Surfing the heatwave: Understanding the influence of marine heatwaves in driving community dynamics and species performance in the North Sea

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Dissertation

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Summary

As a consequence of anthropogenic climate change, the frequency, duration and magnitude of extreme weather events are increasing and expected to continue to do so in the upcoming decades. Among them, marine heatwaves (MHWs) are driving significant ecological changes worldwide, including mass mortalities, shifts in species distributions, and biodiversity reductions. In recent years, growing concerns about MHWs impacts have led to increased research efforts aimed at defining, categorising, and exploring their consequences across different levels of biological organisation from individuals to communities.

Despite the increasing attention given to MHWs in research, much remains unknown. First, the unpredictable nature of MHWs makes it challenging to accurately quantify their effects on communities. Besides, most studies on potential effects of climate change on organisms focus on rising mean temperatures, often neglecting the biological responses to thermal fluctuations, which can differ from those under constant temperature conditions. Research on MHWs has largely concentrated on coral reefs and fish, with less attention given to organisms at the base of the food web, such as plankton. This thesis aimed to quantify the effects of MHWs at the level of individuals, populations and communities using holoplankton and meroplankton as model organisms. The thesis was divided into two main blocks reflecting objectives and methodological approaches. The first block used historical time series data to quantify associations between MHWs and mesozooplankton temporal dynamics in the North Sea. The second block used laboratory experiments to investigate how current and future MHWs might affect the survival, growth, and phenology of meroplanktonic decapod crustacean larvae.

The first objective was to evaluate MHWs effects on the mesozooplankton communities of the North Sea. For this purpose, the Helgoland Roads time series, one of the world's richest marine datasets, was used, and a new method based on a modified before-after-control-impact design (BACI) was applied. The goal was to quantify zooplankton responses to MHWs by using a robust design with multiple controls and impacted replicates. This included assessing the season-dependent effects of MHWs, considering that seasonal variations play a crucial role in shaping many communities worldwide. The results revealed that the structure and densities of the mesozooplankton community were mainly impacted by spring and autumn MHWs. Interestingly, there was no consistent indication that MHWs always affected taxa negatively. On the contrary, several taxa (e.g., copepods) showed an increase in abundance during or after the MHWs.

The second objective was to explore whether MHWs could cause shifts in copepod phenology, a group affected by seasonal MHWs. There was no consistent evidence of changes in phenological traits in response to MHWs occurring before the bloom, suggesting that copepods did not undergo a phenological shift and consistently experienced MHWs during their bloom. Over time, five out of six taxa experienced a significant increase in the number of MHW days and intensity during their blooms. The bloom duration of nearly all taxa was correlated with several MHWs components, including the number of MHW days during the bloom and the MHW temperature increase rates. Overall, a higher proportion of MHW days and a rapid temperature rise resulted in shorter bloom durations.

Within the experimental approach, the first objective focused on the larval performance of the European shore crab, *Carcinus maenas* an important predator in the North Sea benthic food web. Using a factorial experiment, larvae were exposed to heatwaves with varying onset timings, durations, and intensities, including those mimicking realistic (18 and 21 °C) and future (24 °C) heatwaves. The results indicated stage-dependent sensitivity to heatwaves: development to the megalopa stage was faster but survival and dry mass significantly decreased when larvae were exposed to intense heatwaves occurring later in the larval phase. Importantly, larval performance could not always be predicted by the average temperature experienced during the heatwaves. This underscores that when heatwaves affect sensitive stages, data from experiments conducted at constant temperatures may not reliably predict responses to heatwave conditions.

The second objective of the laboratory experiments was to quantify the effects of MHWs on the larval performance of the invasive crab *Hemigrapsus sanguineus.* This was motivated by the hypothesis that MHWs could facilitate biological invasions. Unlike *C. maenas*, *H. sanguineus* benefited from earlier and longer heatwaves, which positively affected larval survival. Interestingly, exposure to prolonged cold summer temperatures led to an extension of development through an alternative developmental pathway that resulted in higher megalopa dry mass than under a normal pathway. This experiment highlighted that ontogenetic patterns of thermal tolerance and developmental plasticity are crucial mechanisms driving responses to MHWs.

This thesis provides a comprehensive analysis, through time series and laboratory experiments, of how MHWs may influence community dynamics and species performance in a coastal area that has experienced numerous heatwaves in recent decades. In summary, this thesis reveals that MHWs impacts on zooplankton communities vary by season, underscoring the need for season-specific studies in communities shaped by seasonal variation. Within the zooplankton community, copepods are unable to adjust their phenology in response to MHWs occurring before their bloom, meaning they consistently experience the MHWs effects. The lack of a phenological shift, combined with rising MHW days and temperatures increase rates, can lead to faster and more or less intense blooms, depending on the taxa and season, with potential repercussions for higher trophic levels. The thesis also demonstrates that MHWs effects on species performance differ from those of general warming, highlighting that MHWs components are interconnected and must be studied together to fully understand organism responses. Species resilient to warmer temperature or invasive species are likely to benefit from MHWs, often at the expense of native species that will face increased stress, eventually leading to their competitive exclusion by species better adapted to MHWs. Because MHWs impacts can vary widely depending on the species studied, there is a need for careful consideration when applying climatological definitions of MHWs to organisms. As MHWs continue to grow stronger, more frequent and longer, understanding the link between their components and their ecological and socio-economic consequences will become increasingly crucial.

Zusammenfassung

Als Folge des anthropogenen Klimawandels nehmen Häufigkeit, Dauer und Intensität extremer Wetterereignisse zu und werden voraussichtlich auch in den kommenden Jahrzehnten weiter zunehmen. Zu diesen Wetterereignissen zählen marine Hitzewellen (MHWs), die weltweit signifikante ökologische Veränderungen verursachen, einschließlich Massensterben, Verschiebungen in der Verbreitung von Arten und einem Rückgang der Biodiversität. In den letzten Jahren haben wachsende Bedenken hinsichtlich der Auswirkungen von MHWs zu verstärkten Forschungsbemühungen geführt, die darauf abzielen, ihre Folgen auf verschiedenen Ebenen der biologischen Organisation von Individuen bis hin zu Gemeinschaften zu definieren, zu kategorisieren und zu erforschen.

Trotz der zunehmenden Aufmerksamkeit, die MHWs in der Forschung erhalten, bleibt vieles unbekannt. Zum einen macht die unvorhersehbare Natur von MHWs es schwierig, ihre Auswirkungen auf Gemeinschaften genau zu quantifizieren. Außerdem konzentrieren sich die meisten Studien über die potenziellen Auswirkungen des Klimawandels auf Organismen auf höhere Durchschnittstemperaturen und vernachlässigen oft die biologischen Reaktionen auf Temperaturschwankungen, die sich von denen unter konstanten Temperaturbedingungen unterscheiden können. Die Forschung zu MHWs hat sich weitgehend auf Korallenriffe und Fische konzentriert, während Organismen an der Basis des Nahrungsnetzes, wie Plankton, weniger Beachtung gefunden haben. Diese Dissertation hatte zum Ziel, die Auswirkungen von MHWs auf der Ebene von Individuen, Populationen und Gemeinschaften unter Verwendung von Holoplankton und Meroplankton als Modellorganismen und -gemeinschaften zu quantifizieren. Die Arbeit wurde in zwei Hauptblöcke unterteilt, die die Ziele und methodischen Ansätze widerspiegeln. Der erste Block nutzte historische Zeitreihen, um die Zusammenhänge zwischen MHWs und der zeitlichen Dynamik von Mesozooplankton in der Nordsee zu quantifizieren. Der zweite Block verwendete Laborexperimente, um zu untersuchen, wie aktuelle und zukünftige MHWs das Überleben, das Wachstum und die Phänologie von meroplanktonischen Dekapodenlarven beeinflussen könnten.

Das erste Ziel war es, die Auswirkungen von MHWs auf die Mesozooplankton-Gemeinschaften der Nordsee zu bewerten. Zu diesem Zweck wurde die Helgoland Roads-Zeitreihe, eine der weltweit reichhaltigsten marinen Datensammlungen, verwendet und eine neue Methode basierend auf einem modifizierten Vorher-Nachher-Vergleich (BACI, Before-After-Control-Impact) verwendet. Ziel war es, die Reaktionen des Zooplanktons auf MHWs zu quantifizieren und sie von denen auf allmähliche Erwärmung zu unterscheiden, indem ein robustes Design mit mehreren Kontroll- und betroffenen Replikaten verwendet wurde. Dies beinhaltete die Bewertung der saisonabhängigen Auswirkungen von MHWs, da saisonale Schwankungen eine entscheidende Rolle bei der Gestaltung vieler Gemeinschaften weltweit spielen. Die Ergebnisse zeigten, dass die Struktur und Dichte der Mesozooplankton-Gemeinschaft hauptsächlich durch MHWs im Frühling und Herbst beeinflusst wurden. Interessanterweise gab es keine konsistenten Hinweise darauf, dass MHWs die Taxa immer negativ beeinflussen. Im Gegenteil, mehrere Taxa (z. B. Copepoden) zeigten während oder

nach den MHWs eine Zunahme der Abundanz. Im Gegensatz dazu fanden sich keine eindeutigen Hinweise auf Auswirkungen von Sommer- und Winter-MHWs.

