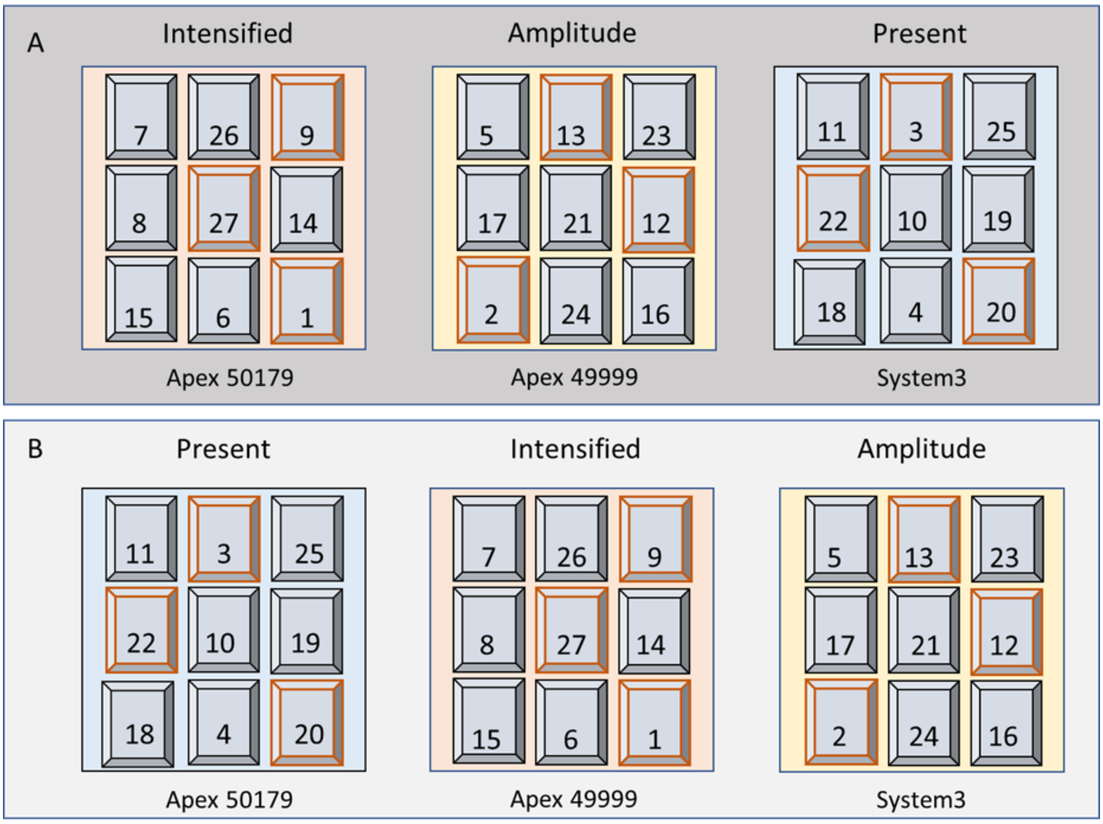


Figure 11. **A**) The positioning of the treatments during the first 18 days of the experiment (16.7.2020 – 3.8.2020). **B**) The positioning of the treatments for the remaining 18 days of the experiment (4.8.2020 – 21.8.2020). The aquaria with red borders were equipped with temperature loggers throughout the experiment.

The 27 crabs were distributed randomly among the three experimental treatments on July 10th, 2020. Carapace width (mm) and weight (g) were measured on July 16th when the experiment started. ANOVA on initial wet weight and carapace width did not yield any significant differences between treatment groups (initial wet weight: $F_{2,24} = 0.556$, $p > 0.581$; initial carapace width: $F_{2,24} = 0.282$, $p > 0.757$; Figure 12, A and B).

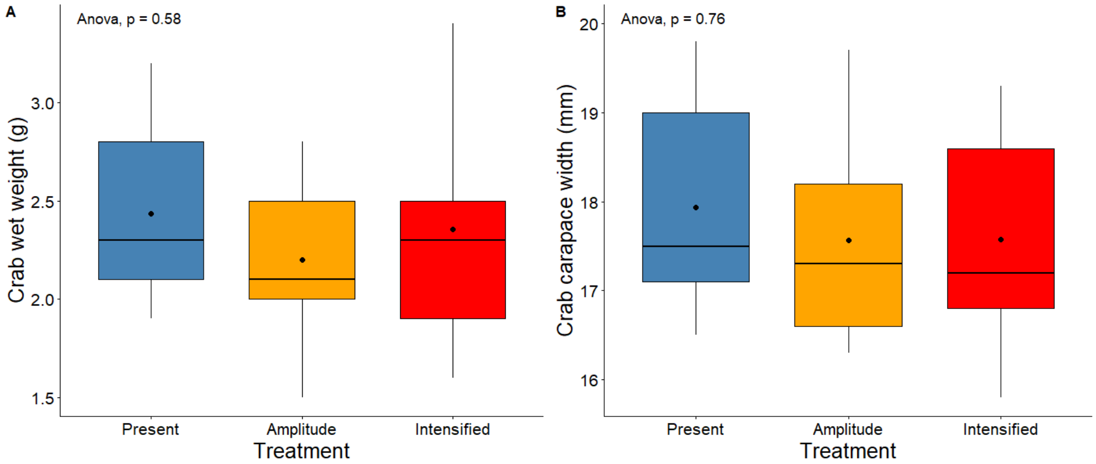


Figure 12. The initial wet weight (**A**) and carapace width (**B**) in the treatments *Present*, *Amplitude* and *Intensified*. Boxplots show the median, including upper and lower quartile. The mean value for each treatment is shown as a black dot (N = 9).

2.3.4. Maintenance and response variables

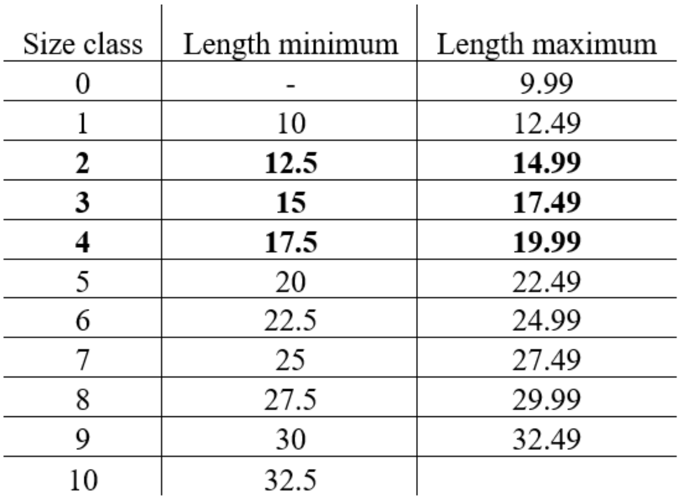
The aquaria were cleaned every second feeding event (every 6 days), during which individual crabs were placed in a separate aquarium of the same water temperature as in their respective treatment. The walls of the aquaria were gently scrubbed with a brush to remove algal growth while the terracotta pot and artificial eelgrass were scrubbed off in a separate bucket. Additionally, algal growth that had formed in the inflow tubing was removed. The water in the aquaria was then filtered using a self-made cloth sieve that collected most of the smaller loose particles and all pieces of mussel shells that had not been removed during previous feedings.

Temperature, pH_{NBS}, salinity, and flow were measured during the experiment with varying intervals. Temperature was manually measured every day during the phase's onset and decline, and every other day during in the pre-heatwave, maintained heatwave and post-heatwave phases. Salinity and pH_{NBS} were measured every six days and the water inflow was adjusted every third day, at which point the aeration stones were also checked and adjusted if necessary. The crabs were maintained in optimal conditions and the response variables crab growth and feeding were evaluated at the start, during and at the end of the experiment. The feeding on fresh blue mussels was transformed into mussel dry weight consumed by crabs following an establishment of mussel size to mussel dry weight correlation (see 2.3.4.1).

2.3.4.1. Size to dry-weight correlation of mussels

Collected blue mussels were sorted into different size classes according to the length of the shell (Table 1). Mussels from each size class were frozen over the course of the experimental period with a total of fifty frozen mussels per collection.

Table 1. Mussel size classes according to the length of the shell. Mussels in size classes 2–4 were fed to *Rhithropanopeus harrisii* during the experiment (given in bold).



Size class	Length minimum	Length maximum
0	-	9.99
1	10	12.49
2	**12.5**	**14.99**
3	**15**	**17.49**
4	**17.5**	**19.99**
5	20	22.49
6	22.5	24.99
7	25	27.49
8	27.5	29.99
9	30	32.49
10	32.5	

A total of 439 frozen mussels were measured (Vernier caliper), dissected, and then dried (24 hours, 80 °C) in a drying cabinet, after which the dry weight (Mettler AE 260 delta range, 0.0001 g) of each dissected mussel was determined (Figure 13).

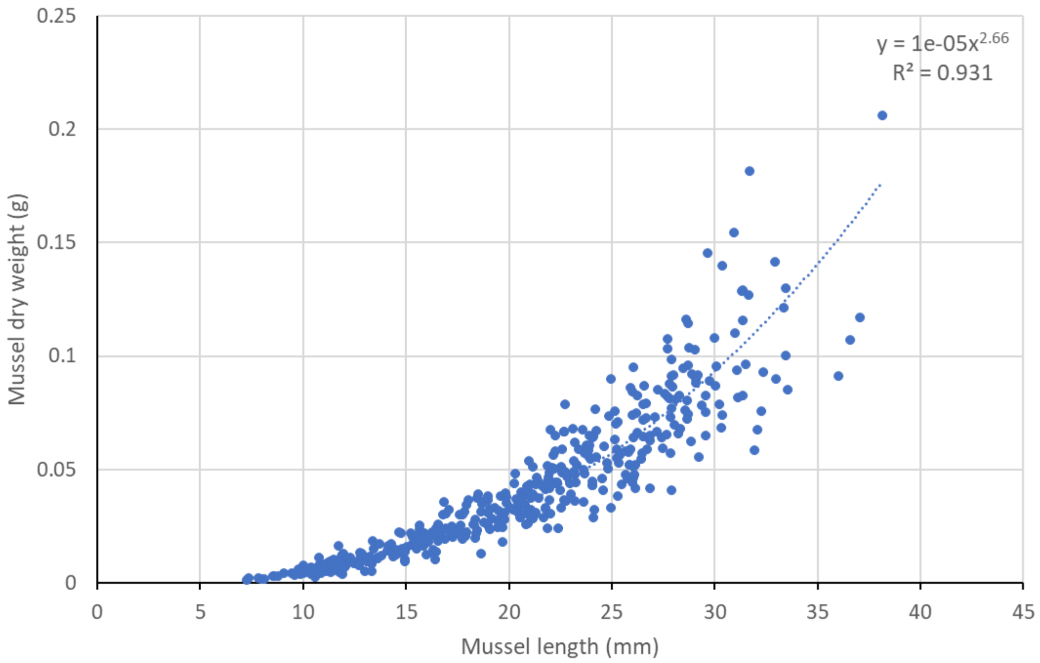


Figure 13. Soft tissue dry weight (g) of 439 mussels of *Mytilus trossulus* from the Sea of Åland plotted over shell length (mm) and fitted to a power function.

2.3.4.2. Growth

Wet weight and carapace width of all *R. harrisii* individuals were measured eight times over the experimental period on July 16th, 21st, 25th and 28th, and on August 3rd, 9th, 15th and 21st, often in connection with the cleaning of the aquaria. The crabs were weighed (Sartorius TE2101, 0.1 g) after careful drying with a towel. The carapace width was measured to the nearest 0.1 mm (Vernier caliper).

At the end of the experiment, the dry weight of each individual mud crab was determined. For this, mud crabs were frozen for three days or more and then dried (24 hours, 80 °C) in a drying cabinet and weighed (Mettler AE 260 delta range, 0.0001 g).

2.3.4.3. Feeding

During acclimatisation, prey preference and mussel size preference were tested on the crabs. Based on these trials, mussels of sizes 12.5–20.0 mm (smaller or equal to the maximum carapace width of the experimental mud crabs) were determined to constitute a prey of suitable size. These results were further supported by other studies, with blue mussels being a likely prey for *R. harrisii* in the Baltic Sea (Forsström et al. 2015; Jormalainen et al. 2016) and mud crabs preferring to consume small or medium sized prey as they are not likely to open blue mussels that are larger than themselves (Forsström et al. 2015; Engström 2020).

The mud crabs were provided with live mussels that were freshly placed into the aquaria every third day, at which point the previous mussel batch was removed from the aquaria. In total, twelve feeding events were conducted. During the feeding occasions 3–12, the crabs were provided with mussels of three different size classes: 12.5–14.99, 15.0–17.49 and 17.5–19.99 mm (see above Table 1). During the feeding occasions 3–5, a total of 9 mussels were provided (three from each size class), but this number was increased to a total of 12 mussels instead (during the feeding occasions 6–12), to ensure that no crab would be able to consume all provided mussels at a single feeding interval. During the feeding occasions 1 and 2, larger mussels were also provided (< 25 mm; see section 4.5). The size class of the remaining mussels after each feeding was measured (Vernier caliper) and the number of consumed mussels was counted.

To estimate the average dry weight in terms of mussel soft tissue that an individual mud crab had consumed over a three-day interval, soft tissue dry weight (g) and shell length (mm) of 439 mussels were measured and fitted to a power function (see above Figure 13). The mean sizes of the consumed mussels (means of the different size classes were: 13.84, 16.31 and 18.71 mm), which were then used to transform each mussel eaten into a size-shell-specific amount of mussel dry tissue weight consumed.

2.3.5. Statistical analysis of experimental data

The data from the experimental part were analysed in R (version 3.6.3, R Core Team 2020). To check for significant differences between the treatments in overall feeding and growth (wet weight and carapace width), one-way ANOVAs were applied. Significant results from the one-way ANOVAs were followed by a *post hoc* Tukey test to check for pair-wise differences.

A one-way repeated measures ANOVA (within-subjects ANOVA) with the fixed factor temperature treatment (three levels: *Present, Amplitude, Intensified)* was applied to test the effect of feeding over time (function ‘aov’, package ‘car’) with significant results being followed by a *post hoc* Tukey test.

Before running any parametric analyses, the normality of residuals was verified using a Shapiro-Wilk normality test as well as graphical tools in R (qqplots and histograms), and homogeneity of variance was verified using Levene's Test for Homogeneity of Variance. Additionally, for the repeated measures ANOVA, the sphericity was tested using Mauchly’s test of Sphericity. Where assumptions for parametric analyses were not met, the non-parametric Kruskal-Wallis test was applied, with significant results being followed by Dunn's *post hoc* test.

3. Results

3.1. Long-term dataset

3.1.1. Means and trends

There is a significant trend towards warmer SST, both annually and during the summer months of July and August (annual: $F_{1, 50} = 57.98$, $p < 0.001$; July–August: $F_{1, 50} = 10.95$, $p = 0.00174$; Figure 14A). Over the last two decades, the temperature in July and August has only fallen below the long-term mean of 17.26 °C in the years 2000, 2007, 2009 and 2015 (Figure 14B), with a negative deviation of less than -0.5 °C only.

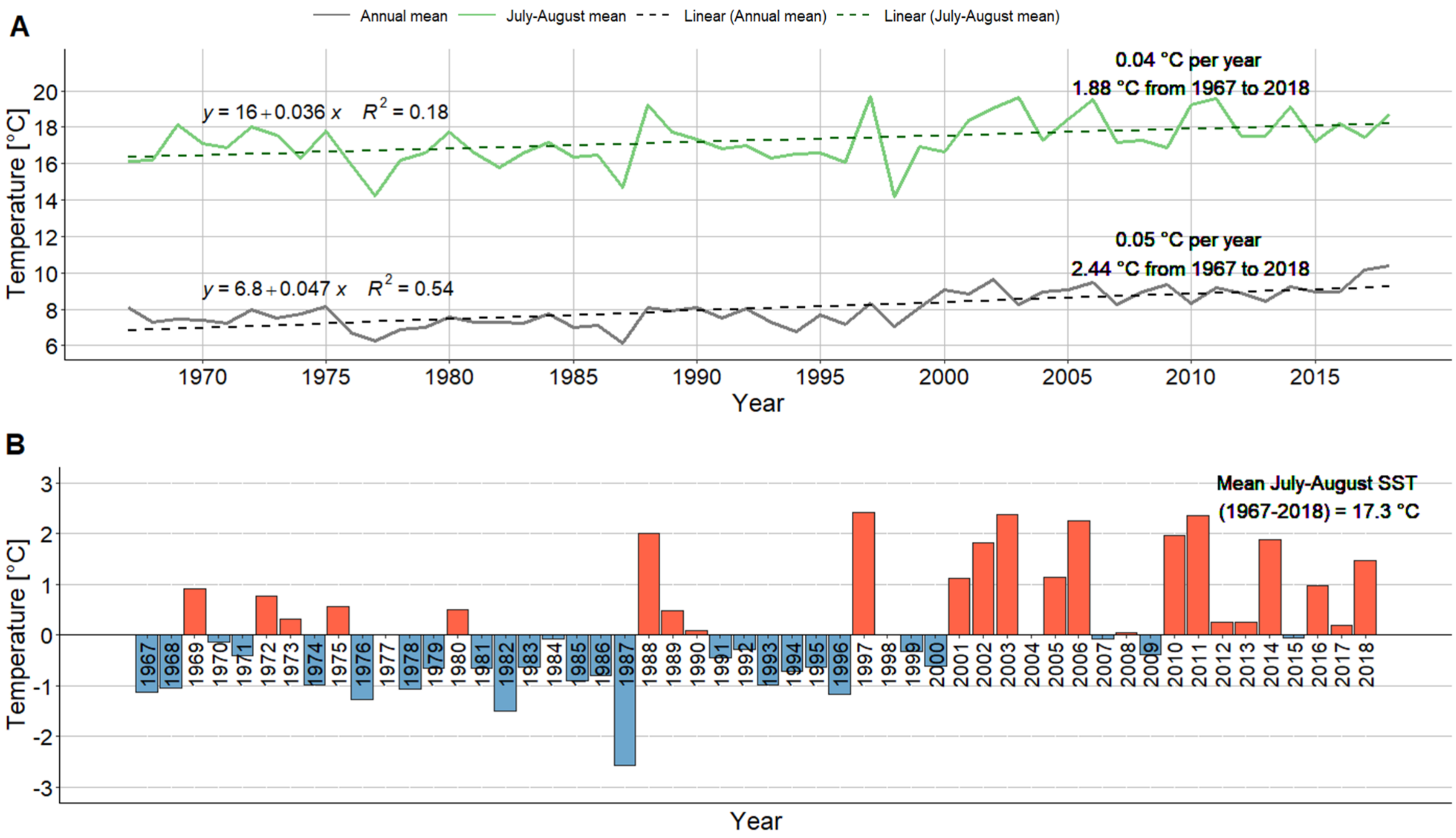


Figure 14. A) Annual mean SST (five metres depth) between 1967 and 2018 as retrieved from the long-term dataset and mean SST for the warmest months, July and August (i.e., the experimental period). There is a significant trend towards warmer SSTs, both when examining annual and July–August means. **B) The** July to August mean SST from 1967 to 2019 is 17.26 °C and shown here are deviations from July–August mean SST for each year. Since 2000, only three years have had mean temperatures below average.