Das zweite Ziel war es, zu untersuchen, ob MHWs zu Verschiebungen in der Phänologie von Copepoden führen könnten, einer Gruppe, die von saisonalen MHWs betroffen ist. Es gab keine konsistenten Hinweise auf Veränderungen in phänologischen Merkmalen als Reaktion auf MHWs, die vor der Plankton-Blüte auftraten, was darauf hindeutet, dass Copepoden keine phänologische Verschiebung durchliefen und MHWs während ihrer Blütezeit konsistent erlebten. Im Laufe der Zeit erfuhren fünf von sechs Taxa eine signifikante Zunahme der Anzahl der MHW-Tage und der Intensität während ihrer Blütezeit. Die Blütedauer fast aller Taxa korrelierte mit mehreren MHW-Komponenten, einschließlich der Anzahl der MHW-Tage während der Blüte und der MHW-Temperaturanstiegsrate. Insgesamt führte ein höherer Anteil an MHW-Tagen und ein schneller Temperaturanstieg zu einer kürzeren Blühdauer.

Im experimentellen Ansatz konzentrierte sich das erste Ziel auf die Larvalentwicklung der Europäischen Strandkrabbe, *Carcinus maenas*, einem wichtigen Raubtier im benthischen Nahrungsnetz der Nordsee. In einem faktoriellen Experiment wurden die Larven Hitzewellen mit unterschiedlichen Beginnzeiten, Dauern und Intensitäten ausgesetzt, einschließlich solcher, die realistische (18 und 21 °C) und zukünftige (24 °C) Hitzewellen nachahmen. Die Ergebnisse zeigten eine stufenabhängige Empfindlichkeit gegenüber Hitzewellen: Die Entwicklung zum Megalopa-Stadium verlief schneller, aber die Überlebensrate und die Trockenmasse nahmen signifikant ab, wenn die Larven intensiven Hitzewellen ausgesetzt waren, die später in der Larvenphase auftraten. Wichtig ist, dass die Larvalentwicklung nicht immer durch die durchschnittlich während der Hitzewellen erlebte Temperatur vorhergesagt werden konnte. Dies unterstreicht, dass Daten aus Experimenten bei konstanten Temperaturen möglicherweise nicht zuverlässig auf die Reaktionen auf Hitzewellenbedingungen schließen lassen, wenn Hitzewellen empfindliche Stadien betreffen.

Das zweite Ziel der Laborexperimente war es, die Auswirkungen von MHWs auf die Larvalentwicklung der invasiven Krabbe *Hemigrapsus sanguineus* zu quantifizieren. Dies wurde durch die Hypothese motiviert, dass MHWs biologische Invasionen begünstigen könnten. Im Gegensatz zu *C. maenas* profitierte *H. sanguineus* von früheren und längeren Hitzewellen, die das Überleben der Larven positiv beeinflussten. Während die Exposition gegenüber verlängerten kalten Sommertemperaturen zu einer Verlängerung der Entwicklung durch einen alternativen Entwicklungsweg führte, entwickelten sich die Larven, die MHWs ausgesetzt waren, über einen kürzeren Weg und erreichten das Megalopa-Stadium schneller. Dieses Experiment hob hervor, dass ontogenetische Muster der Temperatur-Toleranz und der Entwicklungsbiologische Plastizität entscheidende Mechanismen sind, die die Reaktionen auf MHWs steuern.

Diese Dissertation bietet eine umfassende Analyse, wie MHWs durch Zeitreihen und Laborexperimente die Dynamik der Gemeinschaften und die Leistung von Arten in einem Küstengebiet beeinflussen können, das in den letzten Jahrzehnten zahlreiche Hitzewellen erlebt hat. Zusammenfassend zeigt diese Dissertation, dass die Auswirkungen von MHWs auf Zooplankton-Gemeinschaften je nach Jahreszeit variieren, was die Notwendigkeit von

jahreszeitenspezifischen Studien in von saisonalen Schwankungen geprägten Gemeinschaften unterstreicht. Innerhalb der Zooplankton-Gemeinschaft sind Copepoden nicht in der Lage, ihre Phänologie als Reaktion auf MHWs anzupassen, die vor ihrer Blüte auftreten, was bedeutet, dass sie die Auswirkungen der MHWs konsistent erleben. Das Fehlen einer phänologischen Verschiebung, kombiniert mit steigenden MHW-Tagen und Temperaturanstiegsraten, kann zu schnelleren und mehr oder weniger intensiven Plankton-Blüten führen, abhängig von den untersuchten Taxa und der Jahreszeit, mit potenziellen Auswirkungen auf höhere trophische Ebenen. Die Dissertation zeigt auch, dass die Auswirkungen von MHWs auf die Leistung von Arten sich von denen der allgemeinen Erwärmung unterscheiden und dass MHW-Komponenten miteinander verbunden sind und ganzheitlich untersucht werden müssen, um die Reaktionen von Organismen vollständig zu verstehen. Arten, die gegen hohe Temperaturen widerstandsfähig sind oder invasive Arten sind, werden wahrscheinlich von MHWs profitieren, oft auf Kosten einheimischer Arten, die einem erhöhten Stress ausgesetzt sind und schließlich durch besser an MHWs angepasste Arten verdrängt werden könnten. Da die Auswirkungen von MHWs je nach untersuchter Art stark variieren, ist eine sorgfältige Abwägung bei der Anwendung klimatologischer Definitionen von MHWs auf Organismen erforderlich. Da MHWs weiterhin stärker, häufiger und länger werden, wird das Verständnis der Verbindung zwischen ihren Komponenten und ihren ökologischen und sozioökonomischen Folgen immer wichtiger.

Manuscript overview

This dissertation is based on the following manuscripts, written by Margot M F Deschamps in collaboration with other authors.

Manuscript 1

Deschamps M. M., Boersma M., Giménez L., 2024. Responses of the mesozooplankton community to marine heatwaves: challenges and solutions based on a long-term time series. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.14165

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Authors contribution:

MMD: Conceptualisation, Formal Analysis, Investigation, Methodology, Writing, Validation

MB: Data Curation, Writing, Validation, Supervision

LG: Conceptualisation, Data Curation, Methodology, Writing, Validation, Supervision

Manuscript 2

Deschamps M. M., Boersma M., Giménez L., Beyond warming: copepods face marine heatwaves during blooms due to unchanged phenological timing in the North Sea

Status: Draft

Authors contribution:

MMD: Conceptualisation, Formal Analysis, Investigation, Methodology, Writing, Validation

MB: Data Curation, Writing, Validation, Supervision

LG: Conceptualisation, Data Curation, Methodology, Writing, Validation, Supervision

Manuscript 3

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GT: Conceptualisation, Experimentation, Methodology, Writing, Validation, Supervision

Manuscript 4

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LG: Conceptualisation, Formal Analysis, Methodology, Writing, Validation, Supervision

MB: Writing, Validation, Supervision

GT: Conceptualisation, Experimentation, Methodology, Writing, Validation, Supervision

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If someone had told me that one day I would spend four years in self-imposed exile on a tiny island in the middle of the North Sea to complete a PhD, I probably would have laughed! I was supposed to stay for six months, just enough time to complete a master's thesis. And here I am, nearly four years later, still in the same place, reaching the end of a major chapter in my life. This journey was made possible with the help of many. This section is for them.

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« N’oublie jamais, celui qui croit savoir n’apprend plus. »

Le pacte des Marchombres – Pierre Bottero

Table of Contents

List of Figures

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 4: Supplementary Material

CHAPTER 5

CHAPTER 5: Supplementary Material

CHAPTER 6

CHAPTER 6: Supplementary Material

CHAPTER 7

List of Tables

CHAPTER 1

CHAPTER 3

CHAPTER 3: Supplementary Material

CHAPTER 4

CHAPTER 4: Supplementary Material

CHAPTER 5: Supplementary Material

CHAPTER 6: Supplementary Material

GENERAL INTRODUCTION
&
OBJECTIVES

CHAPTER

1

1. Global changes & extreme weather events

The world is changing.

Human activity started to impact our environment long before the industrial revolution (Ruddiman, 2003; Smith & Zeder, 2013). During the 21st century, these changes have intensified dramatically, affecting every aspect of the Earth from the hydrosphere and atmosphere, to the biosphere (Council et al., 1999).

It is now well established that anthropogenic climate change poses a major threat to ecosystems worldwide (IPCC, 2022). This phenomenon, driven primarily by the burning of fossil fuels, along with activities such as industrialization and deforestation, has led to a rapid increase in the concentration of greenhouse gases in the atmosphere, resulting in rising temperatures (IPCC, 2022). The consequences of this warming are profound and far-reaching, disrupting weather patterns with repercussions on biodiversity globally. While global warming is known to alter mean environmental conditions beyond temperature, such as increasing average precipitation and rising sea levels (Jevrejeva et al., 2016; Lambert et al., 2008), these are not the only outcomes. Global warming has also heightened the likelihood of surpassing critical thresholds leading to the increased occurrence of extreme weather events, including droughts, floods, cold spells, and heatwaves (IPCC, 2022; Meehl & Tebaldi, 2004; NAS, 2016). Although such extreme events occur naturally in the climate system, there is growing evidence that their increased intensity, frequency, and duration can be directly linked to anthropogenic activities (Planton et al., 2008; Smale et al., 2019; Trenberth et al., 2015).