3.1.2. *Climatology and thresholds*

Mean SST is at its warmest in August and based on the climatology (Figure 15), the seasonality peaks on August 7th. For the long-term dataset, climatology and the 90th threshold value were extracted from a leap year (366 days), with the baseline period set to January 1st, 1967 to December 31st, 2018 (Figure 15).

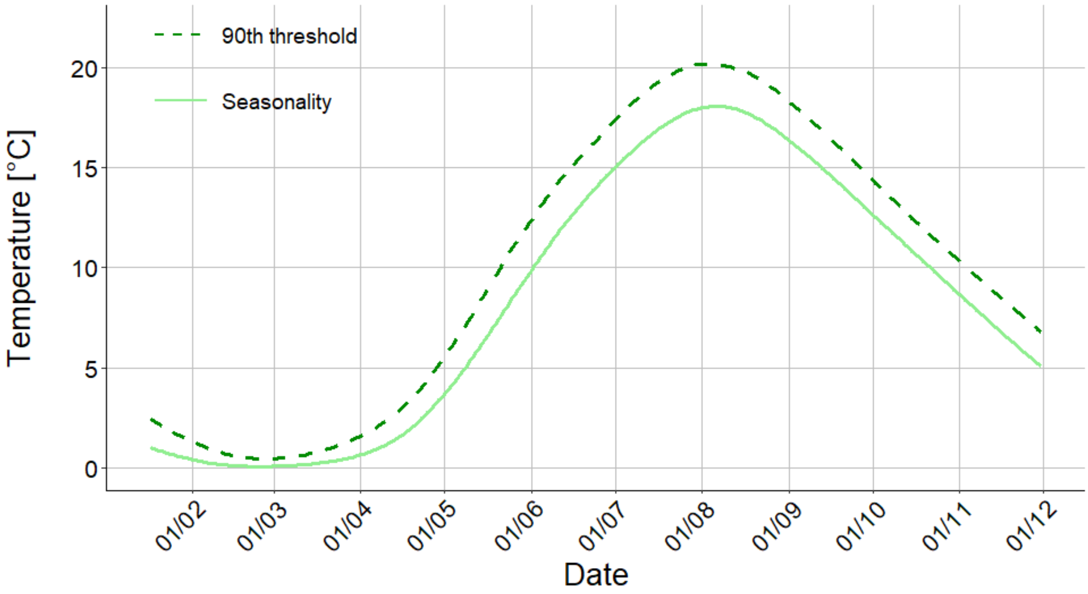


Figure 15. Climatology and threshold (90th percentile) for the long-term dataset, obtained with the 'heatwaveR' package with the baseline period set to January 1st, 1967 to December 31st, 2018.

3.1.3. *Event detection and characterisation*

A total of 63 marine heatwave events were registered from the long-term dataset between 1966 and 2019 (see Appendix; Figure A2 and Table A1). The maximum number of events occurred in 2006 and 2014, while many years did not register a marine heatwave at all. A total of 44 marine heatwave events (70% of the total number of events) occurred between 2000 and 2019. The frequency of marine heatwave events increased significantly with time ($F_{1, 51} = 20.45$, $p < 0.001$; Figure 16A), while the intensity ($F_{1, 61} = 2.03$, $p = 0.159$; Figure 16B) and the duration ($F_{1, 61} = 2.87$, $p = 0.0953$; Figure 16C) showed no significant trends between 1967 and 2019. The number of marine heatwaves (start date) observed per month appears to be highest during the summer months, with most events being recorded in August (10 events). A total of 36 marine heatwaves (57%) occurred during the months of May and August (start date; Figure 16D).

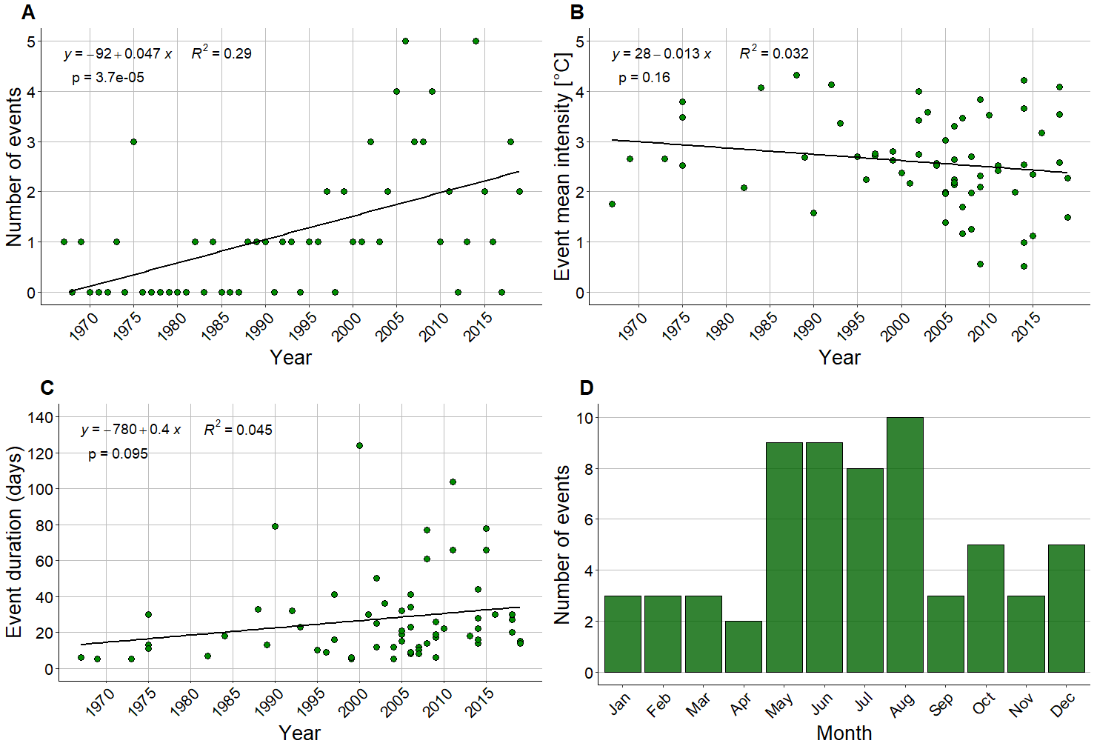


Figure 16. Linear regression on the long-term dataset between time and **A**) the number of marine heatwave events per year, **B)** mean intensity of events and **C)** heatwave duration. **D)** The number of heatwaves per month (start date) represented as bar plots.

3.2. High-resolution dataset

3.2.1. Means and trends

Between 2008 and 2019, there was no significant trend towards warmer SST between May and November or during the summer months of July and August (May–November: $F_{1,\,10} = 1.656$, p = 0.227; July–August: $F_{1,\,10} = 0.00127$, p = 0.972; Figure 17A). Mean SST in July to August across all years was 18.1 °C, and the years 2010, 2011, 2014 and 2018 stood out as years with particularly high mean summer SST (Figure 17B, See Appendix; Figure A3). Maximum SST between 2008 and 2019 occurred in late July and early August (Figure 18, See Appendix; Figure A3), which was also the period when the mean SST were highest.

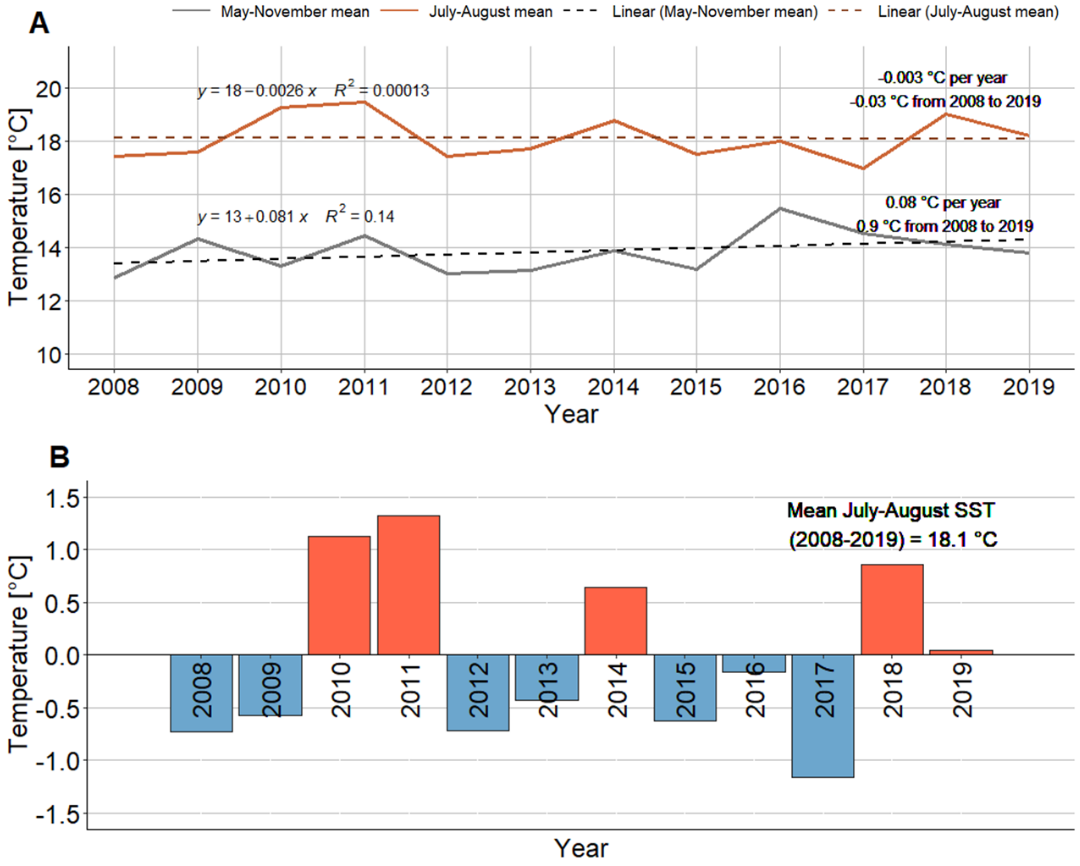


Figure 17. A) The May–November mean SST between 2008 and 2019 from the high-resolution dataset and the SST for the warmest months, July and August (i.e., the experimental period). **B)** The mean SST in July–August between 2008 and 2019 is 18.11 °C and the figure shows the deviation from the mean during each year. The number of conducted measurements varies with missing days in 2008 (21), 2009 (6), 2010 (2) and 2012 (11), see also Figure 6.

3.2.2. Climatology and thresholds

From the 11th of May until the 20th of November, values for the climatology and threshold are calculated (Figure 18) with the baseline period set to 16th of July 2008 to the 15th of July 2019.

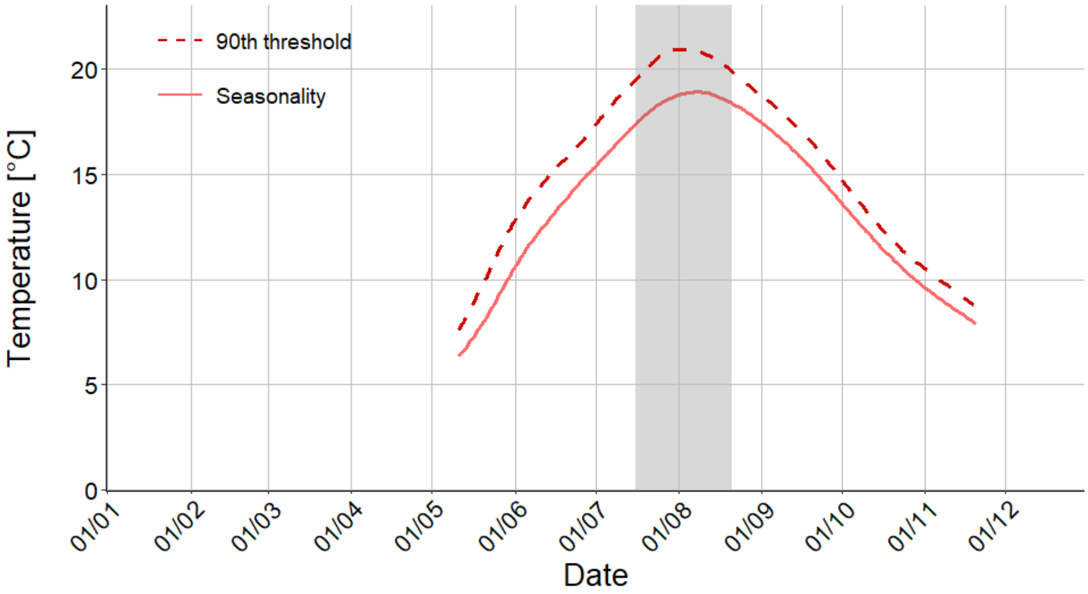


Figure 18. The climatology and threshold (90th percentile) for the high-resolution dataset from the 11th of May until the 20th of November, obtained with the 'heatwaveR' package with the baseline period set to the 16th of July 2008 to the 15th of July 2019. The grey area represents the experimental period.

3.2.3. *Event detection and characterisation*

A total of 14 marine heatwave events were registered in the high-resolution dataset over the period 2008 to 2019 between May and November (see Appendix; Figure A5 and Table A2). The years with the most registered heatwave events were 2011 and 2018, with three events per year each. The frequency and mean intensity of marine heatwave events showed non-significant increases over time (frequency: $F_{1,10} = 2.45$, $p = 0.148$, Figure 19A; mean intensity: $F_{1,12} = 0.0456$, $p = 0.834$, Figure 19B). The duration of marine heatwaves was between 6 and 23 days and showed a non-significant decrease over time ($F_{1,12} = 0.197$, $p = 0.665$; Figure 19C). The month of July (start date) had the most registered marine heatwave events (Figure 19D, see Appendix; Figure A4), and six marine heatwaves (40% of heatwaves registered between May and November) began during the months of July and August (Figure 19D).

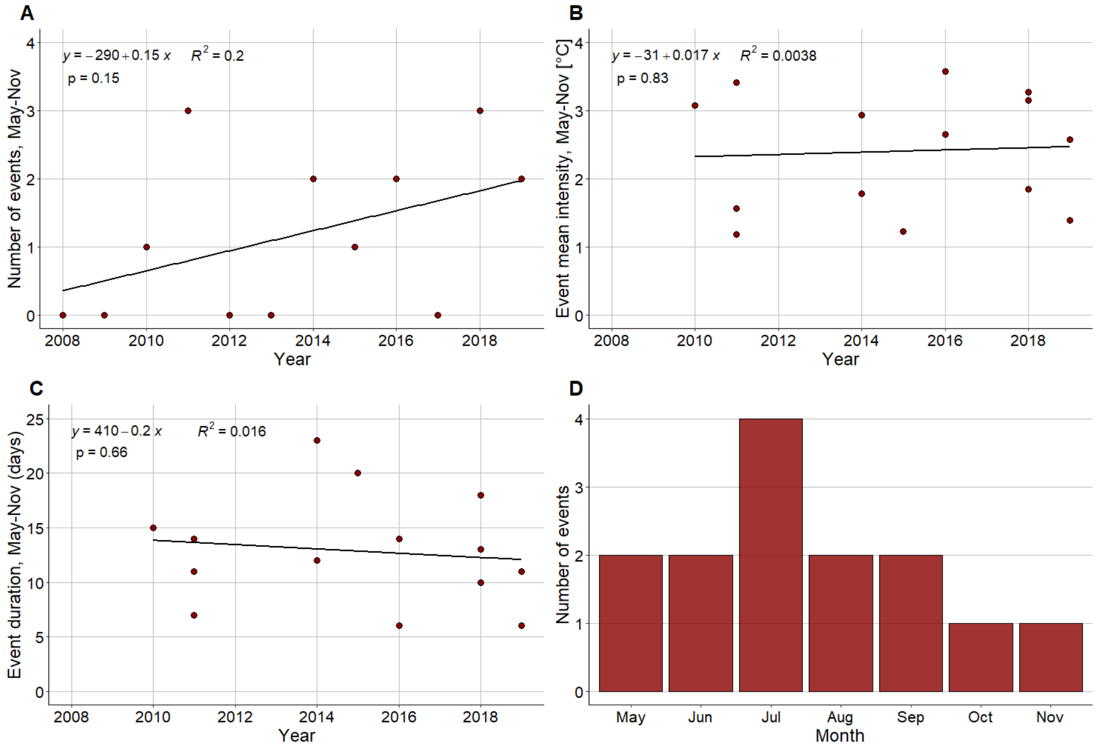


Figure 19. Linear regression on the high-resolution dataset between time and **A**) the number of marine heatwave events per year, **B)** mean intensity of events and **C)** heatwave duration. **D)** The number of heatwaves per month (start date) represented as bar plots.

3.3. Dataset comparison

All days with measurements between 2008 and 2019 during May and November in which both the long-term and high-resolution dataset provided coverage were compared with each other. The temperature measurements lined up almost perfectly (See Appendix; Figure A6). A Pearson correlation analysis was applied to examine the relationship between the means (seasonality) and the 90th percentiles of the long-term and the high-resolution dataset between May 11th and November 20th (Figure 20) which is the period for which both climatologies provide coverage. The climatologies differ from each other, with the high-resolution registering warmer seasonality values, particularly from August onwards, and higher threshold values at the end of July and beginning of August (Figure 20). Nevertheless, the climatologies in the two datasets were significantly correlated ($R^2 = 0.99$, $p < 0.001$) and so were the 90th thresholds ($R^2 = 0.99$, $p < 0.001$). In addition to this, the mean number of detected marine heatwaves per year (1.19 events) in the long-term dataset was almost equal to the mean number of detected marine heatwaves per year in the high-resolution dataset (1.17 events).