In the literature, an extreme weather event is defined as *"an event that is rare at a particular place and time of the year"* (IPCC, 2021). While this definition appears straightforward, Stephenson (2008) wrote that *"extreme events are generally easy to recognise but difficult to define."*. Indeed, the concept of what constitutes "rare" and what constitutes "extreme" is more complex. Generally, an event is considered extreme when a variable of interest exceeds a predefined threshold (McPhillips et al., 2018; Stephenson, 2008). However, the criteria for such thresholds vary across studies. Some use an absolute threshold and classify an event as extreme when the daily maximum temperature exceeds this threshold over consecutive days. Although this approach effectively measures the severity of extreme events, it is specific to a particular period (e.g., summers, when absolute temperatures are high) and sector (e.g., wildlife, human health, agriculture), which limits their broader applicability (Perkins & Alexander, 2013). To overcome these limitations, other studies have adopted a relative threshold, typically defined as a higher percentile in the variable distribution over a base period. While more arbitrary than the absolute threshold (Walsh et al., 2020), the relative threshold facilitates comparisons between studies and regions and allows extreme events to occur at any time of the year (Hobday et al., 2016).

One particular and well-studied extreme event is the heatwave, characterised by discrete periods of unusually high temperature. Heatwaves are increasing in frequency, magnitude, and duration (Meehl & Tebaldi, 2004; Perkins et al., 2012), with projections indicating that they will continue to do so in the coming decades, raising serious ecological concerns (Domeisen et al., 2023; Holbrook et al., 2020; Perkins-Kirkpatrick & Lewis, 2020). Mass mortalities, habitat loss, shifts in species distributions, and reductions in biodiversity in response to heatwaves have been reported in all living compartments worldwide, including birds, mammals, insects, and plants (Ruthrof, 2018; Trondrud et al., 2023). Heatwave impacts can extend beyond ecological damage, as they compromise essential ecosystem goods and services, leading to socio-economic consequences (García-León et al., 2021; Smith et al., 2021). For instance, heatwaves can severely affect provisioning services by disrupting food supply. The 2018 European heatwave and associated drought caused an 8 % drop in global cereal production, leading to livestock feed shortages and increases in commodity prices such as soft wheat and barley (Beillouin et al., 2020; Brás et al., 2021). Cultural services are also affected, not only through loss of iconic species such as the cockatoo (Ruthrof, 2018) but also through a decline in tourism, as regions impacted by heatwaves can become less attractive for recreational activities (Smale et al., 2019). Finally, in terms of regulating ecosystem services, heatwaves can be detrimental to deciduous forests, ultimately reducing carbon sequestration (Krasnova et al., 2022). While the above-mentioned effects of heatwaves primarily highlight terrestrial ecosystems, heatwaves may affect all of the Earth's ecosystems, including rivers, lakes, and oceans (Mouthon & Daufresne, 2006; Smith et al., 2021; Woolway et al., 2021).

1.1. Marine heatwaves

As a consequence of atmospheric warming, ocean surface waters have been warming at an alarming rate of 0.15 °C per decade over the past 40 years (IPCC, 2021), and sometimes at rates two to three times higher in specific regions, such as high latitudes, or even some temperate regions such as the coastal North Sea (Amorim et al., 2023). Alongside this gradual long-term warming and similarly to their atmospheric counterpart, the magnitude, frequency, and duration of marine heatwaves (hereafter MHWs) have also increased significantly (Frölicher et al., 2018; Oliver et al., 2018).

The term “marine heatwave” was first introduced in the literature by Pearce et al. (2011), right after the severe MHW that occurred off the Western Australia, referred to as the “Ningaloo Niño”, in 2011. With the devastating effects of this MHW on marine communities (Bosch et al., 2022; Caputi et al., 2019; Chandrapavan et al., 2019; Lenanton et al., 2017; Wernberg et al., 2013), the term was first applied to understand the biological and ecological implications. Following this event, growing concerns about MHW impacts have led to increased research efforts aimed at defining, categorising, and exploring their consequences across different levels of biological organisation from individuals to communities. This surge in research and the subsequent increase in publications were facilitated by the development of standardised terminology and a growing consensus on the definition of MHWs.

1.1.1. Definitions & consensus

To enable comparative analyses across different regions and time periods, a standardised definition of MHWs was necessary. Hobday et al. (2016) proposed a definition, which is now widely accepted and remains the most commonly used across various sectors to this day.

Drawing from the atmospheric definition by Perkins & Alexander (2013), MHWs were initially defined as *“a discrete, prolonged, anomalously warm water event”* (Hobday et al., 2016). However, like the definition for extreme weather events (see Section 1), this qualitative approach posed challenges for comparing MHWs across different times and locations, as it lacked clear criteria for what constitutes "discrete," "prolonged," and "anomalously warm". Building on the definitions, Hobday et al. (2016) introduced a quantitative definition, specifying that an event is classified as a MHW if the temperature at a specific location and time exceeds the 90th percentile (Q90) of a baseline climatology (i.e., anomalously warm) for a duration of five days or more (i.e., prolonged). Moreover, if the amount of time between two events is equal to or less than two days, the two events will be considered as one and unique MHW (i.e., discrete) (Fig. 1.1). The choice of a relative threshold was made to allow MHWs to be detected across all seasons and spaces (See Section 1). Since a MHW is an extreme event, and extreme events by nature must be rare (IPCC, 2021), a high percentile threshold was necessary to prevent the detection of too many events. The five-day duration strikes a balance between defining events that are too short or too long. Indeed, shorter durations tended to result in an excessive number of MHWs in tropical regions compared to other areas, while longer durations led to fewer than one MHW event per year in many regions (Hobday et al., 2016). Therefore, this compromise ensures a more consistent and meaningful definition of MHWs across different geographical areas. Nonetheless, it is important to emphasize that, from a biological standpoint, strictly adhering to this five-day threshold may overlook the potential impacts of shorter events on organisms with short generation times (e.g., bacteria, protists) while overestimating those for organisms with long generation times (e.g., large mammals).

Until 2018, the quantitative definition of MHWs was relatively simplistic, distinguishing only between the presence or absence of a heatwave. However, in today's world, categorising and naming extreme events has become standard practice, allowing for consistent comparisons across different regions while also enhancing scientific and public awareness (Hobday et al., 2018). For example, hurricanes are categorised from 1 to 5 based on wind speed and potential damage, while earthquakes are classified by magnitude using the Richter scale. To maintain consistency with the quantitative definition, Hobday et al. (2018) developed a system for naming and categorising MHWs using relative thresholds instead of absolute values. This system defines categories based on multiples of the Q90 threshold (Fig. 1.1).

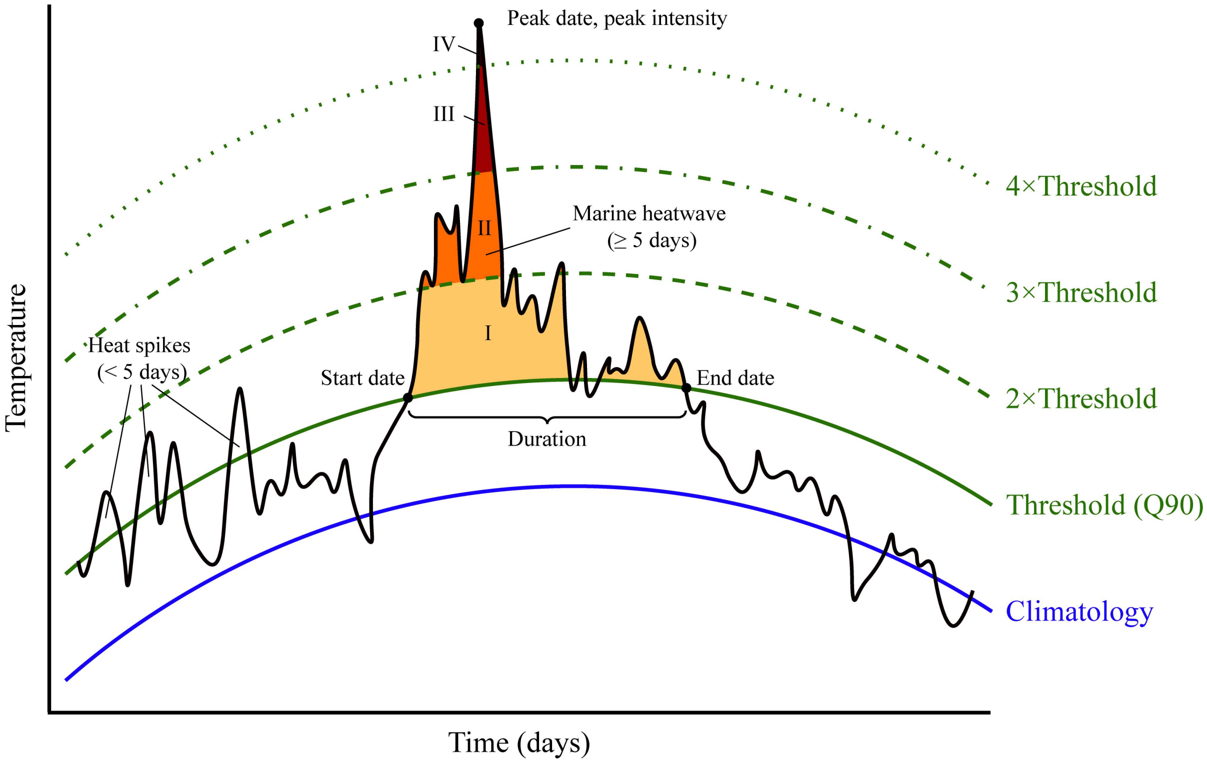

Figure 1.1. Definition of MHWs from Hobday et al. (2016). The black line represents the daily temperature. The peak intensity (i.e., maximum intensity) is calculated as the difference (in °C) between the maximum temperature of the event and the climatological mean for this day. Colours inside the MHW represent the categorisation for MHW as defined by Hobday et al. (2018). Multiples of the 90th percentile (Q90) of the mean climatology define each category from I to IV: I: moderate (< twice the difference), II: strong (twice the difference), III: severe (three times the difference), and IV: extreme (four times the difference).