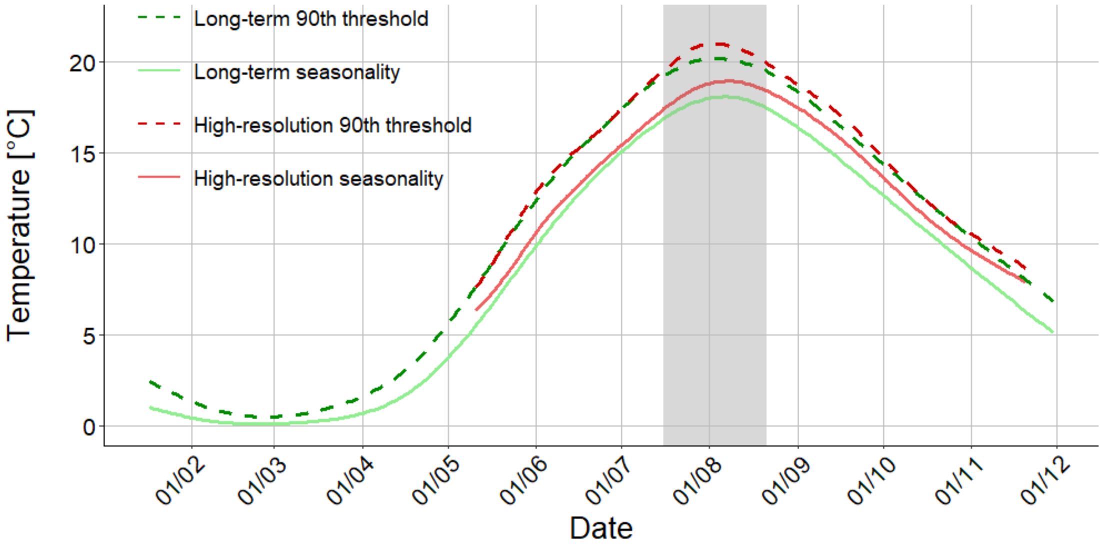


Figure 20. Comparison between the long-term and high-resolution dataset climatologies and 90th thresholds. The grey area represents the experimental period.

During the periods for which both datasets provide coverage, the long-term dataset detected 15 events with a summed duration of 467 marine heatwave days, while the high-resolution dataset detected 14 events with a summed duration of 180 days (Figure 21). With this, the number of days registered as marine heatwaves in the long-term dataset was 160 % higher than the corresponding number of registered days in the high-resolution dataset.

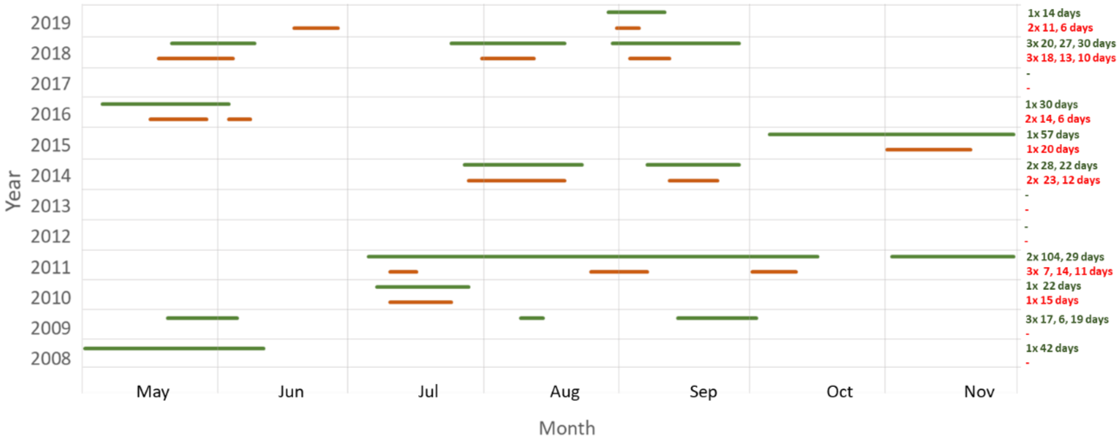


Figure 21. Timing and duration of detected heatwave events in the two datasets (green = long-term dataset, red = high-resolution dataset) in the periods for which both datasets provide coverage.

3.4. Experimental results

3.4.1. *Temperatures over the experimental period*

The intended temperatures for each respective treatment were reached in the experimental units over the course of the experiment (Figure 22). Over the manual measurements, the maximum temperature deviation from an intended temperature in an experimental unit was ±0.3 °C.

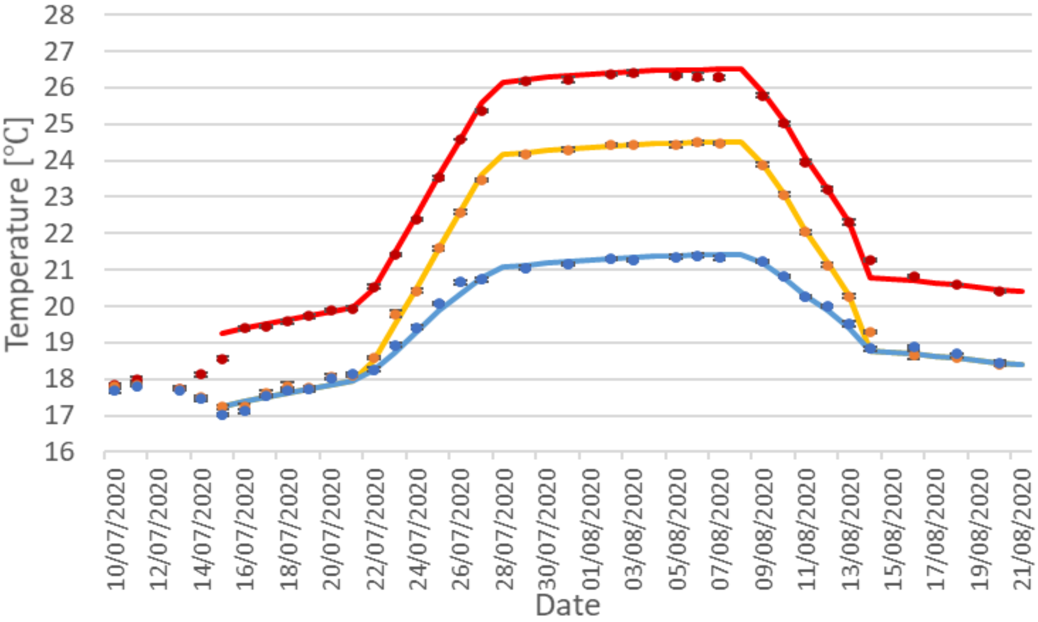


Figure 22. Intended temperatures for the different temperature treatments (*Present* = Blue, *Amplitude* = Yellow, *Intensified* = Red) in lines and the manually measured data as dots. For manually measured data, means over all measured units (N = 9) with SDs are shown.

3.4.2. *Mortality of R. harrisii*

All crabs survived the entire experimental period, although one individual in the *Present* treatment was possibly injured or disabled since it laid on its back for the entire experimental period and did not consume any blue mussels. Although the suboptimal condition of the crab was noted at an early stage, the aquarium was kept in the water bath to not significantly change the flow of water or lighting conditions for the surrounding aquaria. However, this individual was excluded from any further analyses.

3.4.3. *Feeding over the experimental period*

The sum of mussel dry weight consumed over the entire experimental period is not significantly different between treatments ($F_{2, 23} = 0.427$, $p = 0.66$; Figure 23). Mud crabs in the *Amplitude* treatment consumed the least blue mussels on average, although not significantly less per day and over the entire experimental period (Figure 23, see Appendix; Figure A9).

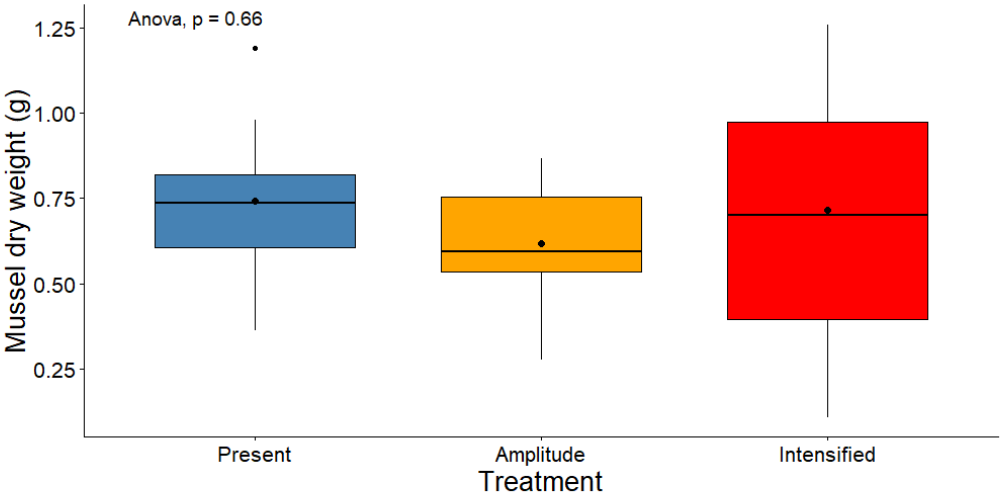


Figure 23. Sum of the dry weight blue mussel consumed by *Rhithropanopeus harrisii* over the 36-day long experimental period. Boxplots display the median, upper and lower quartile (75th and 25th percentile) and whiskers (1.5 times the interquartile range), *Present N = 8, Amplitude N = 9, Intensified N = 9*. The means for each treatment are represented as dots.

The repeated measures ANOVA showed no significant interaction between treatment and time (Treatment*Time: $F_{10.52, 121} = 1.714$, $p = 0.0813$; Figure 24). Yet, there is a significant effect of time without considering the different temperature treatments ($F_{5.26, 121} = 6.783$, $p < 0.001$). Although the combined effect of treatment and time did not yield significant results, the amount of mussel tissue consumed in the *Amplitude* and *Intensified* treatments during the maintained heatwave is higher than during the pre-heatwave and recovery phase (Figure 24).

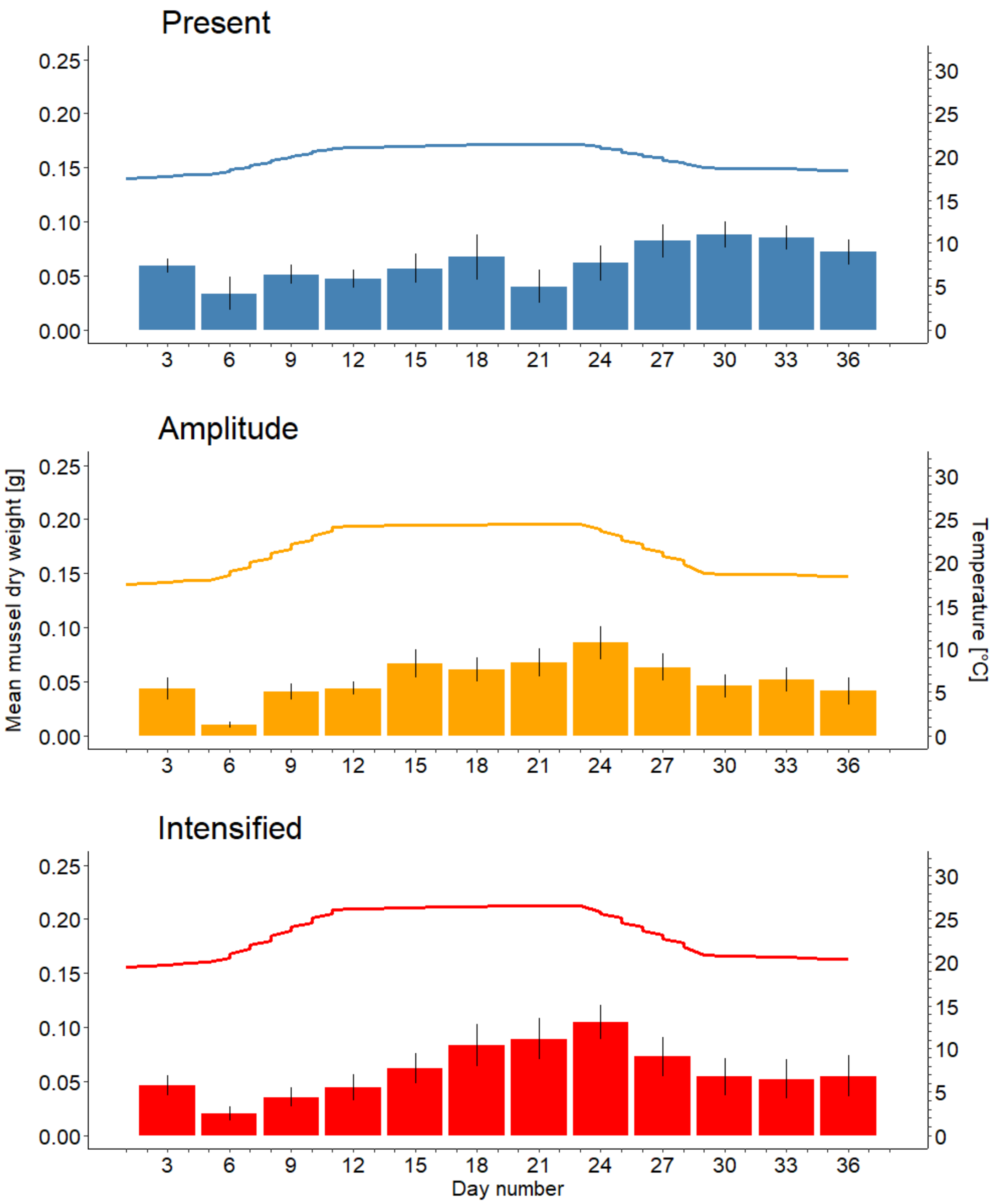


Figure 24. Mussel dry weight consumed by individual *Rhithropanopeus harrisii* during the 36-day long experimental period (*Present* N = 8, *Amplitude* N = 9, *Intensified* N = 9). Error bars show the standard errors of group means.

3.4.4. Size and growth of R. harrisii

The wet weight and carapace width of individuals of *R. harrisii* were evaluated at the end of the experiment. ANOVA on final wet weights and carapace widths did not yield any significant differences between treatment groups (final wet weight: $F_{2, 23} = 1.06$, $p = 0.36$; final carapace width: $F_{2, 23} = 0.583$, $p = 0.57$; see Appendix, Figure A8). The change in wet weight and carapace width over the experimental period was evaluated using the non-parametric Kruskal-Wallis test, since the residuals were not normally distributed. The Kruskal-Wallis test yielded no significant differences for the change in wet weight and carapace width between treatments (change in wet weight: H(2) = 0.438, p = 0.803; change in carapace width: H(2) = 1.92, p = 0.383; Figure 25, A and B).

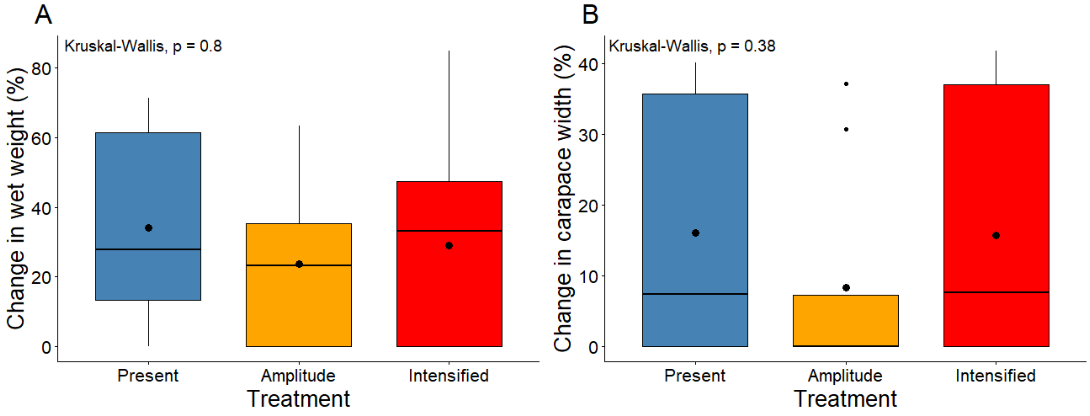


Figure 25. Change in wet weight **(A)** and carapace width **(B)** of *Rhithropanopeus harrisii* in the treatments *Present* (N = 8), *Amplitude* (N = 9) and *Intensified* (N = 9). Boxplots show the median, including the upper and lower quartile. Means are shown as a black dot.

Three (*Present*), two (*Amplitude*) and four (*Intensified*) crabs moulted over the experiment in the treatments, respectively, and changes in the wet weight of *R. harrisii* mainly occur in conjunction with moulting. No significant changes in wet weights of the individuals that did not moult occurred in the treatments over the experimental period (Figure 26).

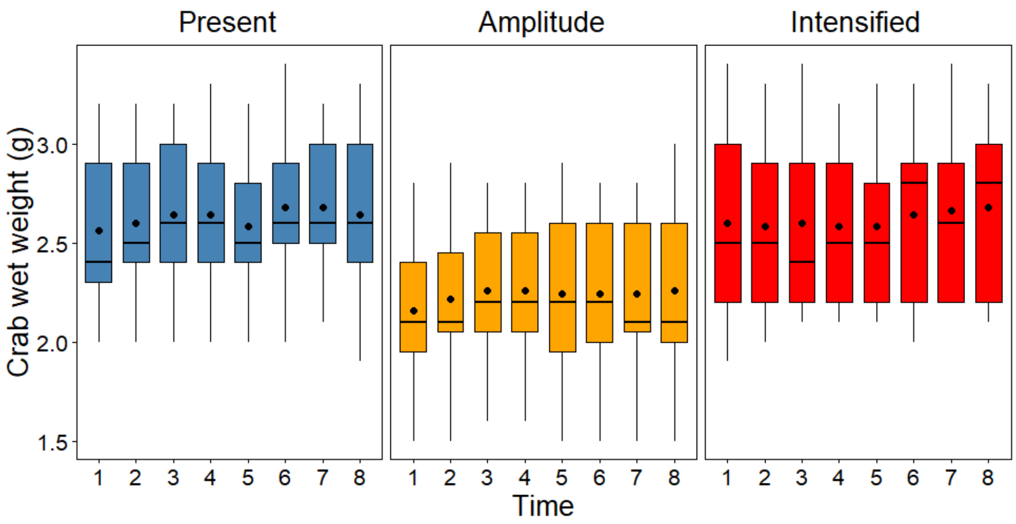


Figure 26. Wet weight of *Rhithropanopeus harrisii* over the experimental period of 36 days in response to the treatments: *Present* (N = 5), *Amplitude* (N = 7) and *Intensified* (N = 5). The wet weight of all individuals was evaluated eight times over the experimental period. Crabs that moulted during the experimental period were excluded from this figure. Boxplots show the median, including the upper and lower quartiles. Mean are shown as black dots.

4. Discussion

4.1. Summary of the main findings

Over the past 52 years, a significant trend towards warmer SST, both, annually and during the summer months of July to August, was observed. The long-term dataset shows a significant increase in the frequency of marine heatwaves over the past 52 years. The mean duration of marine heatwaves was 27.3 days, and the majority of marine heatwave events occurred between May and August (start date). The maximum intensity of a marine heatwave event registered was 5.9 °C above climatology and occurred on the 30th of May 2018 (SST of 15.3 °C). The highest SST ever registered occurred on the 2nd of August 2018 during a marine heatwave event that lasted for 27 days. SST at that time was 23.1 °C (5.1 °C above the daily climatology), and the mean intensity of the event was 3.5 °C.

The high-resolution dataset shows no significant changes in heatwave metrics over the past 12 years. The mean duration of marine heatwaves was 12.9 days, and the month with the most registered heatwaves was July (start date). The maximum intensity of a marine heatwave was 4.9 °C above climatology and occurred on the 3rd of August 2018 (SST of 23.8 °C) during a marine heatwave event with a duration of 13 days and mean intensity of 3.2 °C. This is also the highest SST ever registered in this dataset. The maximum onset and decline rate of a marine heatwave event registered in the high-resolution dataset was 1.2 °C and 0.7 °C per day, respectively.

The output from the high-resolution climatology was further used to determine the baseline conditions and the metrics intensity and duration for the experimental treatments. The temperature treatments were consequently based on events and baseline conditions that *R. harrisii* could have experienced in the field already and in realistic scenarios in the near future.

The overall amount of mussel tissue consumed by *R. harrisii* under the applied heatwave treatments did not vary significantly between treatments, and neither did the overall growth (wet weight and carapace width) of *R. harrisii*. Repeated measures ANOVA found a significant time effect: Generally, mud crabs consumed more mussel tissue as the heatwave progressed, and then gradually decreased feeding as temperatures cooled down.

4.2. Trends in SST and marine heatwave metrics

The increasing trend in SST, both annually (2.44 °C) and during the summer months (1.88 °C) between 1967 and 2018, aligns with reported observations of warming in the Baltic Sea (Mackenzie and Schiedek 2007; Belkin 2009; HELCOM 2013). However, the annual warming trend of the present study might be overestimated due to more missing values in recent decades, particularly so during winter months. The heatwave modelling detected an increase in the frequency of heatwave events over the past 53 years (1967–2019). The mean duration of a marine heatwave increased from 12.7 days to 32.9 days. As the 'heatwaveR' package (Schlegel and Smit 2018) does not account for any existing warming or cooling trends in the dataset (Schlegel et al. 2019), the observed increases in frequency and duration may mainly be explained by the significant warming trend in the dataset (Oliver et al. 2018, 2021; Oliver 2019).

The climatology from the high-resolution dataset gave a very accurate picture of the average conditions and the marine heatwave events that had occurred in the Archipelago Sea during the last 12 years. Still, there was no visible trend in SST between 2008 and 2019, nor in the heatwave metrics, most likely due to the too short coverage of data (Hobday et al. 2016). However, a trend in SST would likely appear as the length of the dataset increases, assuming that the Baltic Sea is warming (Belkin 2009; HELCOM 2013), as seen in the long-term dataset. The measurements from the long-term and the high-resolution datasets overlapped between 2008 and 2019 during May to November, with up to three measurements per month, conducted on the 1st, 11th and 21st (±2–3 days) each month. The temperature measurements were nearly uniform, despite not being conducted during the same time of the day. This uniformity between the datasets in the last decade supports the credibility of the earlier measurements from the long-term dataset, indicating that the significant trend towards warmer surface waters observed in the long-term dataset should not be dismissed despite the low measurement frequency. Climatology for the two datasets were aligned in the first half of the year but from August onwards, the high-resolution climatology deviates and remains slightly warmer for the rest of the climatological period. The threshold values deviate during the warmest period at the end of July and the beginning of August but otherwise align well. These differences can in part be explained by the high-resolution climatology being based on the last decade, a period that has on average registered warmer air (Arneth et al. 2019) and SST (Bindoff et al. 2019) than the decades that preceded it.

4.3. Effects of marine heatwaves on *R. harrisii* (eco-physiological)

The overall consumption of blue mussels by *R. harrisii* under the heatwave treatments did not vary significantly between the treatments, indicating that *R. harrisii* is tolerant to the temperatures that it was exposed to. *R. harrisii* is an ectotherm organism and its physiological processes are therefore affected by changes in their thermal environment (Hartnoll 1982; Deutsch et al. 2008). Hegele-Drywa and Normant (2014) studied the physiological functioning of *R. harrisii* in the Gulf of Gdańsk, and showed that the metabolic rate of *R. harrisii* increased significantly when kept at 20 °C as opposed to 15 °C, with locomotor activity, moulting rate and food consumption also showing detectable changes. The thermal requirement for reproduction and embryotic development for *R. harrisii* has been determined to be around 20 °C (Christiansen and Costlow 1975; Forward 2009; Hegele-Drywa and Normant 2014). In the present study, *R. harrisii* in the different treatments were kept at 21.5 °C, 24.5 °C and 26.5 °C respectively for 13 days, with no significant changes in food consumption or growth being noted, indicating that temperatures above 20 °C do not favour nor harm physiological processes of *R. harrisii*. This is further supported by earlier studies that have shown *R. harrisii* to be tolerant to temperatures between 0–34 °C, or even slightly higher than 34 °C for up to two weeks (Costlow et al. 1966; Turoboyski 1973; Forward 2009). The mussel consumption did not vary significantly over time within the treatments. However, there was a non-significant trend in mussel consumption of *R. harrisii* that followed the thermal regimes applied, showing more mussel consumption and therefore energy uptake with warmer temperatures. This is likely imposed by higher energetic demands at higher temperatures (Doney et al. 2012; Hegele-Drywa and Normant 2014). Growth rates of ectotherms are expected to increase in a warming ocean (Doney et al. 2012) and previous studies show increased metabolic rates and food consumption of *R. harrisii* at higher temperatures (Hegele-Drywa and Normant 2014). Despite strong temperature differences, *R. harrisii* in the warmer treatments neither grew nor consumed significantly more, which could possibly be explained by limited food availability (Doney et al. 2012). The crabs never consumed all provided mussels, but showed a preference for the smaller size classes, with mussels left unopened often belonging to the largest size class provided. The crabs may have opted for the smaller mussels since these require less energy to open than larger mussels with more durable shells that could potentially do damage to their claws (Juanes and Hartwick 1990). Hence, the crabs may have been limited in food and could potentially have consumed a greater number of smaller mussels if these had been provided. There was no significant difference between treatments in the final wet weight or carapace width, nor in the change in wet weight or carapace width over the experimental period. The experimental period might have been too short to detect the growth of *R. harrisii*, seeing as increases in carapace width occurs in conjunction with moulting only, which adult crabs usually undergo only once per year (Turoboyski 1973). Moulting also affects feeding since crabs stop eating a few days prior to moulting (Turoboyski 1973), but despite this, the overall consumption was higher (non-significant) in the treatments with more moulting crabs (*Intensified* and *Present*).

4.4. Implications for marine life in the Archipelago Sea

Species with high degree of tolerance towards environmental stress are favoured in the Baltic Sea (Bonsdorff et al. 1996; Bonsdorff and Pearson 1999), and this trait can often also be found in successfully established invasive species (Sareyka et al. 2011; Bates et al. 2013). Species of varying environmental tolerances and origin are found in the brackish Baltic Sea (Kautsky and Kautsky 2000; Ojaveer et al. 2010) and although *R. harrisii* appears to remain unaffected, many other species in the Archipelago Sea will most probably suffer from the heat stress associated with marine heatwaves (Roth et al. 2010; Takolander et al. 2017; Pansch et al. 2018). Additionally, responses to gradual changes in abiotic variables (Rousi et al. 2019) or extreme events (Pansch et al. 2018) are species-specific, or even intra-specific (Reusch et al. 2005; Lago-Lestón et al. 2010). The capacity of marine heatwaves or heat stress to alter ecosystems by shifting species abundance or community composition (Sorte et al.

2010) thus depends on species-specific temperature tolerances and optima (Wahl et al. 2020), but also on the potential of species to adapt to higher temperatures (Nasrolahi et al. 2016; Vajedsamiei et al. 2021).

The heat stress associated to marine heatwaves may be detrimental to sessile cold-water species inhabiting coastal waters. For example, blue mussels (*Mytilus spp.*) are abundant and have an important role in benthic and pelagic ecosystems (Westerbom et al. 2002), and bladderwrack (*Fucus vesiculosus*) is an important foundation species providing functions and structure to the coasts (Kautsky et al. 1992; Wikström and Kautsky 2007). The seagrass *Zostera marina* has an important structural and functional role on soft bottoms in the Baltic Sea (Boström and Bonsdorff 1997; Boström et al. 2014), and in the Archipelago Sea, it mainly reproduces asexually through clonal growth (Boström et al. 2014). In *Z. marina*, the genetic diversity is central to its resilience towards marine heatwaves (Reusch et al. 2005; Ehlers et al. 2008). These species all in large part inhabit the depths most susceptible to warming (Boström and Bonsdorff 1997; Kautsky and Kautsky 2000). *Mytilus spp.* inhabiting coastal waters in the Baltic Sea are experiencing temperature stress, since energetic balance for *M. trossulus* turns unfavourable at 17°C (Westerbom et al. 2019). These temperatures are exceeded in the Archipelago Sea during the summer months (see Appendix; Figure A3) and on top of that, *M. trossulus* in the Archipelago Sea is presently living at the edge of its tolerance with respect to salinity (Westerbom et al. 2002). These combined effects may cause increased mortality for *M. trossulus* during warm periods in summer (Westerbom et al. 2019).

The invasion of the heat tolerant *R. harrisii* may have implications on Baltic Sea ecosystems and affect the abundance of organisms across many trophic levels (Lokko et al. 2018). For example, the crab could, as a burrower, effectively rework sediment through bioturbation (Lokko et al. 2018). In soft bottom habitats such as eelgrass habitats, this can potentially affect the functioning of the eelgrass community (Gagnon and Boström 2016). Engström (2020) demonstrated that the burrowing behaviour of *R. harrisii* disturbs the eelgrass through uprooting of eelgrass shoots. A study of littoral hard bottom macroinvertebrate communities from the northern Baltic Proper suggests that *R. harrisii* is already decreasing the prey species diversity and richness through its predatory behaviour (Forsström et al. 2015). Jormalainen et al. (2016) showed that the presence of *R. harrisii* has led to a decrease in amphipod and isopod populations associated with the *Fucus* community.

R. harrisii prefers to prey upon small- and medium-sized prey, suggesting that the crab could potentially alter the prey population size structure (Forsström et al. 2015). Crabs are mobile but generally not good hunters, as they only move around along the bottom and sudden movements are not part of their nature. Hence, they tend to feed on sessile organisms, macrophytes or detritus (Bourdeau and O'Connor 2003), but blue mussels also represent a likely prey. However, previous studies in the Archipelago Sea suggest that *R. harrisii* might prefer soft shelled crustaceans over *M. trossulus* (Forsström et al. 2015; Engström 2020), and other crab species have shown similar preferences (Buck et al. 2003). Crabs might avoid hard shells because of the risk of craw damage (Juanes and Hartwick 1990), however, blue mussels in the northern Baltic are dwarfed by the low-salinity conditions and have thinner shells (Kautsky et al. 1990; Riisgård et al. 2014) which implies a decreased shell stability and hence a lower pressure is needed to break the shells (Kossak 2006). The only real predators on blue mussels in the Archipelago Sea is the Eider duck, *Somateria molissima* (Kautsky and Kautsky 2000; Westerbom et al. 2002) and the Roach, *Rutilus rutilus* (Lappalainen et al. 2004), and *R. harrisii* may intensify the predation pressure on *M. trossulus*. The European green crab, (*Carcinus maenas)* has experimentally been shown to prevent recruitment of juvenile *M. edulis* in the North Sea, due to their efficiency as predators (Christie et al. 2020). Similarly, increased predation pressure by *R. harrisii* may cause a threat to blue mussel beds and to mussel recruitment since they are known to prefer predating upon the smaller mussels (Forsström et al. 2015; Engström 2020). *R. harrisii* migrates towards warmer surface waters during summer (Hegele-Drywa and Normant 2014), and the coastal mussel beds that are already weakened by heat stress (Kossak 2006; Westerbom et al. 2019) might then represent attractive foraging areas.

The introduction of a non-indigenous species can also have minimal or even positive effects on the recipient ecosystem, and in the Baltic Sea a non-indigenous species contributes to more functional- and species diversity (Olenin et al. 2017). In the Archipelago Sea, *R. harrisii* adds to a functional diversity that is already present rather than bringing in something completely new (Aarnio et al. 2015). Added diversity can be seen as positive, but in the case of a widely successful invader it also contributes to the homogenization of ecosystems, meaning that differences in species composition between regions is reduced (Olden et al. 2004). Invasive crabs commonly impact native communities via predation (Grosholz and Ruiz 1996), but community impacts of a crab may also as much occur if the invader serves as a preferred prey for native consumers. *R. harrisii* is consumed by common predators, such as the Eurasian perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*) and fourhourned sculpin (*Myoxocephalus quadricornis*) (Fowler et al. 2013), and in this way contributes to secondary production. It is likely that heat tolerant non-indigenous species such as the investigated mud crab will perform better than native species when exposed to the SST changes and fluctuations expected with climate change (Sorte et al. 2010). Yet, whether *R. harrisii* will benefit from the warming conditions in the Baltic Sea in any way remains to be seen and potentially tested in mesocosm experimental studies in the Archipelago Sea.

4.5. Methodological strengths and limitations

At present, there are no projections for marine heatwaves for the Archipelago Sea. Yet, the treatments applied in this study are realistic, with motivated baselines and, in the case of the first two treatments, amplitudes that already can be seen in the high-resolution dataset. There have been other experimental studies in the Baltic Sea that have based treatments on historical climate data to evaluate how organisms or marine communities are affected by extreme events. Pansch et al. (2018), for instance, evaluated the effect of marine heatwaves on benthic communities and Saha et al. (2020) looked at responses to heatwave among foundation macrophytes. Here, the authors used metrics from 15-years of temperature data recorded from the Kiel Fjord, Germany (Western Baltic Sea), to define their treatments for the experimental approach based on rates of increase and decrease in SST. The methods used to determine the baselines and treatments for the experimental approach in this study resemble the ones applied by Morón (2018), who extracted climatology using the 'heatwaveR' package, from a dataset containing 37 years of SST measurements from Tjärnö, Sweden, and applied these values as a baseline for the treatments. Similarly, the high-resolution dataset climatology was used as a baseline for two of my treatments, with the third treatment starting at an offset of +2 °C, which is a likely future scenario given the projected SST rise in the Baltic Sea (BACC II Author Team

2015). Consequently, the base conditions applied were temperatures that *R. harrisii* could experience in the field now and in realistic scenarios in the future (HELCOM 2013; Meier and Saraiva 2020). The treatment amplitudes and durations as applied by Moron (2018) were extracted and verified from mean metrics in the climatological data. Similarly, the mean metrics for duration and mean intensity in the Archipelago Sea were applied for my first treatment, *Present.* In fact, marine heatwaves with the temperature (±1 °C) applied in the *Present* treatment (21.5 °C) have occurred at the Seili sampling station between July and August in 2010, 2011, 2014 and 2018 respectively.

There are advantages of only basing treatments on local meteorological data, since this keeps treatments realistic to what individual organisms are likely to experience in their environment. The drawback with an exclusively climatological approach is that the physiological traits of the study species are not taken into consideration when defining the treatments. In the current study, it could have been valuable to also account for physiological traits of *R. harrisii*, such as metabolic rates and moulting (Turoboyski 1973; Hegele-Drywa and Normant 2009, 2014), when defining the treatments. This, given that *R. harrisii* is ectothermic, and there was a probability that the projected extreme temperatures in the Baltic Sea would not affect the study species. In addition, changes in the wet weight and carapace width of *R. harrisii* mainly occur in conjunction with moulting (Turoboyski 1973), and hence, these were not ideal response variables. Furthermore, it was not ideal to use an eurythermal study species to evoke a response to temperature. On the other hand, there is at present few studies on this invasive species in Archipelago Sea and this study supports previous observations of Baltic Sea populations of *R. harrisii* being unaffected by extreme temperatures (Turoboyski 1973; Hegele-Drywa and Normant 2014).

The datasets used in the present study had limitations, being suboptimal for heatwave modelling as mentioned in section 2.1.3. Additionally, when the long-term dataset was interpolated, the raw data was in two cases manipulated. This resulted in two events of extreme amplitudes being registered (see Appendix, Figure A2, Table A1, years 1975 and 2015). Importantly, the inclusion of these events did not change the results from the regressions on the long-term dataset in any significant way. Generally, the duration of marine heatwaves in the long-term dataset is probably overestimated, especially so in recent decades. This is partly due to the long-term dataset being based on only a few measurements, with values interpolated (see 2.1.3) and because of the warming trend (Schlegel et al. 2019). It may also be because of the 90th percentile (threshold value) being lower and, hence, comparably lower temperatures may qualify as a marine heatwave event, especially during summer. Yet, the climatology and the marine heatwave events detected by the high-resolution dataset accurately illustrate the realized marine heatwaves that have occurred in the Archipelago Sea. However, it might be that only the most extreme events are registered with this shorter period and more minor events would be registered if the baseline was longer, since it can be assumed that there has been a long-term warming trend as seen in the long-term dataset (Schlegel et al. 2019). There might even be more events between 2008 and 2019 of lesser intensity, that were not registered by this dataset due to the short baseline, or the events registered might actually be of greater intensity.