Based on this definition of MHWs, each event will differ from the others and can be characterised not only by its category but also by a set of specific metrics or components, such as duration, timing, intensity, location, and rates (Hobday et al., 2016) (Table 1.1). Some metrics, like depth, require further calculation. The vertical structure of a MHW is defined by the average temperature anomalies of a T/S profile within the MHW time frame (Zhang et al., 2023). Additionally, the Impact Depth of MHW (IDMHW) or MHW maximum depth, is the depth where 85 % of the maximum cumulative temperature anomaly (scaled heat content anomaly) is located (Zhang et al., 2023). Moreover, while metrics like duration and intensity have received the most attention, others such as the rate of MHW onset and decline are often overlooked despite being equally important. These rates determine the speed at which heat builds up and dissipates during a MHW event, offering crucial insights into the MHW dynamics (Spillman et al., 2021).

Table 1.1. Example of MHW components commonly used to characterise the event. All components can be extracted after the identification of the event using the Q90 threshold based on the climatological baseline.

MHW component	**Name**	**Definition**
Timing	Start date	Date on which the temperature > Q90 threshold
	End date	Date on which the temperature < Q90 threshold
	Peak date	Date on which the MHW reaches the highest temperature anomaly
	Season	Season of the MHW
Intensity	Maximum	Maximum temperature anomaly during the MHW relative to the climatological mean
	Mean	Mean temperature anomaly during the MHW relative to the climatological mean
	Variance	Variation in intensity of the MHW over the duration
	Cumulative	Sum of daily intensity anomalies
Duration	Total duration	Consecutive period of time that temperature exceeds the threshold
	Onset duration	Consecutive period of time between the onset and the maximum intensity of the MHW
	Decline duration	Consecutive period of time between the maximum intensity and the end of the MHW
Rates	Onset rate	Rate of temperature change from the onset of the MHW to the maximum intensity
	Decline rate	Rate of temperature change from the maximum intensity of the MHW to the end
Location	Geographical location	Area of ocean meeting the MHW definition
	Depth	Depth reached during the MHW.

A critical aspect in defining extreme weather events, and by extension atmospheric heatwaves, is the definition of the baseline used to calculate threshold temperature. Indeed, in their definition, Hobday et al. (2016) introduced the Q90 for quantitatively measuring MHWs. However, the concept of what constitutes "abnormal" temperatures remains ambiguous. "Abnormal" could be interpreted as a temperature that is higher than what was “normal” during the same period in the past. This would imply using a consistent (fixed) historical reference period to calculate the Q90 and compare it with current temperature (e.g., over a 30-year period). However, as ocean temperatures rise, the probability of exceeding the Q90 will increase. As a result, all days in a future year might be classified as heatwave days. Therefore, using a fixed baseline in the face of long-term temperature trends risks drifting away from the original concept that a MHW should be an exceptional, rare event. This led to a second measurement of the Q90 based on a shifting baseline that will characterised the “new normal” and accounts for ocean global warming (Amaya et al., 2023; Jacox, 2019).

The selection of a baseline is crucial for effectively communicating and accurately assessing MHW impacts on marine ecosystems. Currently, there is still confusion surrounding the definition of MHWs, leading to frequent miscommunication between scientists and media. This often arises when different types of MHWs are being referenced: extreme conditions compared to historical temperatures using the fixed baseline, and extreme compared to an evolving ‘new normal’ of rising temperatures, using the shifting baseline (Amaya et al., 2023). Some may say that MHWs should be reserved for events identified with the shifting baseline, and that the combination of MHWs and long-term warming should be described with a distinct term such as "total heat exposure" (Amaya et al., 2023). However, this view is not universally accepted. Critics suggest that introducing new terms would only create further confusion and foster the misleading notion that temperature extremes and their related impacts will remain relatively stable (Sen Gupta, 2023). Defining MHWs through the shifting baseline could be seen as contributing to the "shifting baseline syndrome" (Soga & Gaston, 2018), a phenomenon already observed in fisheries where each generation of scientists accepts the stock sizes and species composition at the start of their careers as the baseline. As stocks further decline, this new baseline leads to a gradual perception of resource depletion, making the loss seem less dramatic than it actually is (Pauly, 1995).

Both the shifting and fixed baselines have their merits and the choice should depend on the specific research question being addressed (Amaya et al., 2023). From an ecological perspective, a fixed baseline is essential for understanding how species with long lifespans and limited adaptive capacity may respond to temperature changes in a warming environment, as it accounts for long-term temperature trends (Oliver et al., 2021). In contrast, a shifting baseline (Jacox, 2019) allows to examine how species with short lifespans capable of fast adaptation might experience MHWs.

1.1.2. Temporal variations

Various MHW components described above (Table 1.1) have shown significant changes over time. Since 1982, the average duration of MHWs has increased in 82 % of the global ocean by 1.3 days per decade (Oliver et al., 2018). Additionally, the frequency and intensity have risen by 0.45 events and 0.08 °C per decade, respectively (Oliver et al., 2018). With 87 % of MHWs attributable to anthropogenic warming (Frölicher et al., 2018), the severity of MHWs is expected to continue rising (Oliver, 2019). If global temperatures exceed 2 °C above pre-industrial levels, nearly all MHWs will be driven by human-induced warming, potentially reaching 100 % attribution (Frölicher et al., 2018; Oliver, 2019). Notably, under the RCP8.5 scenario and assuming a fixed baseline, 15 % of the ocean is projected to approach a permanent MHW state by 2100 (Cheng et al., 2023)

Globally, the increasing trend in MHW components is evident across all seasons (Thoral et al., 2022; Wang & Zhou, 2024). However, in the mid and high latitudes of the Northern Hemisphere, the summer months (June to August) usually experience the highest number of MHW days and the highest maximum intensity (i.e., °C above the climatological mean during the MHW) (Wang & Zhou, 2024). Consequently, over the past four decades, the seasonal differences in MHWs have become more pronounced in most regions, with a stronger increase in cumulative MHW intensity during the warm season and a weaker increase during the cold season (Wang & Zhou, 2024).

1.1.3. Spatial variations

Marine heatwaves are characterised not only by their magnitude, duration, and timing but also by their spatial extent and depth. MHWs may be confined, occurring in bays, around small islands, or along coastlines, or they can be widespread, affecting entire regional seas, or even spanning multiple oceans (Holbrook et al., 2020). While most MHWs in the ocean are confined to the mixed layer, it has been shown that a third can extend to depths below the mixed layer, with the majority occurring in the eastern tropical and North Pacific (Koehn et al., 2024). Interestingly, these deeper MHWs tend to have higher maximum intensities and last longer than those restricted to the mixed layer (Koehn et al., 2024). A notable example is the "*Blob*" from 2013 to 2016 in the North Pacific Ocean, which is the largest deep MHW recorded to date, reaching depths of up to 400 meters.

While the overall trend in MHW intensity is increasing and is expected to continue increasing, there are spatial heterogeneities in MHW metrics across regions, with some areas showing more intense and longer MHWs and warming much faster than others. For instance, MHW frequencies generally range from one to three events per year (Oliver et al., 2018; Sen Gupta, 2023; Sun et al., 2023). However, in the eastern tropical Pacific, El Niño events can result in a single MHW lasting up to 60 days (Oliver et al., 2018). The average MHW duration also varies significantly by region: mid and high latitudes have seen an increase of 20 days since 1982, while the central tropical ocean and the Northeast Pacific have experienced an increase of over 30 days (Oliver et al., 2018). Consequently, some regions are projected to reach a permanent MHW state sooner than others (Cheng et al., 2023).

There are also significant spatial variations in MHW intensity (i.e., °C above the climatological mean during the MHW). High intensities have been observed in regions with large sea surface temperature variability, including the five western boundary current regions, which have experienced increases of between +2 and +5 °C since 1982 (Oliver et al., 2018). In contrast, eastern boundary current regions have seen increases of up to 3 °C (Oliver et al., 2018). Furthermore, despite the overall global increase in MHWs, the Eastern Tropical Pacific has shown a notable decline in MHW intensity (Oliver et al., 2018; Wang & Zhou, 2024).