The experimental design could have been improved with more replicates per treatment, and by placing replicates in separate blocks. However, this was not possible due to constraints in laboratory space and equipment. Over the course of the experiment, individuals of *R. harrisii* were fed 12 times at 72-hour intervals. In feeding 1 and 2, the number and size classes of the provided mussels deviated from the other feeding events (see Table 1), with a total of ten mussels with two from each size class (2–6; see Table 1) being provided in feeding 1, and a total of six mussels with one from each size class (2–7; see Table 1) in feeding 2. This was applied because not enough mussels of the correct size class had been collected. Although feeding 1 and 2 differed from the rest, none of the crabs in these two feedings ever came close to consuming all provided mussels, so the food was not limited with the total dry weight of mussels provided being even higher than in the successive feedings (feeding 3–5, see section 2.3.4.3). The consumed dry weight for the crabs in these feedings was calculated using the same method as for the other feeding events.

4.6. Considerations for future research

Temperature time series can be used to detect and characterise past marine heatwave events and to illustrate local temperature variations. Similar analyses that were applied in this thesis could be applied to other time series around the Baltic Sea, particularly in highly productive coastal regions where often good long-term and high-resolution datasets are missing. By using the definition for heatwaves by Hobday et al. (2016), coherent and comparable results can be obtained and an idea of the spatial extent of past events and regions that have been or are likely to be particularly affected can be formed.

Future studies should examine the community responses to marine heatwaves in the northern Baltic Sea, to provide insight into the shifts occurring in ecosystems and to interactions between species. Furthermore, the possible consequences for Archipelago Sea species and communities resulting from both marine heatwaves and generalist non-indigenous species (like *R. harrisii)* should be considered

4.7. Referring to the initial research questions and hypotheses

A common marine heatwave in the Archipelago Sea lasts for 13 days and has an amplitude of 2.4 °C above climatology (Q1a), and both the mean SST and the frequency of marine heatwaves have increased significantly over the last 52 years (Q1b). The impact of marine heatwaves on *R. harrisii*, did not increase with increasing heat intensity (Q2a). Overall, it can be assumed that heatwaves in the Archipelago Sea with the amplitudes applied in the treatments will not harm the recent invader *R. harrisii*, which contradicts my hypotheses H2a and H2b. Since the crabs showed no overall negative effect, the recovery of the mud crabs after the different marine heatwave events was not measurable, and the hypothesis concerning the potential for recovery (H2c) could not be examined in a meaningful way.

5. Conclusions

The results show that the Archipelago Sea SST is warming at a rate of 0.47 °C per decade with the frequency of marine heatwaves also significantly increasing over the last 52 years. Since mean warming is found to be the main driver of the increasing frequency (and duration and amplitude) of marine heatwaves (Oliver 2019), these events will likely have more pronounced impacts on the Baltic Sea in the near future.

R. harrisii seems to be tolerant to the simulated marine heatwaves of current and near-future amplitudes, indicated by the lack of impact on their consumption of blue mussels and their growth. Possibly, the energy uptake during the simulated marine heatwaves could have been used to compensate for heat stress but despite the possible metabolic costs, *R. harrisii* will most probably have an advantage over species that are less tolerant or harmed by heat stress (Sorte et al. 2010; Sareyka et al. 2011). The responses to marine heatwaves may largely be species-specific (Pansch et al. 2018) but have ecosystem-wide consequences (Sorte et al. 2010; Wernberg et al. 2013; Smale et al. 2019). On top of the changes that increased mean SST and marine heatwaves may bring about, the invasion of *R. harrisii* may affect various Archipelago Sea habitats (Gagnon and Boström 2016; Jormalainen et al. 2016). Hence, the effects of marine heatwaves and invasive species on Archipelago Sea communities should be examined, both separately and the possible interactive effects, to gain insight on the ecosystem shifts caused by increasing SST and marine heatwaves, and how this affects species interactions, of native or non-indigenous nature.

6. Ethical considerations

At the end of the experiment, all *R. harrisii* were put down using methods that minimise the amount of stress experienced by the organism. This is done since *R. harrisii* is a non-indigenous species and according to regulations set by the European parliament and of the council (2014), these cannot intentionally be let lose into the environment.

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Swedish summary – Svensk sammanfattning

Identifiering av marina värmeböljor och experimentell undersökning av deras effekter på den främmande arten slamkrabba i Skärgårdshavet

I samband med den pågående klimatförändringen förväntas medelvärdena för ett antal abiotiska variabler i havet (såsom ytvattentemperatur, havsvattennivå, pH-värde och salinitet) förändras (Bindoff et al. 2019). Globalt förväntas dessutom en ökning i såväl frekvensen som varaktigheten för extrema klimathändelser (Bates et al. 2018), till exempel marina värmeböljor. En marin värmebölja definieras som en period på fem eller flera på varandra efterföljande dagar då havsvattentemperaturen överstiger den 90:e percentilen. Detta värde bestäms utifrån lokal klimatologi, och denna baserar sig vanligtvis på minst 30 år av historiska temperaturdata (Hobday et al. 2016). Klimatforskning har hittills till stor del fokuserat på gradvis skiftande medelvärden. Ändå kan en ökad variation, såsom en högre frekvens och kraftigare intensitet av extrema klimathändelser, kan utgöra ett större hot mot arter och ekosystem, eller till och med förstärka effekten av skiftande medelvärden (Helmuth et al. 2014; Vasseur et al. 2014).

Klimatförändringen och introduktion av främmande arter anges bland de största hoten mot biologisk mångfald (Halpern et al. 2008; Sorte et al. 2010) och i nuläget har 195 vattenlevande arter som förekommer i Östersjön klassificerats som introducerade (AquaNIS 2021). Slamkrabban, *Rhithropanopeus harrisii* (Gould 1841) härstammar från Nordamerikas ostkust (Williams 1984), och påträffades i södra Östersjön redan under 1950-talet (Turoboyski 1973). Slamkrabban observerades första gången i Skärgårdshavet år 2009 (Karhilahti 2010), och den har sedan dess etablerat sig och spridit sig snabbt till flera olika habitat (Fowler et al. 2013; Gagnon and Boström 2016; Jormalainen et al. 2016; Engström 2020). Slamkrabban är en opportunistisk mesopredator, och i Skärgårdshavet kan slamkrabban utnyttja ett flertal tillgängliga födokällor, till exempel blåmusslor (*Mytilus trossulus*), och flera arter av märlkräftor och snäckor (Turoboyski 1973). Predatorer har en strukturerande effekt på organismsamhällen, och introducerade predatorer kan ha en särskilt stark inverkan på Östersjöns ekosystem, som byggs upp av relativt få arter och hyser enbart ett fåtal arter i varje ekologisk nisch (Elmgren and Hill 1997; Micheli and Halpern 2005;

Jormalainen et al. 2016). Så här långt har inga experimentella studier utförts kring slamkrabbans känslighet för marina värmeböljor i Skärgårdshavet. Syftet med denna avhandling är att 1) identifiera tidigare värmeböljor i Skärgårdshavet och modellera framtida värmeböljors styrka, baserat på data från två olika databaser över ytvattentemperatur från Själö i Nagu (*N° 60.255278; E° 21.951028*) och att 2) genom akvarieexperiment i Skärgårdshavet undersöka slamkrabbans respons på marina värmeböljor av olika intensitet (en marin värmebölja med genomsnittlig nutida intensitet, en marin värmebölja med ökad temperatur med utgångspunkt i databasernas registrerade högsta amplitud och en marin värmebölja med modellerad temperaturökning för framtiden med ett uppvärmt grundscenario, se figur 10).

Frågeställningarna i avhandlingen är:

1a: Vad kännetecknar en typisk marin värmebölja i Skärgårdshavet med avseende på dess varaktighet och intensitet?

1b: Har medelvärdet för ytvattentemperaturen och frekvensen av marina värmeböljor ökat i Skärgårdshavet under de senaste dryga 50 åren?

2a: Har marina värmeböljors styrka i Skärgårdshavet betydelse för den introducerade slamkrabban, *R. harrisii*?

2b: Kan *R. harrisii* återhämta sig efter en simulerad marin värmebölja, och beror återhämtningsförmågan på värmeböljans intensitet?

Denna avhandling utnyttjar både ett långsiktigt dataset med låg upplösning (1966–2019) och ett kortare dataset (2006–2019) med hög upplösning för att extrahera naturliga variationer i ytvattentemperaturer i Skärgårdshavet och för att identifiera gångna tiders marina värmeböljor samt deras karaktär. Data från modelleringen av de båda dataseten analyserades i R (version 3.6.3, R Core Team 2020), med "heatwaveR" (Schlegel and Smit 2018) som är en "package" som innehåller funktioner som räknar ut och åskådliggör marina värmeböljor enligt definitionen av Hobday et al. (2016). En daglig klimatologi och en lista över detekterade marina värmeböljor levereras av funktionerna. Klimatologin och den 90:e percentilen från datasetet med hög upplösning användes sedan som bas för de experimentella behandlingarna i avhandlingens praktiska del. Trender i ytvattentemperaturen över tid och trender hos marina värmeböljor (deras varaktighet, frekvens och medelintensitet) analyserades med linjär regression.

Den experimentella delen av avhandlingen pågick i totalt 36 dagar (16.7–21.8.2020) och bestod av tre behandlingar som baserade sig på resultat från de existerande dataseten och den statistiska modelleringen (figur 10). Varje behandlingsgrupp bestod av nio replikat (akvarier) och varje akvarium innehöll en slamkrabba av storleken 16–20 mm. De olika behandlingarna utsattes för simulerade marina värmeböljor av tre olika intensiteter (maximal temperatur: 21,5 °C, 24,5 °C och 26,5 °C för de respektive behandlingarna: genomsnittlig nutida intensitet, ökad temperatur med utgångspunkt i de existerande databasernas registrerade högsta amplitud samt framtida modellerad hög temperatur med ett uppvärmt grundscenario). Akvarierna placerades i tre vattenbad där varje akvarium innehöll en halv terracotta-kruka och konstgjort ålgräs som fungerade som strukturer och gömställen för slamkrabborna. Slamkrabborna utfodrades med 72 timmars mellanrum med blåmusslor av storleken 12,5–20 mm (skallängd). Tillväxt hos slamkrabborna (våtvikt i gram och ryggsköldsbredd i millimeter) och födointag (torrvikt blåmussla efter torkning i 80 °C i 24 timmar) användes som responsvariabler. Data från akvarieexperimentet analyserades i R med hjälp av variansanalyser (ANOVA). Envägs-ANOVA användes för att upptäcka statistiskt signifikanta skillnader i tillväxt och födointag mellan behandlingarna och en ANOVA med upprepade mätningar (eng. repeated measures ANOVA) för att testa om behandlingarna hade någon effekt på slamkrabbornas födointag över de tolv utfodringstillfällena, både inom och mellan behandlingarna. Statistiskt signifikanta övergripande resultat följdes upp med *post hoc* Tukey-test för att klargöra inom och mellan vilka behandlingar och mätningstillfällen som det förekom skillnader.

Globalt sett utgör Östersjön ett av de havsområden där ytvattentemperaturen för tillfället stiger snabbast (Mackenzie and Schiedek 2007; Belkin 2009; Meier and Saraiva 2020). En regressionsanalys på långtids-datasetet visar en signifikant stigande trend för ytvattentemperaturen i Skärgårdshavet, och eftersom temperaturökning är en av de främsta drivkrafterna bakom en ökad frekvens (tillsammans med varaktigheten och intensiteten) av marina värmeböljor (Oliver 2019), kommer detta sannolikt att påverka Östersjön allt tydligare inom en snar framtid. Regressionsanalyserna som utfördes på de registrerade marina värmeböljorna i det långsiktiga datasetet (53 år) visar en statistiskt signifikant ökning av frekvensen av marina värmeböljor över tid. Värmeböljornas varaktighet visar en svagt ökande trend över tid, medan värmeböljornas medelintensitet är svagt minskande, även om dessa båda variabler är icke-signifikanta. Majoriteten av de marina värmeböljor som registrerats i det långsiktiga datasetet inträffade under månaderna maj–augusti (startdatum) och medelvaraktigheten var 27,3 dagar med en medelintensitet (som °C över normaltemperaturen) på 2,59 °C. Regressionsanalyserna som utfördes på data från det högupplösta datasetet (12 år) visar inga signifikanta förändringar för varken frekvensen, medelintensiteten eller varaktigheten av värmeböljor över tid. I det högupplösta datasetet har juli månad flest registrerade värmeböljor (startdatum), medan medelvaraktigheten för de marina värmeböljorna är 12,9 dagar och medelintensiteten 2,41 °C varmare än klimatologin.

Slamkrabbornas totala konsumtion av blåmusslor varierade inte signifikant mellan behandlingarna under experimentets gång även om det tycktes finnas en trend för att krabborna i den mellersta temperaturökningen (maximal temperatur 24,5 °C) konsumerade färre blåmusslor än i de andra behandlingarna. Resultaten från ANOVAn med upprepade mätningar visar ingen signifikant skillnad mellan eller inom behandlingarna över tid. Trots detta syns skillnader mellan de olika utfodringstillfällena, främst inom den kraftigaste temperaturökningen, där slamkrabborna konsumerade fler musslor i takt med att värmeböljan framskred och sedan gradvis minskade sin konsumtion när temperaturen sjönk igen (figur 24). Samma mönster kan delvis observeras i den mellersta temperaturökningen (maximal temperatur 24.5 °C). Tidigare studier har visat att slamkrabbans metabolism och födointag ökar vid 20 °C (Hegele-Drywa and Normant 2014), men resultaten från den praktiska delen av min studie indikerar att högre temperaturer inte ökar ytterligare på slamkrabbans konsumtion. Förändringar i våtvikt och ryggsköldsbredd (%) över tid för *R. harrisii* skilde sig inte signifikant mellan de olika behandlingarna. Eftersom slamkrabborna i de olika behandlingarna inte uppvisade någon negativ respons till följd av en värmebölja kunde återhämtningsförmågan inte fastställas.

Extrema händelser såsom marina värmeböljor påverkar levande organismers fysiologi och deras tillväxt, reproduktion och överlevnad och kan driva förändringar i artsammansättning och biodiversitet, och till och med förändra ekosystemens struktur och funktion (Wernberg et al. 2013). Slamkrabban förblir troligtvis i rätt hög grad opåverkad i den framtida Östersjön med såväl högre medeltemperaturer (HELCOM 2013) som fler och intensivare värmeböljor, medan mindre toleranta arter, bland dessa också många infödda arter, kan komma att drabbas negativt (Pansch et al. 2018). Det finns fortfarande få experimentella studier kring marina värmeböljor och deras effekter på arter och samhällen, både globalt och i Östersjön. Den förväntade ökade frekvensen och intensiteten av marina värmeböljor (Oliver et al. 2018) innebär dock att det kommer att behövas allt fler studier kring olika effekter på både infödda och introducerade marina arter för att klarlägga vad som kan ske med arterna själva och hur interaktionerna mellan olika arter och mellan arterna och deras miljö kan komma att förändras i ett framtida hav.

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Appendix

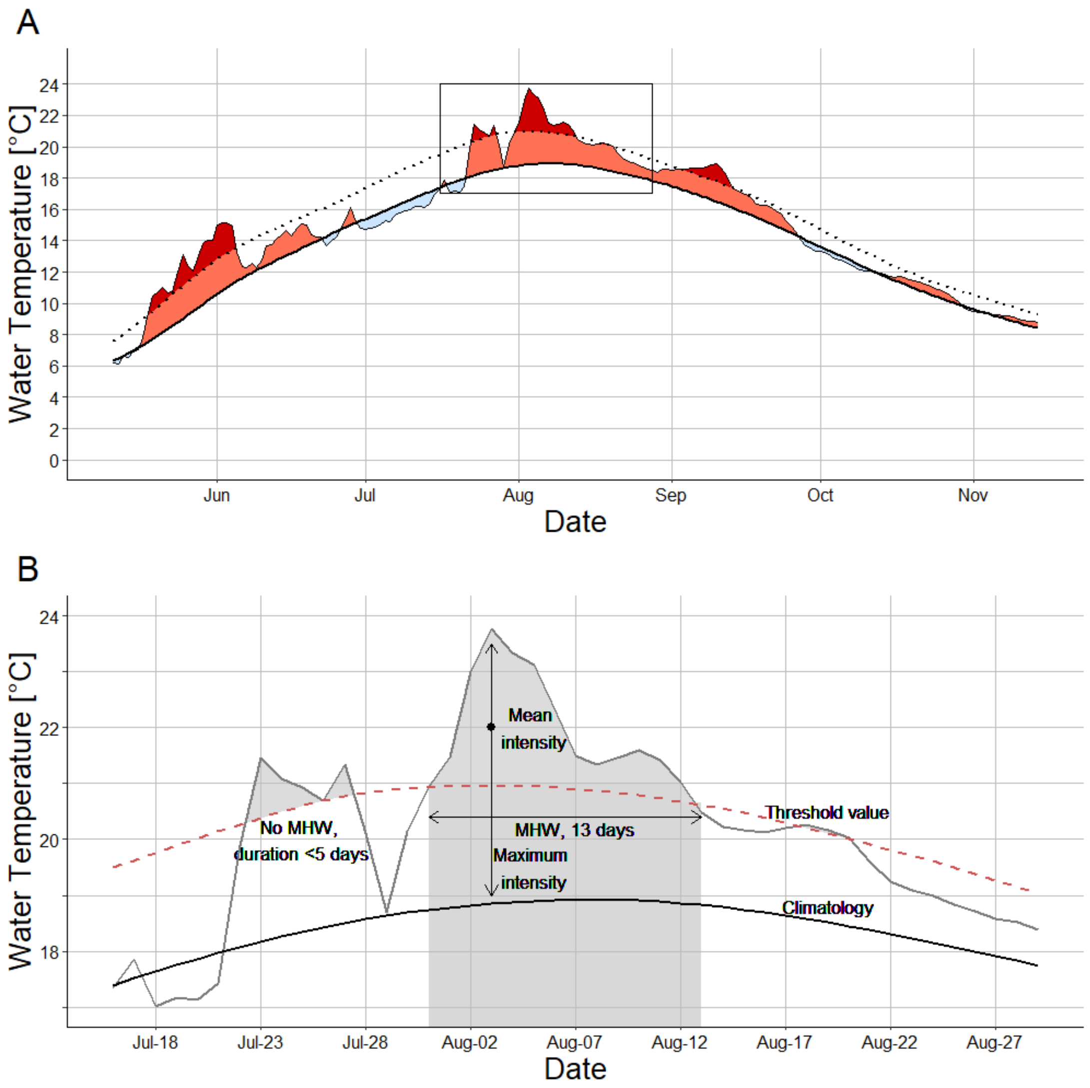
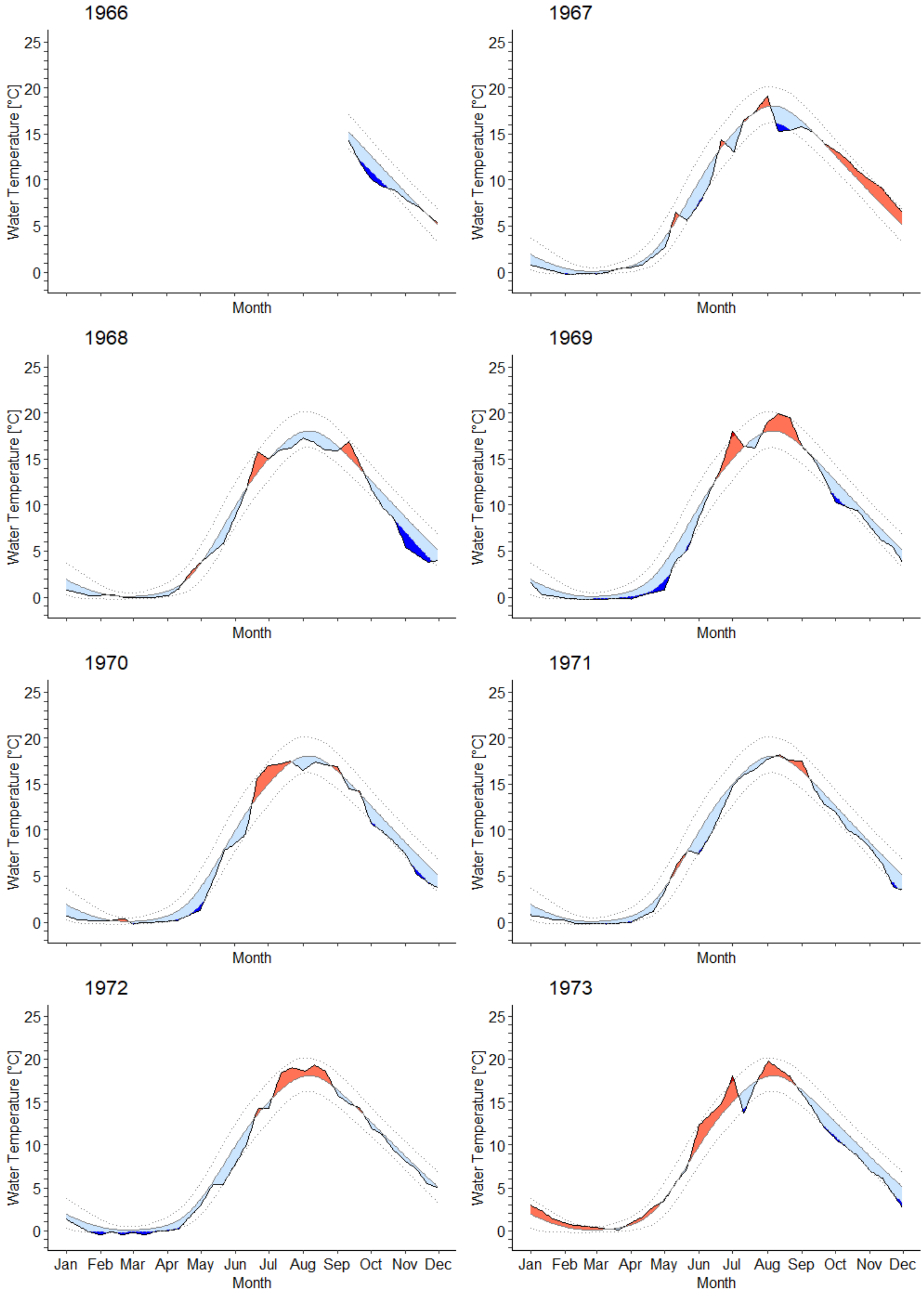


Figure A1. Representation of marine heatwave metrics from a 2018 marine heatwave event at Seili, Archipelago Sea. **A)** The 90th percentile values are the thresholds for a marine heatwave event, and these vary through the year (dotted line), as does the climatological mean (solid black line). The squared off box is the area displayed in figure B. **B)** Temperatures that exceed the threshold value for less than five days are not considered marine heatwaves (*sensu* Hobday et al. 2016). The metrics used in my thesis are mean intensity and maximum intensity, which are given as °C above the climatological mean and duration, given as number of days.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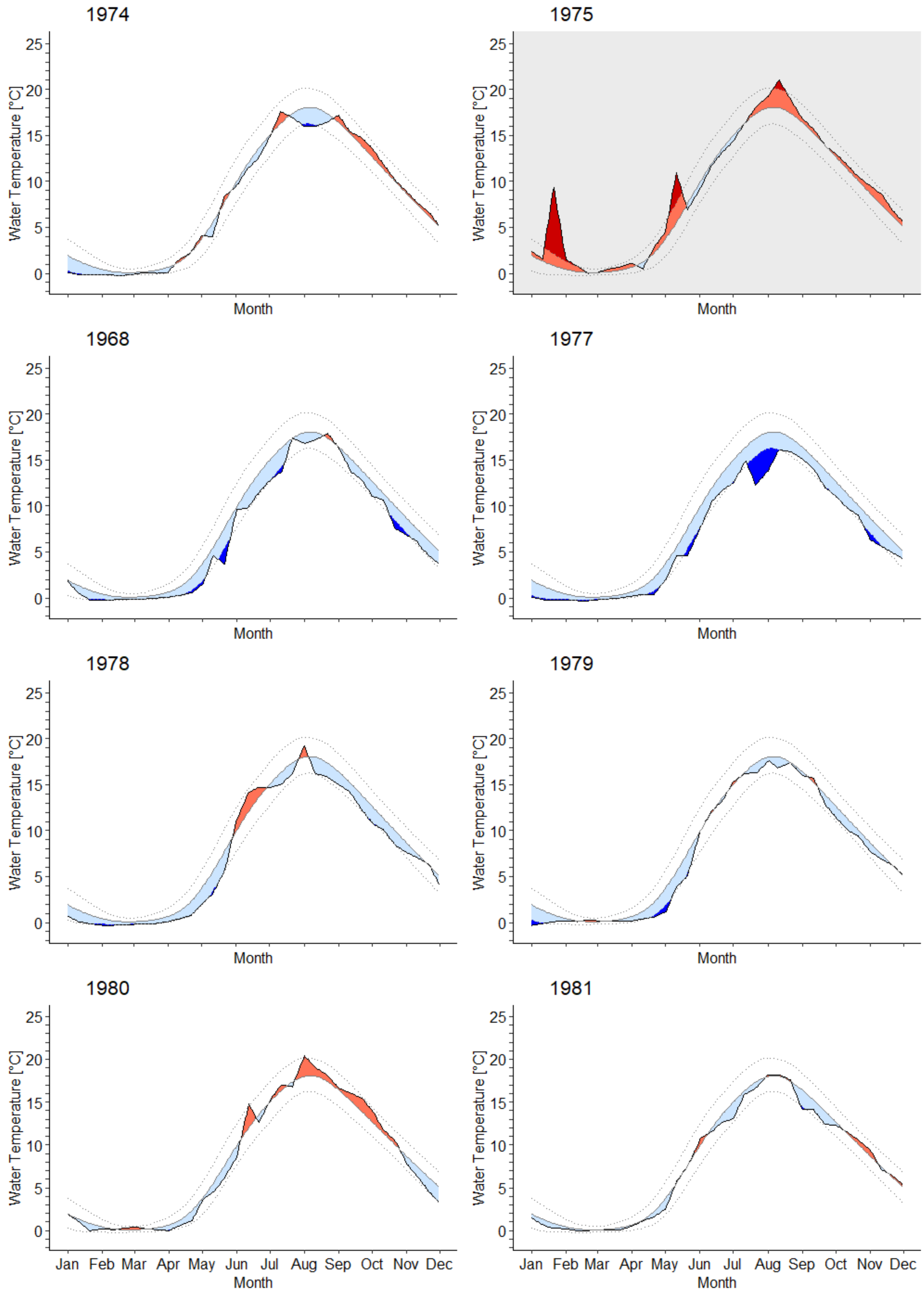
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Water Temperature [°C]
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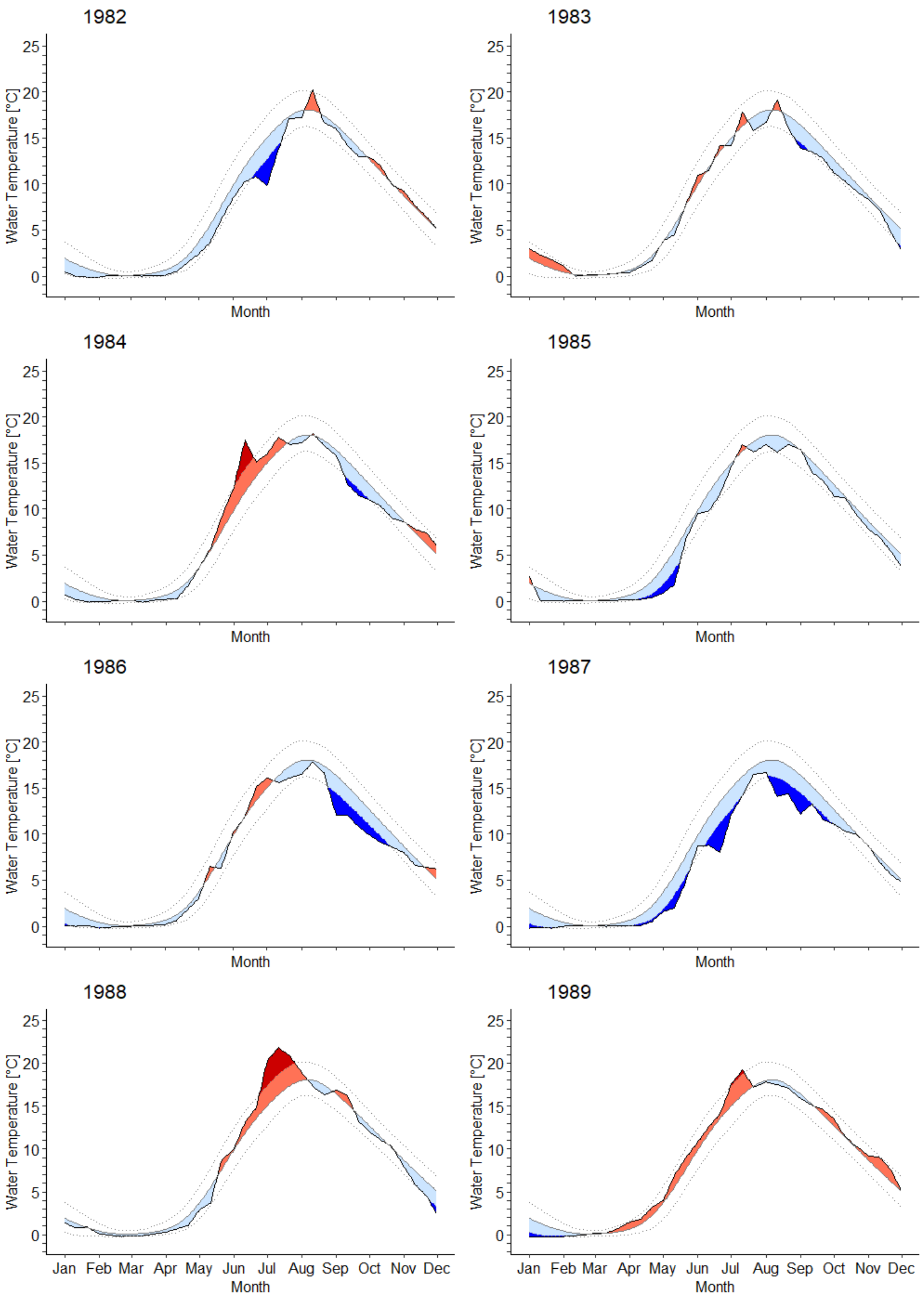
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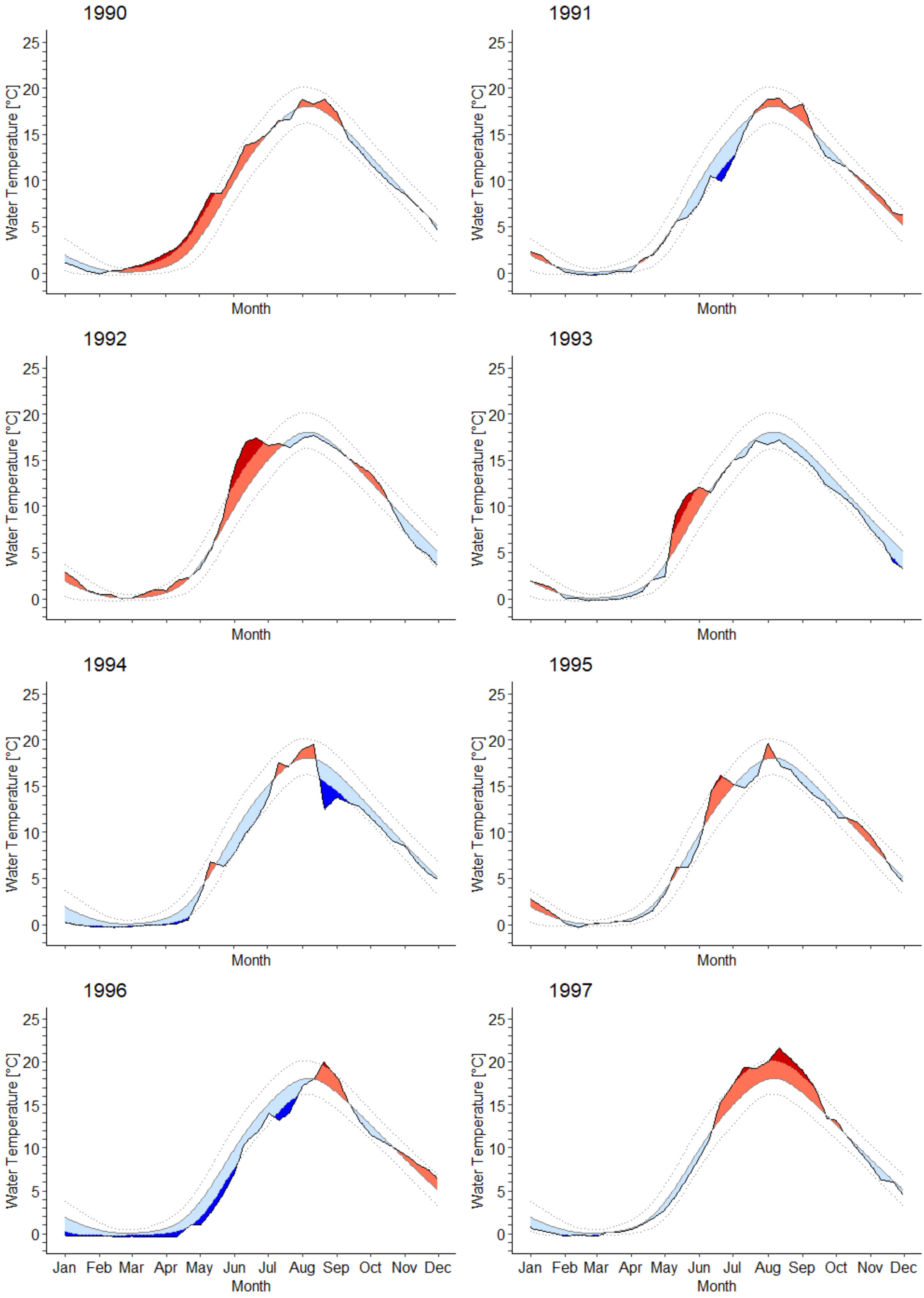
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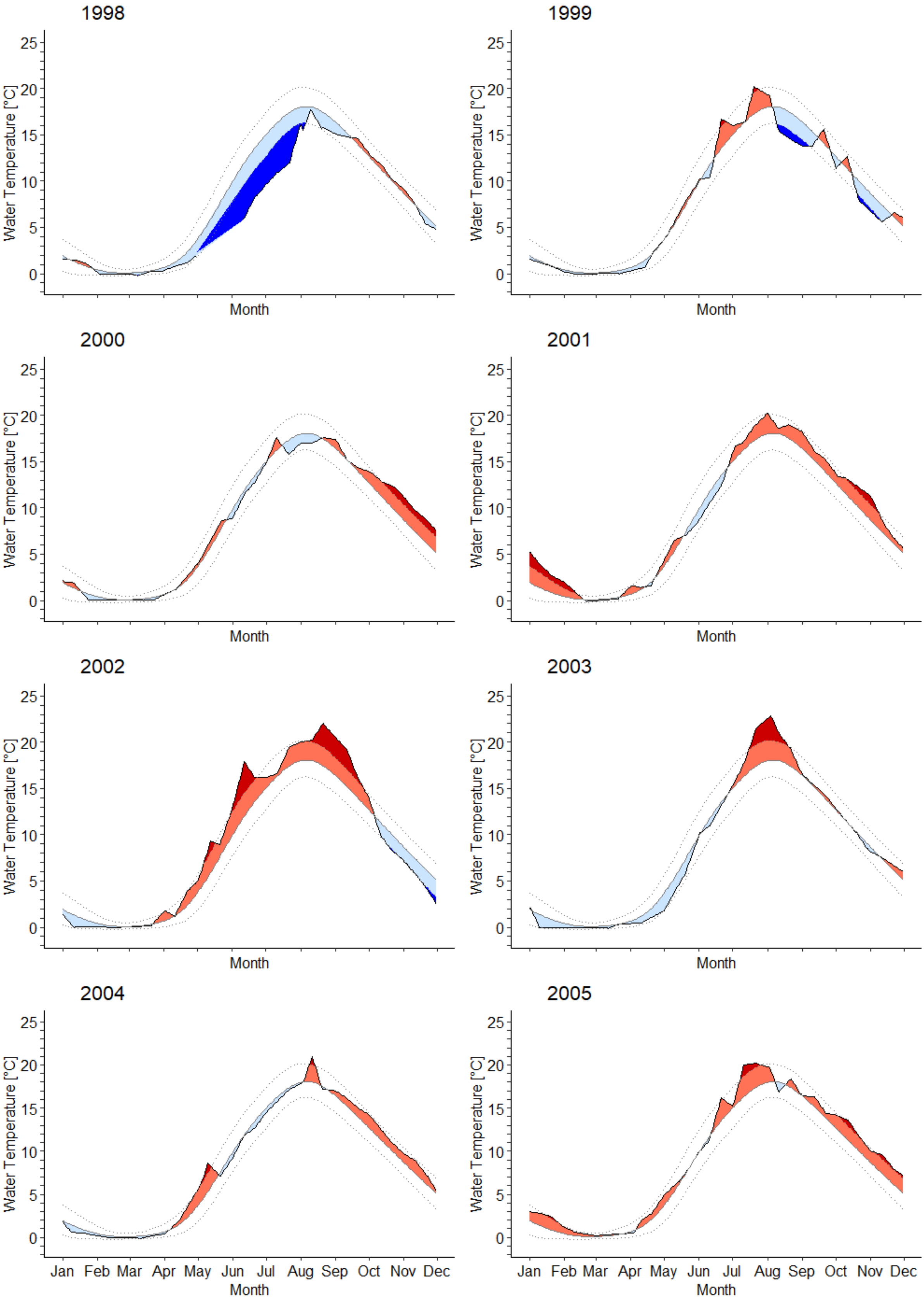
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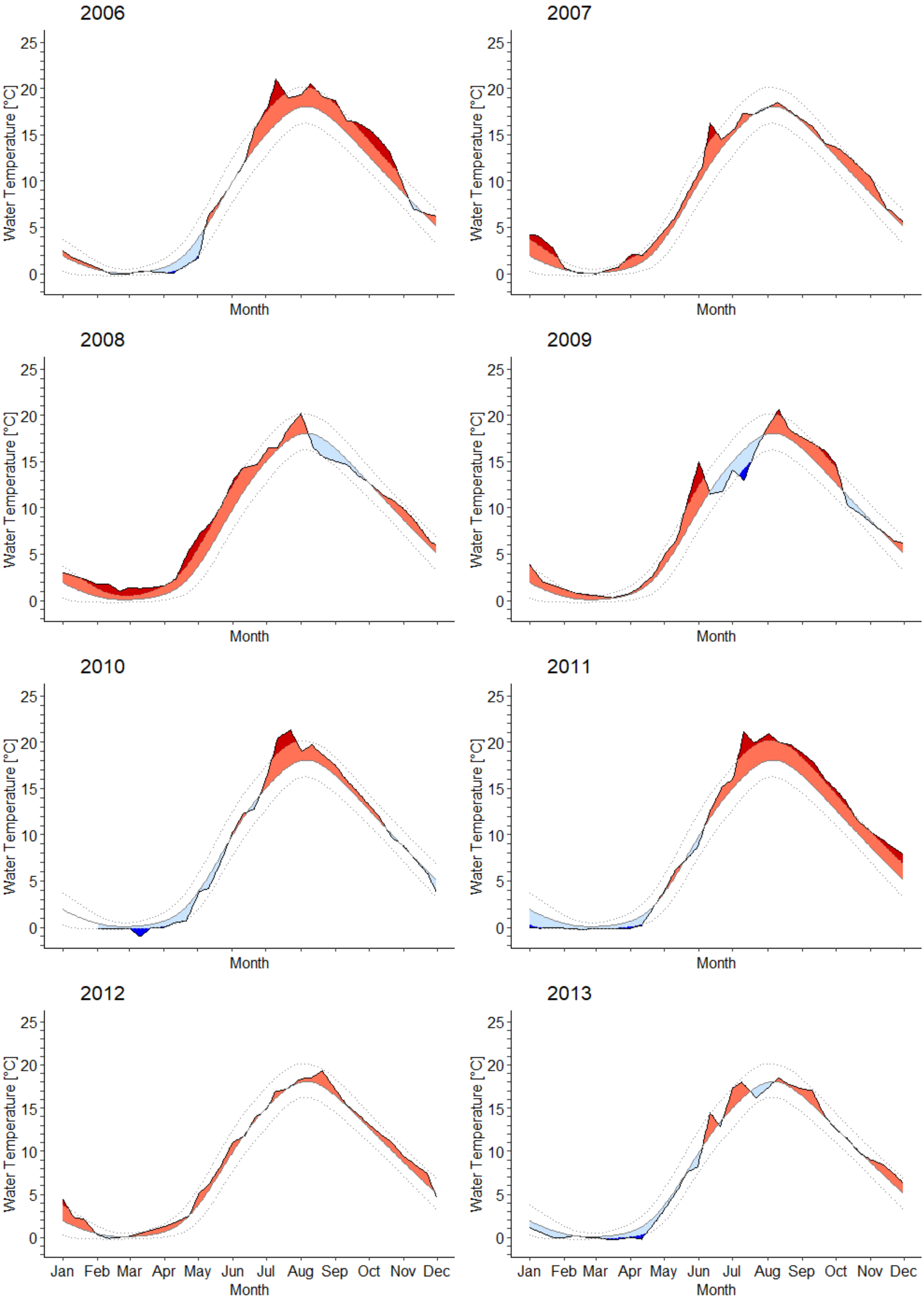
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Water Temperature [°C]
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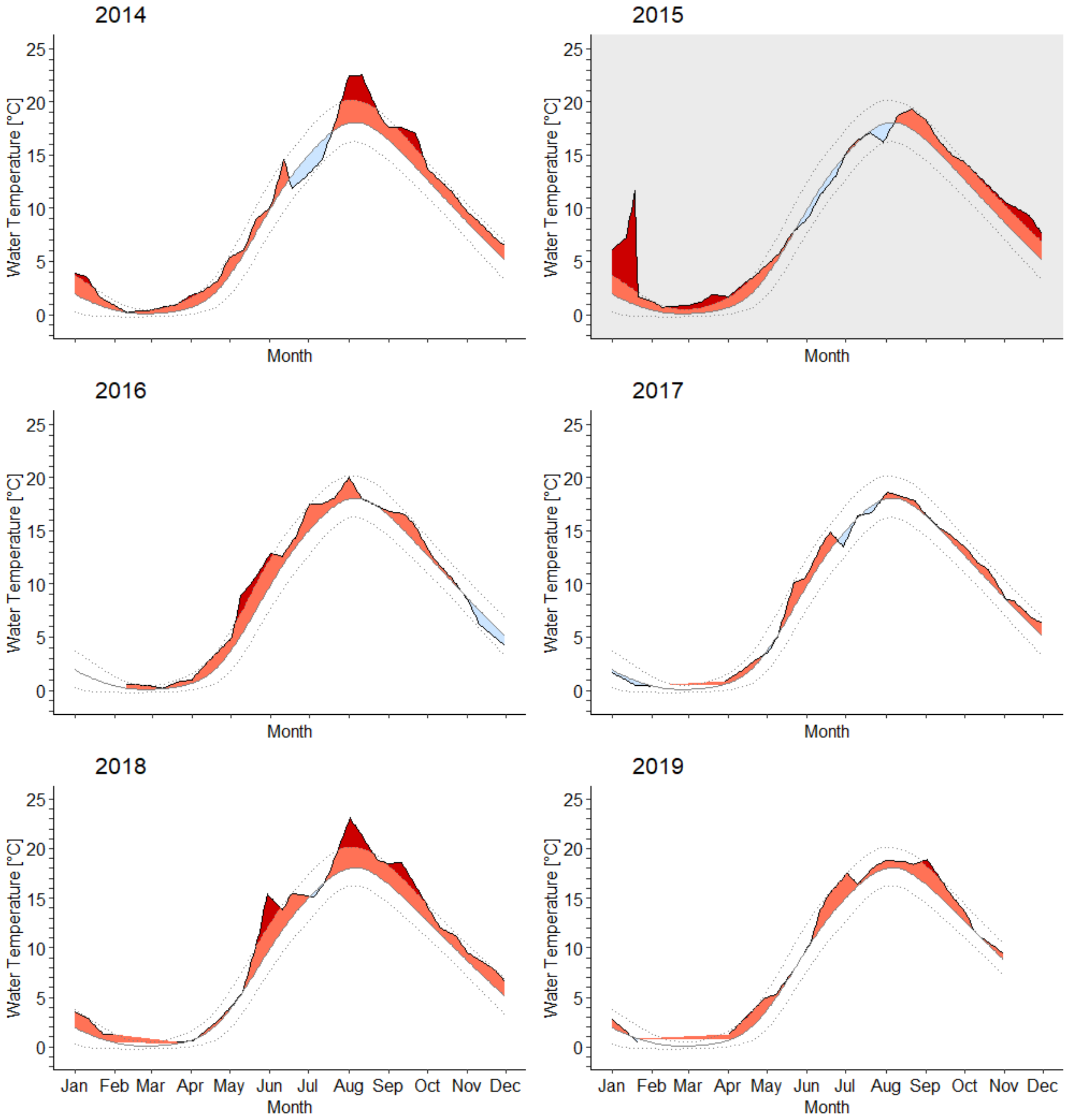