All changes in MHW components over time and space presented above are the results of the MHW computations using a fixed baseline. Therefore, it is important to acknowledge that a change in baseline would result in different trends over time and space (see Section 1.1.1).

1.2. Biological impacts of MHWs

1.2.1. Major MHW events and their impact on marine communities

Numerous MHWs have occurred over the past decades, with some being so intense and prolonged that they have gained significant attention due to their devastating impact on marine ecosystems (Fig. 1.2). The following section discusses the two most significant MHW events that have occurred in recent decades and examines their impacts on marine ecosystems.

The most extensively studied MHW, known as "The Blob," occurred in the Northeast Pacific from fall 2013 to late 2016. This event was characterized not only by unusually warm sea surface temperatures but also by significant changes in various physical properties and processes that persisted for several years. Typical winter storms and wind patterns were weakened, leading to increased ocean stratification and shift in the timing and location of upwelling and downwelling (Cavole et al., 2016). In some areas, this stronger stratification reduced the mixing of colder, nutrient-rich deep water with surface water, resulting in lower nutrient levels in the upper ocean (Zaba & Rudnick, 2016). Additionally, the usual flow of colder water weakened, and the zone where cold Arctic water meets warmer subtropical water shifted farther north than usual (Cavole et al., 2016). Together, these physical and chemical changes triggered cascading effects that spread throughout the marine food web resulting in mass mortality events (Piatt et al., 2020), range shifts of various species, including invertebrates, fish, and top predators (Lonhart et al., 2019; Welch et al., 2023), as well as changes in lower trophic community composition (Arteaga & Rousseaux, 2023; Beltrán-Castro et al., 2020; McKinstry et al., 2022). Among others, phytoplankton community shifted from being dominated by diatoms to being dominated by dinoflagellates, which resulted in an increase in surface chlorophyll (Arteaga & Rousseaux, 2023). At the zooplankton level, the event led to a tropicalisation of the copepod community (Beltrán-Castro et al., 2020) and a shift from a community dominated by crustaceans to one dominated by gelatinous organisms (Brodeur et al., 2019). Spawning failures among meroplanktonic coastal invertebrates were also reported (Shanks et al., 2020). Additionally, the dynamics of ichthyoplankton communities were affected, likely due to changes in larval mortality rates and/or shifts in distribution (Nielsen et al., 2021). These changes could impact the recruitment of commercially important fish species, as seen with sardines, which are favoured by warmer temperatures, and anchovies, which thrive in cooler conditions (Cheung & Frölicher, 2020). Some of these biological responses were short-term while others were long-term and persisted through the following year (Suryan et al., 2021). As "The Blob" moved toward the coast of the Gulf of Alaska and Northern California, not only pelagic ecosystems were affected, but also benthic communities, including intertidal zones and kelp forest ecosystems (Arafeh-Dalmau et al., 2019; McPherson et al., 2021; Sanford et al., 2019).

Another important MHW, known as the "Ningaloo Niño," occurred in the Indian Ocean from 2010 to 2011 and drew considerable attention due to its severe impact on marine and coastal communities. The event led to mass bleaching of corals (Moore et al., 2012), tropicalisation of fish communities (Wernberg et al., 2013), fish, lobster, and abalone mass mortality events (Pearce et al., 2011) and a shift towards warm-water macroinvertebrates species (Smale et al., 2017). While temperatures did not exceed the thermal tolerance of many marine species, the MHW also resulted in a large-scale seagrass die-off (Arias-Ortiz et al., 2018; Strydom et al., 2020; Wernberg et al., 2016) and therefore indirectly affected the associated community through loss of habitat, refuge, and/or food supplies. Top predators declined indirectly in response to these events (Nowicki et al., 2019). The higher temperature of the event combined with higher turbidity also led to a successful recruitment and therefore higher commercial catch of two important prawn species (Pearce et al., 2011).

Most studies on MHW effects on marine communities are concentrated in specific regions that have experienced a single, intense event (Fig. 1.2). For example, about 75 % of the studies exploring MHW impacts on communities using time series data were conducted either during “The Blob” or during the “Ningaloo Niño” (**Chapter 3**, Table S3.1; see also Joyce et al., 2023). Moreover, across all methods used to assess the biological and ecological impacts of MHWs (modelling, laboratory work, or field studies) most research has been conducted in North America and Australia (Joyce et al., 2023). Other continents that have experienced intense MHWs over the last decades such as Africa, Asia, South America, and Europe, have been largely overlooked in research (Fig. 1.2).

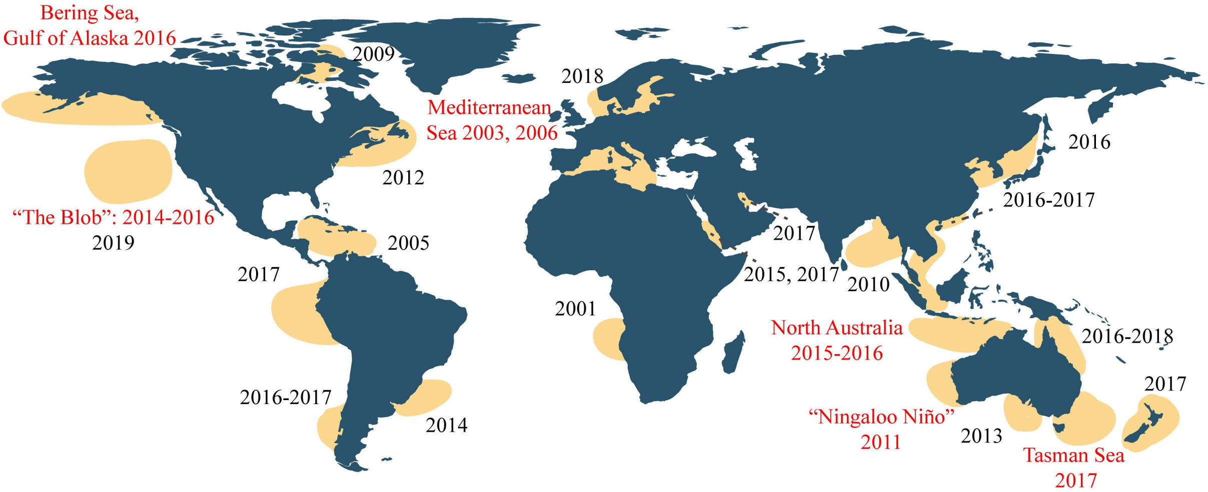

Figure 1.2. Major MHWs recorded since 2000. The most studied MHWs, in terms of impact on marine communities, are highlighted in red. The yellow shapes are approximate areas and do not represent the precise spatial scale of the MHWs. Main sources: Smith et al. (2023), Oliver et al. (2021), Holbrook et al. (2020), Sun et al. (2023)

1.2.2. From individual to populations

Temperature has a significant impact on all biological processes, thereby influencing key aspects of ecological performance such as growth, reproduction, survival, and phenology. This is particularly true for ectotherms as their physiological performance is highly dependent on ambient temperature (Huey & Kingsolver, 1989). The performance response will vary depending on the organism’s functional traits, location, life-history stage, and also the MHW components (Smith et al., 2023).

Within a species’ thermal range, organisms typically perform best at temperatures near the middle of this range, where conditions are optimal (Angilletta, 2009). As temperatures move toward the upper or lower thermal tolerance limits, performance declines, sometimes faster near the upper limits (Huey & Stevenson, 1979). Therefore, stenotherm species (i.e., narrow thermal range) are more likely to be negatively affected by MHWs than eurytherm species (i.e., broader thermal range) (Smith et al., 2023). Moreover, individuals living in areas close to their lower thermal limit may benefit from MHWs if the increased temperatures remain within their thermal range (Smith et al., 2023). Interestingly, many organisms in environments with strong seasonal temperature variability, such as temperate seas, tend to have an optimum temperature higher than the annual mean at their location (Boersma et al., 2016). This pattern can be explained by the fact that their optimum temperature aligns more closely with the most frequent temperature rather than the average. As a result, MHWs may actually benefit many organisms in temperate environments.

Conversely, species already living near their upper thermal limits are likely to suffer from MHWs because of increased thermal stress (Fig. 1.3). As the temperature increases and approaches the upper thermal limits, physiological and biochemical mechanisms will be increasingly stressed, including rises in metabolic rates and energy demands. All of these processes can in turn impact growth, reproduction, and survival (Piatt et al., 2020; von Biela et al., 2019) with consequences at the ecosystem level.