Figure A2. Event lines for marine heatwaves between 1966–2019 retrieved from the long-term dataset using the R package ‘heatwaveR’ (Schlegel and Smit 2018). The black line represents the actual measured temperature each year. The upper grey dotted line represents the 90th percentile and the lower dotted line represents the 10th percentile. Seasonality is demonstrated as the black line between the thresholds. Red = above the 90th percentile (registered as a marine heatwave event by the ‘heatwaveR’ package software if the temperature remains above this level for five or more consecutive days), orange = between the seasonality and 90th percentile, light blue = between the seasonality and 10th percentile, dark blue = below the 10th percentile. Years that include events that are overestimated due to interpolation errors are displayed in grey.

Table A1. Event output for the long-term dataset. Events that are overestimated due to interpolation errors (one measurement in January 1975 from 2 °C to 9.6 °C, and another measurement in January 2015 was changed from 1.7 °C to 11.7 °C) are displayed in grey.

Event number	Duration (days)	Start date	Peak date	End date	Mean intensity (°C)	Max intensity (°C)	Onset rate (°C per day)	Decline rate (°C per day)
1	6	09/11/1967	11/11/1967	14/11/1967	1.75	1.80	0.04	0.03
2	5	29/06/1969	01/07/1969	03/07/1969	2.65	2.98	0.25	0.29
3	5	28/06/1973	01/07/1973	02/07/1973	2.65	2.98	0.18	0.57
4	30	13/01/1975	21/01/1975	11/02/1975	3.49	8.52	0.82	0.37
5	13	04/05/1975	11/05/1975	16/05/1975	3.79	5.49	0.47	0.61
6	11	07/08/1975	11/08/1975	17/08/1975	2.52	3.00	0.19	0.15
7	7	09/12/1982	11/12/1982	15/12/1982	2.09	2.37	0.23	0.14
8	18	01/06/1984	11/06/1984	18/06/1984	4.07	5.69	0.30	0.41
9	33	24/06/1988	11/07/1988	26/07/1988	4.33	5.51	0.19	0.22
10	13	30/06/1989	11/07/1989	12/07/1989	2.69	2.91	0.06	0.32
11	79	26/02/1990	11/05/1990	15/05/1990	1.58	3.09	0.04	0.20
12	32	27/05/1992	11/06/1992	27/06/1992	4.12	5.19	0.17	0.17
13	23	08/05/1993	20/05/1993	30/05/1993	3.37	3.83	0.13	0.13
14	10	12/06/1995	20/06/1995	21/06/1995	2.69	2.83	0.05	0.25
15	9	19/08/1996	20/08/1996	27/08/1996	2.24	2.49	0.31	0.07
16	16	01/07/1997	11/07/1997	16/07/1997	2.72	3.11	0.07	0.13
17	41	03/08/1997	11/08/1997	12/09/1997	2.76	3.60	0.16	0.06
18	5	20/06/1999	21/06/1999	24/06/1999	2.80	3.17	0.47	0.23
19	6	19/07/1999	20/07/1999	24/07/1999	2.63	2.95	0.38	0.15
20	124	12/10/2000	02/01/2001	12/02/2001	2.38	3.34	0.02	0.07
21	30	10/10/2001	01/11/2001	08/11/2001	2.17	2.64	0.04	0.13
22	12	06/05/2002	13/05/2002	17/05/2002	2.74	3.39	0.19	0.26
23	25	30/05/2002	12/06/2002	23/06/2002	4.00	5.90	0.25	0.32
24	50	07/08/2002	21/08/2002	25/09/2002	3.42	4.57	0.17	0.08
25	36	16/07/2003	04/08/2003	20/08/2003	3.59	4.86	0.12	0.17
26	12	02/05/2004	10/05/2004	13/05/2004	2.57	3.28	0.16	0.33
27	5	09/08/2004	11/08/2004	13/08/2004	2.53	3.00	0.39	0.39
28	15	15/01/2005	21/01/2005	29/01/2005	1.39	1.57	0.01	0.07
29	19	08/07/2005	11/07/2005	26/07/2005	3.02	3.71	0.36	0.09
30	21	04/10/2005	12/10/2005	24/10/2005	2.00	2.38	0.07	0.06
31	32	05/11/2005	11/11/2005	06/12/2005	1.96	2.20	0.09	0.02
32	23	26/06/2006	10/07/2006	18/07/2006	3.31	4.83	0.17	0.29

33	8	08/08/2006	10/08/2006	15/08/2006	2.24	2.48	0.15	0.09
34	9	27/08/2006	01/09/2006	04/09/2006	2.14	2.32	0.07	0.11
35	41	16/09/2006	11/10/2006	26/10/2006	2.64	3.05	0.05	0.09
36	34	25/12/2006	09/01/2007	27/01/2007	2.18	2.66	0.05	0.09
37	12	26/03/2007	02/04/2007	06/04/2007	1.16	1.39	0.08	0.06
38	10	07/06/2007	11/06/2007	16/06/2007	3.46	4.49	0.48	0.36
39	8	25/10/2007	01/11/2007	01/11/2007	1.69	1.74	0.01	0.12
40	77	17/01/2008	11/02/2008	02/04/2008	1.25	1.62	0.01	0.01
41	61	12/04/2008	03/05/2008	11/06/2008	2.69	3.26	0.10	0.02
42	14	21/12/2008	31/12/2008	03/01/2009	1.98	2.10	0.02	0.09
43	26	06/02/2009	06/02/2009	03/03/2009	0.57	0.73	-0.02	0.01
44	17	20/05/2009	01/06/2009	05/06/2009	3.83	5.14	0.21	0.55
45	6	09/08/2009	11/08/2009	14/08/2009	2.31	2.60	0.21	0.18
46	19	14/09/2009	22/09/2009	02/10/2009	2.09	2.29	0.05	0.07
47	22	07/07/2010	12/07/2010	28/07/2010	3.53	4.09	0.29	0.11
48	104	05/07/2011	11/07/2011	16/10/2011	2.52	4.81	0.39	0.03
49	66	02/11/2011	01/12/2011	06/01/2012	2.41	2.84	0.04	0.03
50	18	29/12/2013	10/01/2014	15/01/2014	1.99	2.22	0.03	0.13
51	14	04/03/2014	17/03/2014	17/03/2014	0.52	0.59	0.01	0.00
52	16	22/03/2014	02/04/2014	06/04/2014	0.99	1.14	0.04	0.01
53	28	27/07/2014	11/08/2014	23/08/2014	3.65	4.50	0.14	0.20
54	22	07/09/2014	22/09/2014	28/09/2014	2.54	3.19	0.09	0.24
55	44	08/12/2014	19/01/2015	20/01/2015	4.22	10.78	0.21	4.96
56	66	13/02/2015	20/03/2015	19/04/2015	1.12	1.59	0.03	0.01
57	78	05/10/2015	21/12/2015	21/12/2015	2.35	3.08	0.02	3.08
58	30	05/05/2016	09/05/2016	03/06/2016	3.18	3.77	0.37	0.05
59	20	21/05/2018	30/05/2018	09/06/2018	4.09	5.95	0.37	0.33
60	27	24/07/2018	02/08/2018	19/08/2018	3.55	5.10	0.29	0.17
61	30	30/08/2018	11/09/2018	28/09/2018	2.59	3.39	0.12	0.09
62	15	10/04/2019	23/04/2019	24/04/2019	1.48	1.62	0.03	0.01
63	14	29/08/2019	02/09/2019	11/09/2019	2.27	2.63	0.15	0.08

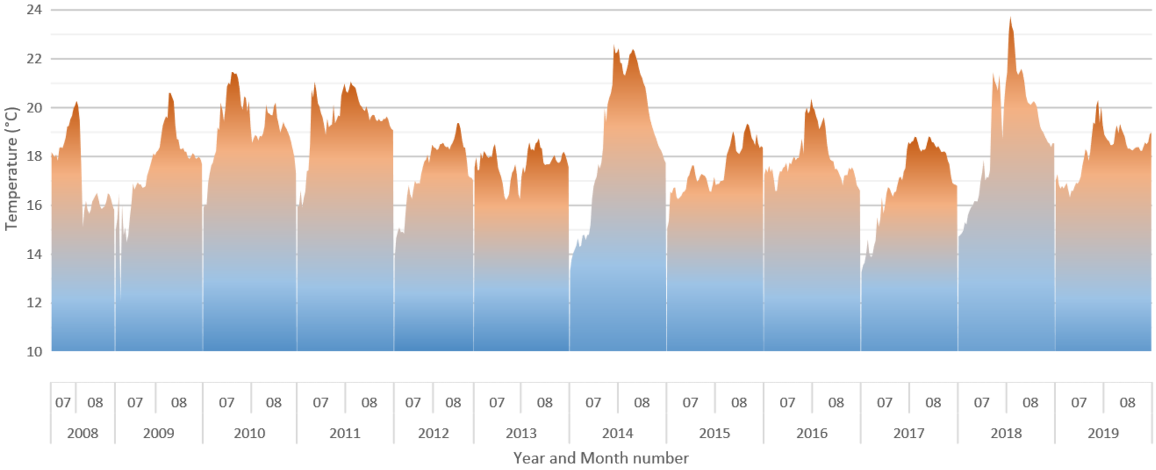


Figure A3. The variability in temperature at five metre depth in July and August between 2008 and 2019. The years 2014 and 2018 have the highest recorded temperatures.