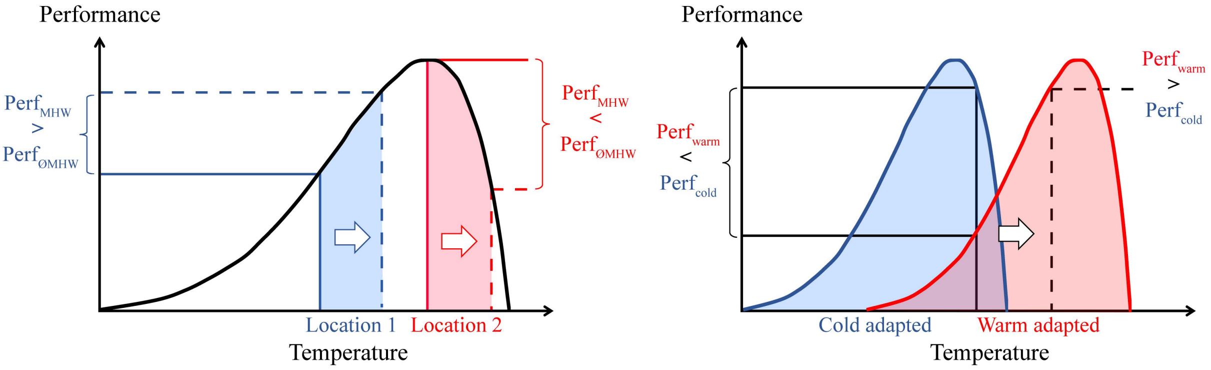

Figure 1.3. Thermal tolerance and species responses to MHWs. Left panel: MHW responses of a species at two different locations: cold edge (blue) and warm edge (red) of the thermal performance curve. Right panel: MHW responses for two species at the same location but with different thermal tolerance ranges: a cold-adapted (blue) and a warm-adapted species (red). The arrows indicate the thermal displacement from the normal thermal conditions (solid line) to the MHW conditions (dotted line). Perf: performance.

In the context of MHWs, the traditional two-dimensional framework of thermal tolerance (performance against temperature) is inadequate. Indeed, temperature fluctuations in a given environment can influence biological systems through mechanisms distinct from those at play in constant environments (Gerhard et al., 2023). This discrepancy can be explained by Jensen's inequality, which originates from nonlinear relationships between temperature and biological responses (Koussoroplis et al., 2017; Ruel & Ayres, 1999). Since MHWs are discrete events, a temporal variable is essential to fully capture their effects on organism performance

(Rezende et al., 2014). For example, survival under MHW conditions depends not just on the intensity but also on the duration of exposure. Shorter thermal events tend to cause less severe declines in performance or survival, and the higher the thermal stress, the shorter the time an organism can endure it (Rezende et al., 2014). This relationship between survival, intensity, and timing is effectively visualised in what is known as a thermal tolerance landscape (Rezende et al., 2014), where the combination of the three variables can explain organisms' responses to temperature changes more comprehensively.

To mitigate the thermal stress caused by MHWs, several strategies can be employed. Mobile species, such as fish and marine mammals, can use thermoregulatory behaviours and relocate to more suitable thermal habitats (Holbrook et al., 2020). Many species can adjust their distributions in response to MHWs by closely tracking changes in ocean temperature, often with minimal delay (Jacox et al., 2020; Pinsky et al., 2013). Additionally, as discussed in Section 1.1.3, not all MHWs affect the entire water column. Species associated with cooler temperatures may relocate to deeper ocean layers (Chaikin et al., 2022), which can serve as thermal refugia during these extreme events.

When relocation in response to MHWs is not possible, organisms must rely on physiological adjustments through phenotypic plasticity (Madeira et al., 2020). These adjustments involve two main strategies: short-term rapid adjustments, known as "heat hardening", which occur following brief exposure to heat stress, and long-term plastic responses, called "acclimatisation", which develop after repeated exposure to heat stress (Bowler, 2005; Moyen et al., 2020; Zhang et al., 2021). Phenotypic plasticity in response to MHWs can also manifest through modifications in the offspring's traits, influenced by the environmental conditions experienced by the parents. This process, known as transgenerational plasticity (Donelson et al., 2018), allows offspring to inherit adaptive traits that enhance their survival. Transgenerational plasticity has been observed in sticklebacks (*Gasterosteus aculeatus*), where offspring reared at elevated temperatures exhibited larger body sizes if their mothers also developed in elevated temperatures (Shama, 2015). Additionally, Chamorro et al. (2023) demonstrated that the parental thermal history significantly influences the thermal tolerance of progeny in the purple sea urchin (*Strongylocentrotus purpuratus*). Females that had been acclimated to MHW thermal conditions during gametogenesis produced offspring that exhibited greater thermal tolerance compared to those from non-acclimated parents.

Population-wise, responses to MHWs can vary widely. Positive effects may include range expansions, increased abundance, and enhanced reproduction (Smith et al., 2023). Conversely, negative impacts can involve recruitment failure due to reproductive issues, range shifts, and mass mortality events, all of which can threaten species persistence (Chandrapavan et al., 2019; Crickenberger & Wethey, 2018; Shanks et al., 2020). MHWs can also create favourable conditions for biological invasions through several mechanisms. First, they can extend the distribution of species beyond their native ranges or support the expansion of already established populations. In years characterised by MHWs, these conditions can sustain populations at the edges of their distribution by opening phenological windows of opportunity (Giménez et al., 2020). Second, species that become invasive often possess certain traits, such as broader thermal tolerances, which may give them an advantage during MHWs. MHWs can therefore facilitate the successful establishment of invasive species through competitive release, as the elevated temperatures often exceed the physiological limits of native species, reducing their competitive abilities (Diez et al., 2012; Gilson et al., 2021; Smith et al., 2023). Field studies have documented the rise of invasive species following MHW events (Arafeh-Dalmau et al., 2019; Thomsen et al., 2019), and experimental research has confirmed these findings for various organisms, including invasive seaweeds (Atkinson et al., 2020), mussels (Xu et al., 2023), oysters (Gilson et al., 2021), and clams (Crespo et al., 2021).

While MHWs can lead to significant shifts in marine populations, it is essential to note that this is not always the case. Indeed, the effects of MHWs can be minimal and, at times, even smaller than the impact of other sources of environmental variability. For instance, Fredston et al. (2023) showed that alteration in fish biomass did not always happen in response to MHWs in the North Atlantic. The 2008 MHW in the North Sea was characterised by a cumulative intensity of 42 °C-days and led to a decline in fish biomass of only 6 %. In contrast, years without MHWs, such as 2011, showed a 97% increase, highlighting that the natural variability of the ecosystem and/or the sampling variability can be stronger drivers of biomass changes in many regions (Fredston et al., 2023). The authors also analysed changes in abundance and biodiversity in the presence and absence of MHWs and did not find any common and systematic effect across all North Atlantic ecosystems. It is true that the implicit assumption of a common response to MHWs across all ecosystems might not be valid, as different ecosystems contain species that may respond differently to the same MHW conditions (Payne, 2023). However, the study from Fredston et al. (2023) underscores the need for caution when interpreting the effects of MHWs on biodiversity.

1.2.3. The case of marine invertebrates

As discussed in the previous section, the predicted increase in frequency and magnitude of heatwaves has become particularly alarming for many marine organisms. Among these, invertebrates may be especially affected, as beyond physiological stress, facilitation of biological invasions, and habitat alteration, certain specific stages of their development can be vulnerable to temperature fluctuations.

Instead of developing from the egg to an adult-like juvenile, many marine invertebrates produce a larval phase that may differ entirely from the adult and juvenile counterparts in terms of habitat, morphology, or behaviour (Carrier et al., 2017). This biphasic life cycle that alternates between larvae and adult, occurs commonly among invertebrates in both terrestrial and aquatic ecosystems (Rieger, 1994). Larvae acquire form and functional capabilities through morphogenesis, differentiation of larval tissue, and growth (McEdward, 1995). At the end of the larval phase, the larvae undergo a radical transformation (i.e., metamorphosis) into juveniles where the morphology and function are similar to those of an adult (McEdward, 1995). Transitions between phases can also involves changes in habitat. Among others, bentho-pelagic life cycle can be seen in bivalves, echinoids, and crustaceans where the larval phase drifts in the water column (meroplankton larvae), while juveniles and adults settle on the seafloor (Pechenik, 1999; Rieger, 1994). For many invertebrates, larvae contribute to range expansion (Giménez et al., 2020; Kelley et al., 2013; Yamada et al., 2021), connectivity between populations (Cowen et al., 2006), and can drive recovery of local populations from mass mortalities (Giménez et al., 2020). Therefore, they are crucial for dispersion, recruitment success and survival of populations (McConaugha, 1992). More than their ecological importance, some may refer to them as "the weakest links" in an organism's life cycle due to their high sensitivity to extreme heat events (Pandori & Sorte, 2019).

Stress tolerance is expected to increase with age, with maturation of regulatory functions occurring during development, including organisms' capacities to withstand environmental fluctuations in temperature (Pandori & Sorte, 2019; Pörtner & Farrell, 2008). Consequently, larval stages are often more sensitive to temperature changes and exhibit a narrow subset of the species' thermal niche, making them 'weak links' in the life cycle (Pandori & Sorte, 2019). Stage-specific sensitivity to temperature or other environmental variables, such as salinity or food limitation are also widespread in many invertebrates. Transitions between ontogenetic stages are particularly sensitive to environmental factors such as temperature

(Uriarte et al., 2019). Enhanced mortality typically occurs near the start and end of the larval phase (Anger, 1991; Dunn et al., 2016; Sulkin & McKeen, 1989) and early embryos appear to be more tolerant to temperature increases than later stages (Balogh & Byrne, 2020; Gall et al., 2021). Stressful environmental conditions at a particular life stage can then be carried over into subsequent stages. For instance, larval size or quality may influence post-settlement success, impacting juvenile growth and survival (Emlet & Sadro, 2006; Giménez et al., 2004; Pechenik, 2006). Subsequently, as the phenotype of an individual is affected by the phenotype or environment of its parent (Badyaev & Uller, 2009), thermal stress in adults can also be carried over to the offspring and negatively impact their thermal tolerance, as seen with the intertidal mussel *Mytilus californianus* (Waite & Sorte, 2022).

In response to environmental stress, many marine invertebrates exhibit a wide range of phenotypic plasticity, including morphological, physiological, behavioural, life-history and developmental (McAlister & Miner, 2017). Among them, decapod crustaceans constitute a highly diverse order, with more than 17,500 species (Decanet, 2024). In terms of developmental plasticity, alternative developmental pathways can occur in many decapod crustaceans such as shrimps and crabs (Criales & Anger, 1986; Giménez & Torres, 2002; Pestana & Ostrensky, 1995). For instance, under osmotic stress and food limitation, some crab species like *Neohelice granulata* can shift to a longer developmental pathway involving five zoeal stages, compared to the usual four under natural conditions (Giménez et al., 2004; Giménez & Torres, 2002; Pestana & Ostrensky, 1995). This alteration can have significant consequences for later life stages, as megalopa originating from the longer pathway exhibit higher biomass and produce larger juveniles (Giménez et al., 2004). Ultimately, crabs that follow the longer pathway may initially have higher fitness compared to those from the shorter pathway settling in the environment at the same time, as their larger size reduces the risk of cannibalism by conspecifics (Giménez et al., 2004).

While MHW effects on decapod crustacean adult stages have been widely studied in field observations or in laboratory experiments (Monteiro, et al., 2023), their effects on early stages are yet to be understood. To date, field observations are limited to a few studies (McKinstry & Campbell, 2018; Monteiro et al., 2024; Morgan et al., 2019) and while valuable, most of them broaden their focus to the entire zooplankton community, setting aside specific impacts on larvae. Moreover, although laboratory experiments have been conducted (Giménez et al., 2021; Marochi et al., 2022; Nour et al., 2022), they remain limited in scope. These studies explored, for the first time, the concurrent effects of MHW temperatures and other variables on crustacean larval stages, offering initial warnings about the impact of marine heatwaves as a multiple stressors on sensitive life stages. However, in Section 1.1.1, it was noted that MHWs can be characterised by a set of components, and while this is widely recognised, experimental studies on the effects of MHWs on larvae have focused solely on one component, such as the intensity, with the cumulative effects of other components being overlooked.

2. The North Sea ecosystem

The significant warming trend observed in the North Sea (Amorim et al., 2023) suggests that MHWs could become more frequent and severe in this region. Additionally, the recent rise in atmospheric heatwaves across continental Europe (Russo et al., 2015) is likely to influence sea temperatures in the coastal North Sea, as there is a strong correlation between marine and atmospheric heatwaves (Giménez et al., 2024). These atmospheric events often occur simultaneously or just before a MHW, indicating a strong coupling between the two heatwaves (Giménez et al., 2024). However, to date, existing research on MHWs in the North Sea primarily focuses on their patterns, trends, and occurrence (Borgman et al., 2022; Giménez et al., 2024; Mohamed et al., 2023); so far, no study has investigated their potential impact on the biological levels in the North Sea ecosystem.

2.1. The Helgoland Roads Time Series

To understand the MHW effects on marine communities, field observations, including time series, are essential. By collecting data over extended periods, one can identify patterns and trends in species abundances, population dynamics, and regime shifts. Without time series, the understanding of the complex impacts of MHWs on marine biodiversity would be severely limited.

In marine ecosystems, long-term datasets that include both temperature and biological data are rare. For instance, out of 232 time series identified in the North Atlantic, only 21 have been collecting both biological and temperature data since before 1990 (O'Brien et al., 2017). Even when available, such datasets often have high spatial resolution, but this typically comes at the cost of lower temporal resolution, which is essential for detailed MHW analysis (Table 1.2). Because of the immense effort required to maintain long-term data collection, the sampling frequency is typically on a weekly or monthly basis. Few time series include both temperature and biological data over a prolonged period with a resolution finer than a week.

Table 1.2. Time series including both biological and temperature data and started before 1990 (O'Brien et al., 2017). Grey cells indicate the longest and the highest-resolution time series. BATS: Bermuda Atlantic Time Series, CPR: Continuous Plankton Recorder, EcoMon: Ecosystem Monitoring Program, SEAMAP: South East Area Monitoring and Assessment Program, SMHI: Swedish Meteorological and Hydrological Institute.

Time series	**Location**	**Start**	**Resolution**
BATS	Northwest Atlantic	1988	1/month
Radiales	Northwest Iberian Coast	1988	1/month
Svelogsbanski transect	South Iceland	1960s	2/year
Plymouth L4	Western English Channel	1988	1/week
CPR	North Atlantic	1931	1/month
EcoMon	Northwest Atlantic (continental shelf)	1977	6-7/year
SEAMAP	Gulf of Mexico	1982	3/year
Helgoland Roads	German Bight	1962	3/week
Arkona Basin (IOW)	South Baltic Sea	1979	5/year
Pärnu Bay	Gulf of Riga	1957	1/month to several/weeks
Bothnian Bay	Baltic Sea	1979	1/year
Gulf of Finland	North Baltic Sea	1979	1/year
North Baltic Sea	North Baltic Sea	1979	1/year
Eastern Gotland Basin	Central Baltic	1959	3/year
Gdansk Basin	Baltic	1986	3 or 6/year
Bornholm	Baltic	1979	7/year
Southern Gotland Basin	Baltic	1979	7/year
SMHI	Baltic	1982	Maximum 1/month
Saronic Gulf	Aegan Sea	1987	1/month
Gulf of Naples	Tyrrhenian Sea	1984	1/week since 1995
Gulf of Trieste	Northern Adriatic Sea	1970	1/month

In this context, the Helgoland Roads time series is considered one of the most valuable marine time series in the world. Situated in the southern North Sea near the island of Helgoland in the German Bight (Fig. 1.4), the Helgoland Roads is characterised by shallow depths (6–8 meters deep) with a well-mixed water column. This makes the area particularly susceptible to

MHWs, which can simultaneously impact both the bottom habitat and the water column, thereby affecting the entire marine community. Since 1962, the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research has been conducting daily sampling at Helgoland Roads to collect pelagic data such as phytoplankton, nutrient concentrations, and hydrographic parameters, including temperature (AWI, 2023; Wiltshire et al., 2010).

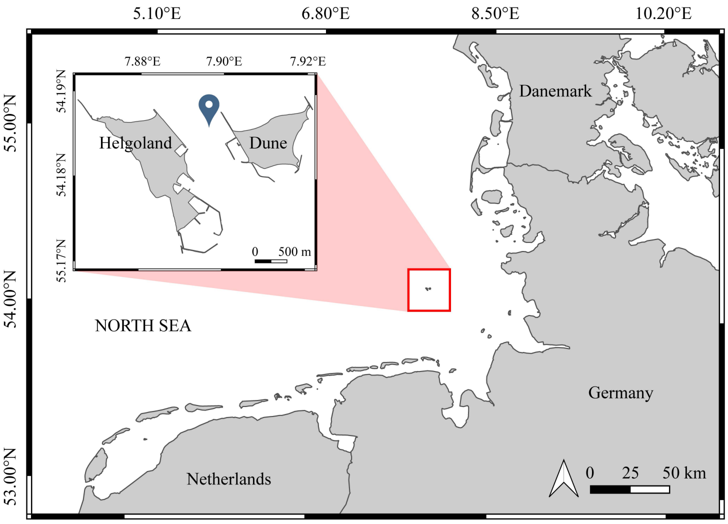

Figure 1.4. Location of the island of Helgoland in the German Bight, southern North Sea (red rectangle) and the Helgoland Roads sampling site (blue dot).

2.1.1. Warming trend & MHW events

At Helgoland Roads, long-term changes in sea surface temperature have been observed since 1962, with an increase of 0.3°C per decade, a higher rate than that observed in both the North Atlantic and North Sea (Amorim et al., 2023). Alongside this ongoing warming trend, a recent study has identified all MHWs that have occurred since 1962 (Giménez et al., 2024). The authors demonstrate that the intensity, the number of MHW days, as well as the average duration of MHWs have increased over time, specifically after 1990 (Fig. 1.5). While MHWs were recorded throughout the year, seasonal variation was also observed, with a higher MHW frequency in spring and at the end of summer/beginning of autumn (Giménez et al., 2024). As observed in other regions in the Northern Hemisphere (Wang & Zhou, 2024), most of the most intense heatwaves occurred during the summer.

Sea surface temperature anomalies at Helgoland Roads are positively correlated with those at Sylt Roads in the Wadden Sea and the wider North Sea (Amorim et al., 2023). This suggests that MHWs recorded at Helgoland Roads occur on a wider spatial scale. Therefore, while Helgoland Roads is a single point within the expansive surface area of the German Bight, the observed correlations with a broader regional scope underscore the relevance of using MHWs recorded at Helgoland Roads to understand the general MHW pattern in the German Bight.