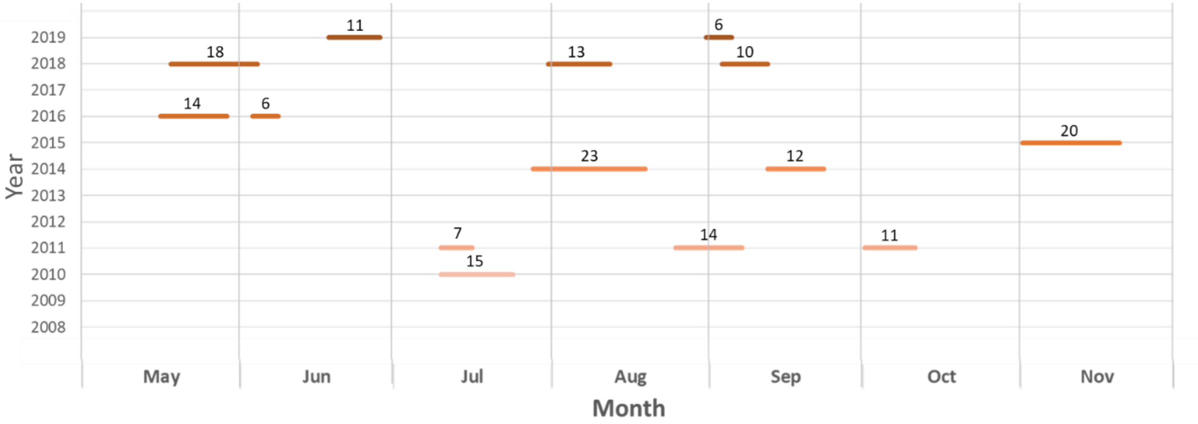
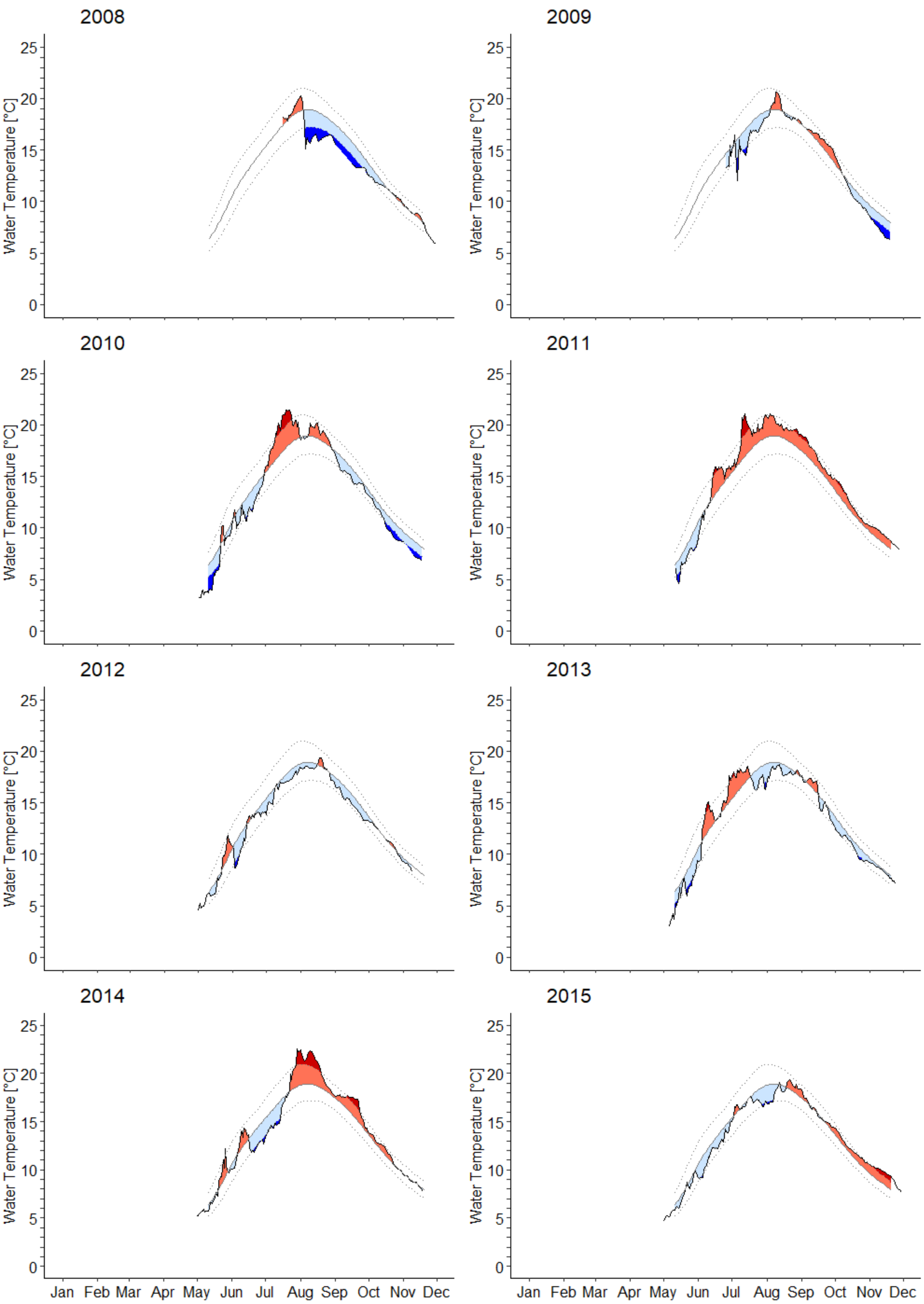


Figure A4. The timing and duration of registered marine heatwaves in the high-resolution dataset during the period 2008 to 2019 between May and November. Heatwaves had lengths between 6 and 23 days and the years with the most days with temperatures registering as marine heatwaves are 2018 and 2011, which are also the years with the most heatwave events (three events, respectively).


2008
2009
2010
2011
2012
2013
2014
2015
Water Temperature [°C]
0
5
10
15
20
25
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

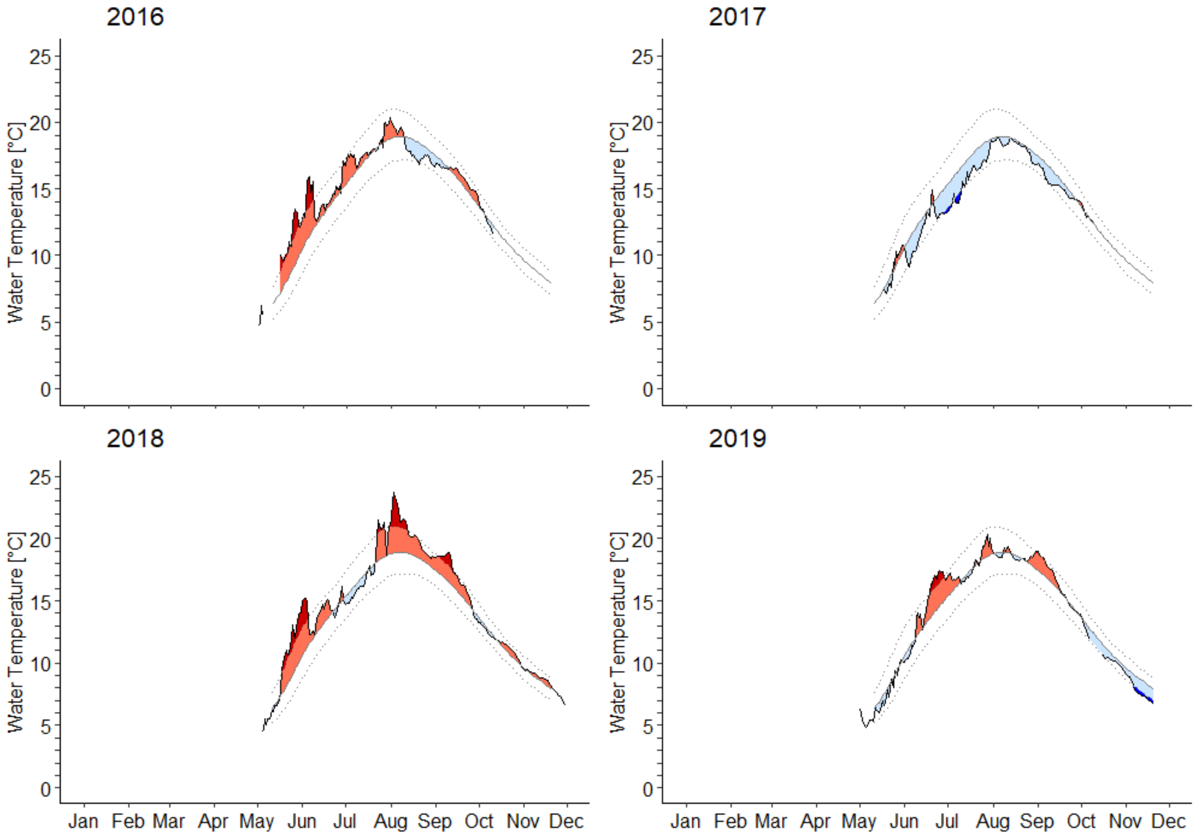


Figure A5. Event lines for marine heatwaves between 2008 and 2019 retrieved from the high-resolution dataset using the R package 'heatwaveR' (Schlegel and Smit 2018). The black lines represent the actual temperature measurements each year. The upper grey dotted line represents the 90th percentile and the lower dotted line represents the 10th percentile. Seasonality is demonstrated as the black lines between the thresholds. Red = above the 90th percentile (registered as a marine heatwave event by the 'heatwaveR' package software if the temperature remains above this level for five or more consecutive days), orange = between the seasonality and 90th percentile, light blue = between the seasonality and 10th percentile, dark blue = below the 10th percentile.

Table A2. Event output for the high-resolution dataset.

Event number	Duration (days)	Start date	Peak date	End date	Mean intensity (°C)	Max intensity (°C)	Onset rate (°C per day)	Decline rate (°C per day)
1	15	10/07/2010	19/07/2010	24/07/2010	3.08	3.71	0.16	0.29
2	7	10/07/2011	12/07/2011	16/07/2011	3.41	4.19	0.44	0.43
3	14	25/08/2011	27/08/2011	07/09/2011	1.57	1.73	0.14	0.03
4	11	01/10/2011	06/10/2011	11/10/2011	1.18	1.29	0.04	0.05
5	23	28/07/2014	29/07/2014	19/08/2014	2.94	3.97	1.16	0.11
6	12	12/09/2014	21/09/2014	23/09/2014	1.79	2.22	0.09	0.46
7	20	01/11/2015	20/11/2015	20/11/2015	1.23	1.47	0.03	NA
8	14	16/05/2016	26/05/2016	29/05/2016	2.65	4.18	0.26	0.60
9	6	03/06/2016	05/06/2016	08/06/2016	3.58	4.47	0.86	0.66
10	18	18/05/2018	01/06/2018	04/06/2018	3.28	4.43	0.23	0.47
11	13	31/07/2018	03/08/2018	12/08/2018	3.15	4.90	0.88	0.31
12	10	03/09/2018	10/09/2018	12/09/2018	1.85	2.40	0.15	0.34
13	11	18/06/2019	22/06/2019	28/06/2019	2.58	2.95	0.24	0.19
14	6	31/08/2019	01/09/2019	05/09/2019	1.39	1.48	0.09	0.05

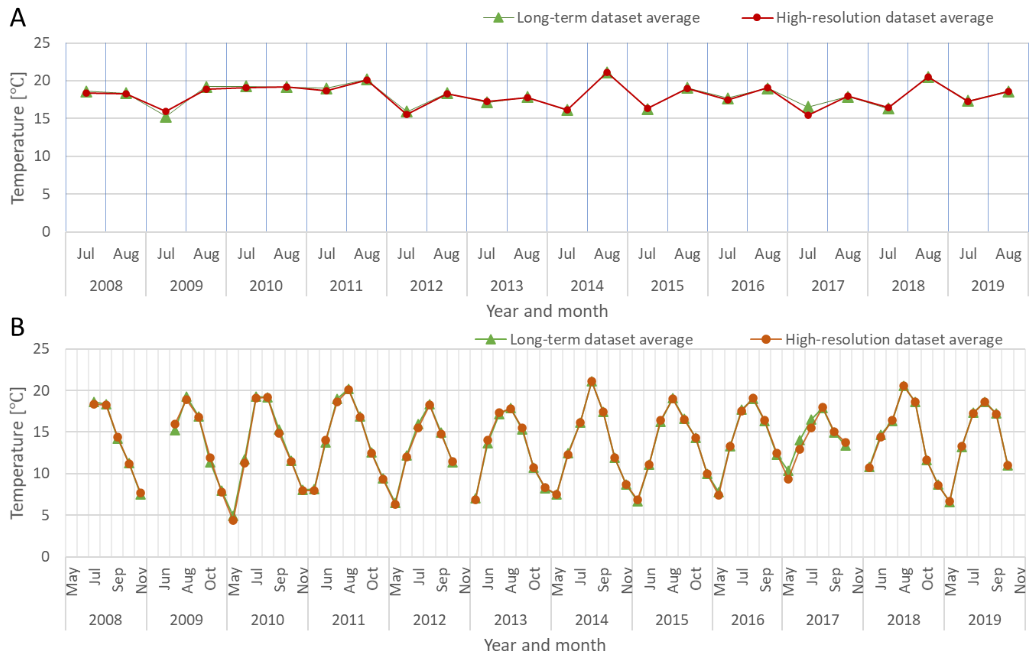


Figure A6. A) Comparison of the mean temperature in July and August from 2008–2019 based on three monthly measurements from each dataset (long-term and high-resolution data set). **B**) Comparison of the mean temperature from each dataset in the months May–November between 2008 and 2019 (during periods when both datasets provided coverage

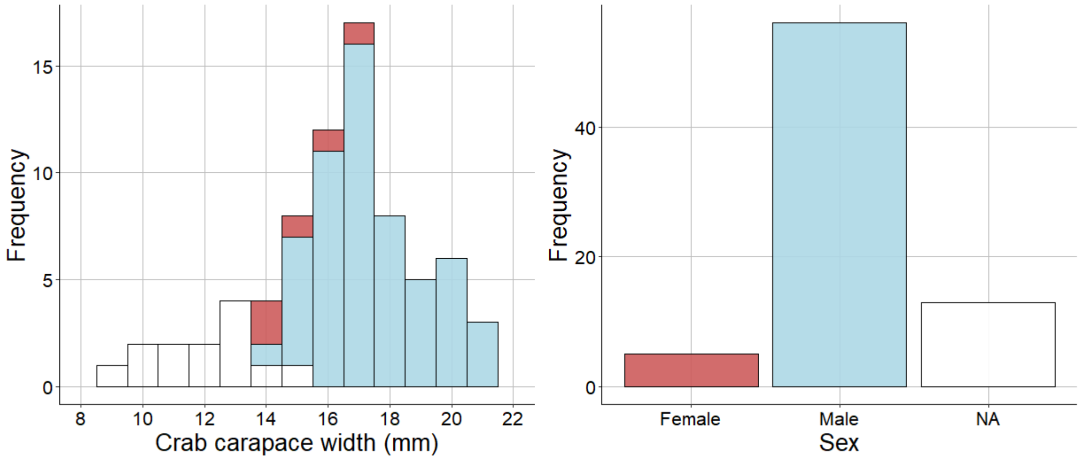


Figure A7. A total of 74 crabs with carapace widths between 9.0 and 21.5 mm were collected between the 30th of June and 13th of July 2020 from Godby's small boat port by Färjsundet (N° 60.24067; E° 20.00799). The majority of the crabs were identified as males, with the smaller crabs being difficult to determine.

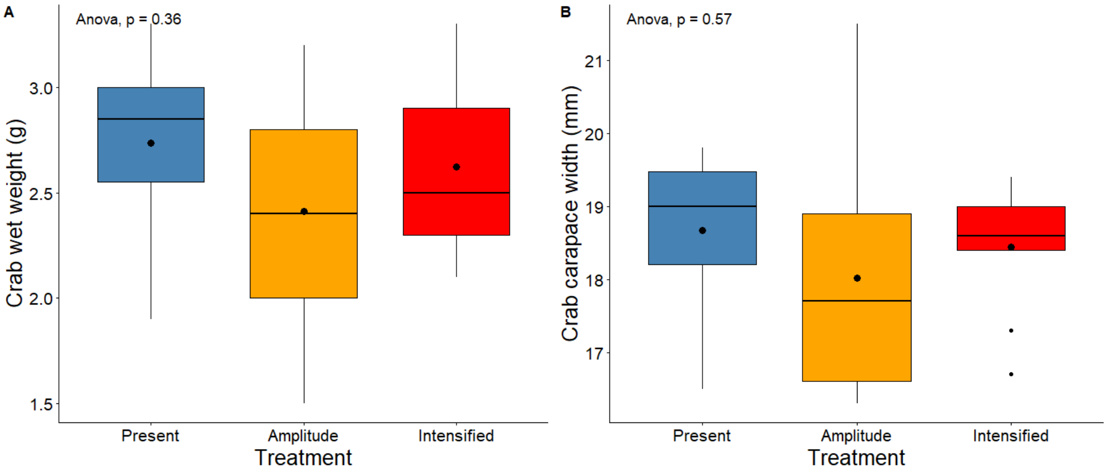


Figure A8. The final wet weights **(A)** and carapace widths **(B)** of *Rhithropanopeus harrisii* in the treatments *Present* (N = 8), *Amplitude* (N = 9) and *Intensified* (N = 9). Boxplots show the median, including the upper and lower quartile. Means are shown as black dots.

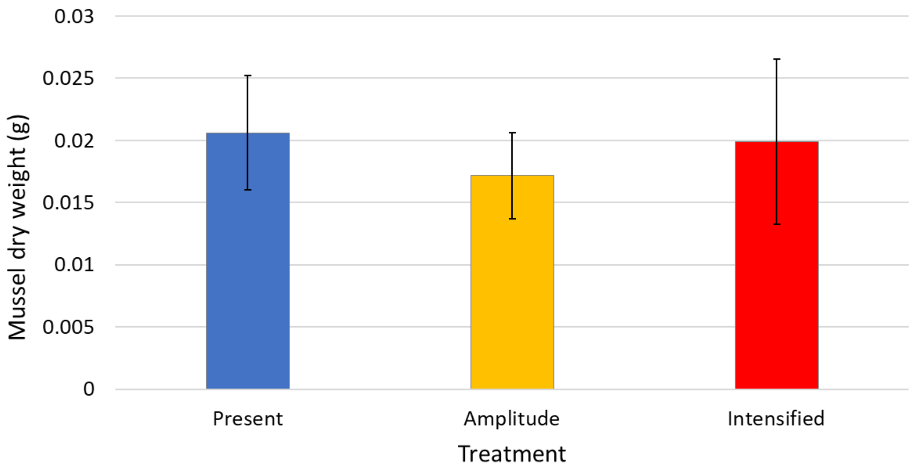


Figure A9. Mussel dry weight consumed by individual *Rhithropanopeus harrisii* during the 36-day (presented are daily means) for the three treatments (*Present* (N=8), *Amplitude* (N=9), *Intensified* (N=9); with 95% confidence intervals).