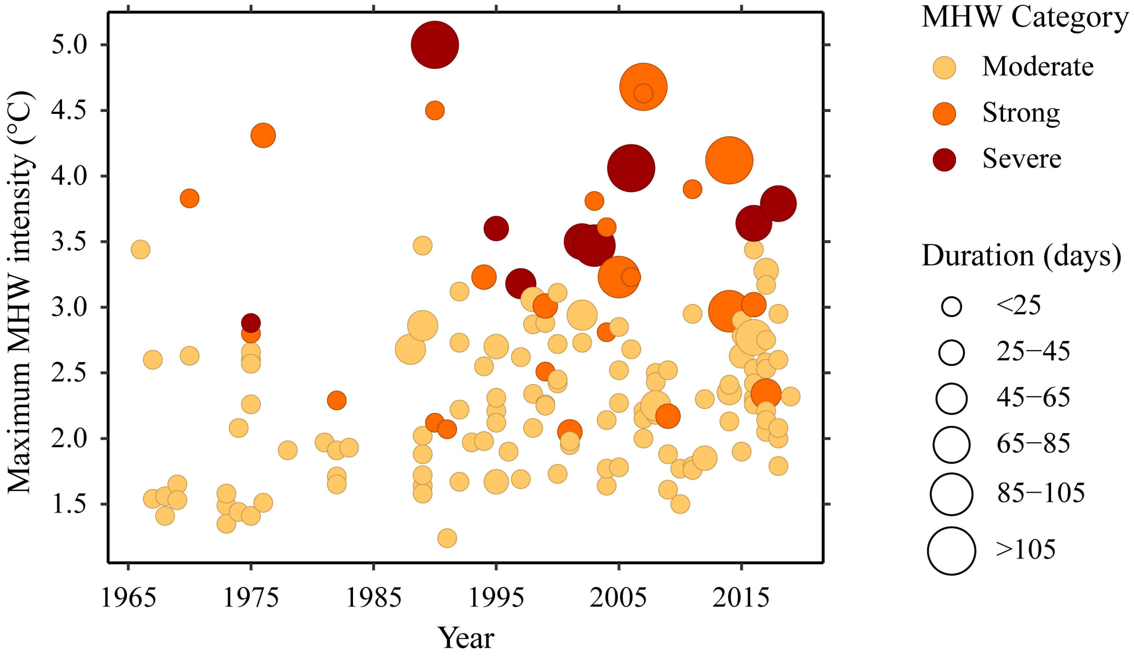

Figure 1.5. MHWs detected at Helgoland Roads from January 1962 to January 2019 using a fixed baseline. The figure was made using data collected from Giménez et al. (2024).

2.1.2. Zooplankton

In 1975, the Helgoland Roads time series was expanded to include meso- and macro-zooplankton (Greve et al., 2004). Zooplankton samples are collected three times a week and counted. The mesozooplankton species compartment is sampled using a Nansen net (150 µm, aperture 17 cm, and net length 100 cm) fitted with a flowmeter. The complete monitoring method was described by Greve et al. (2004).

Long term changes in the zooplankton community, and more specifically mesozooplankton (i.e., zooplankton from 0.2 to 20 mm) also occurred at Helgoland Roads, often linked to the long-term warming (Boersma et al., 2015; Deschamps et al., 2023; Marques et al., 2023). For the whole mesozooplankton community, two major shifts were observed since the beginning of the time series. During the 1980s, the abundance of most of the taxa including hydrozoans, ctenophores, cladocerans, and most of the copepods taxa, increased followed by a sharp decrease in abundance and biodiversity after the mid-2000s (Di Pane et al., 2023)

For copepods, drastic changes were observed, including a decline in the percentage of calanoid copepods relative to total abundance and an increase in copepod diversity during the late 1980s (Boersma et al., 2015). Changes were largely driven by decreases in the calanoids *Temora longicornis*, *Acartia* spp., *and Pseudo/Paracalanus* spp., while the opposite trend was noted for the cyclopoids *Oithona* spp., and *Corycaeus* spp. Additionally, changes in the functional community of copepods in response to warming have been documented, with smaller copepods with a short development time becoming more abundant at the expense of larger copepods with longer development time (Deschamps et al., 2023). Alongside these community shifts, changes in the phenology of key copepod taxa have been observed, with several important species showing earlier peaks of abundance in response to warming (Corona et al., 2024).

At Helgoland Roads, while most mesozooplankton taxa experienced sharp declines, decapod larvae showed a significant increase from 2006 onward (Di Pane et al., 2023; Marques et al., 2023). Within the decapod group, significant changes in the relative abundance of larvae were also observed. Larvae of the European shore crab, *Carcinus maenas* experienced the greatest decline in relative abundance (Marques et al., 2023). Meanwhile, larvae of the non-native species *Hemigrapsus* sp. (including *H. sanguineus* and *H. takanoi*) have increased since 2010 (Marques et al., 2023).

3. Gaps, objectives, and thesis outline

Despite the increasing attention given to MHWs in research, significant gaps in knowledge remain, and many important questions are yet to be addressed (Harvey et al., 2022; Joyce et al., 2023; Smith et al., 2023). Taxonomically, research tends to concentrate on well-known, charismatic species that are easier to monitor, leaving significant gaps in our understanding of lesser-studied taxa (Joyce et al., 2023). Additionally, much of the research focuses on the adult life stages of organisms, overlooking earlier stages that are crucial for recruitment success (Monteiro et al., 2023). In terms of field observations, many regions remain underexplored (see section 1.2.1), limiting our understanding of global MHW impacts (Joyce et al., 2023). Moreover, studies also tend to focus on abundance and diversity indices, overlooking the impact of MHWs on the phenology of the organisms. Experimentally, the general approach used to investigate MHW effects on a biological system often neglects the temporal scale inherent to a fluctuation, and most studies tend to focus on a single component of MHWs, paying insufficient attention to how multiple MHW components interact (see gaps in knowledge & methods for detailed gaps and hypotheses). Additionally, most studies investigate very intense MHWs in summer, when temperatures can exceed the thermal optimum for many organisms. Unfortunately, whether it is through experiments or field observations, the impacts of MHWs during other seasons, such as winter, are not well studied.

The general objective of this thesis is to investigate the effects of MHWs on community dynamics and species performance in the North Sea, with a focus on zooplankton organisms. The work is structured into two main blocks, reflecting distinct objectives and methodological approaches. **The first objective** concerns the effects of MHWs on mesozooplankton and is addressed in block I. This block, composed of **Chapters 3** and **4**, uses historical time series data to quantify associations between MHWs and mesozooplankton temporal dynamics in the North Sea. **The second objective** is the quantification of the effects of MHW components on larval development of two key brachyuran crabs of the North Sea. This objective is addressed in block II, composed of **Chapter 5** and **6.** This block moves from the community and time series analysis to focus on the levels of individuals and populations. Here, laboratory experiments were used to investigate how current and future MHWs might affect the survival, growth, and phenology of decapod crustacean larvae.

In what follows, **Chapter 2** presents the **Gaps in knowledge & methods**, including the general approaches used so far to investigate biological system responses to fluctuations, as well as the methods and model systems used throughout the thesis. **Block I**, including **Chapter 3** and **4**, addresses the impact of MHWs on mesozooplankton communities in the North Sea. **Block II**, comprising **Chapter 5** and **Chapter 6**, focuses on the impact of MHWs on populations and individuals. Finally, **Chapter 7** provides a **General Discussion**, synthesising key findings, exploring implications, and suggesting future research directions.

Gaps in knowledge & methods

CHAPTER

2

1. General approaches to studying MHW impacts on biological systems

Nowadays, the primary methods for studying biological responses to MHWs include small- and large-scale laboratory experiments, as well as field observations (Joyce et al., 2023). Each of these approaches has unique strengths and limitations. Laboratory experiments, such as microcosms, offer highly controlled conditions and allow for numerous replicates, increasing statistical reliability. However, this control comes at the cost of reduced ecological realism, and microcosms generally focus on single-species systems, limiting their ability to capture complex trophic interactions (Boyd et al., 2018; Gerhard et al., 2023). In contrast, large-scale experiments, like mesocosms provide greater ecological realism and facilitate the study of trophic interactions while still maintaining some environmental control (Stewart et al., 2013). However, the higher costs and logistical complexities associated with mesocosms often result in fewer replicates, thus reducing statistical power (Boyd et al., 2018; Gerhard et al., 2023). Finally, field observations offer the highest degree of realism and can encompass a wide array of environmental variables. Yet, the inherent complexity of natural systems makes it difficult to isolate the specific effects of MHWs. Additionally, climate variability can complicate the task of drawing clear connections between MHWs and biological responses.

Although each approach can be used independently, with the choice largely depending on the specific research question, combining field observations with laboratory experiments within a broader framework can significantly improve the understanding of how biological systems respond to MHWs. However, to achieve this integration effectively, several key factors must be considered.

First, the environment should not be viewed as static but rather dynamic. Natural ecosystems are characterised by variability in environmental conditions (hereafter fluctuations), whether predictable, such as seasonal or daily light cycles (Reed et al., 2010), or unpredictable, like extreme weather events, including MHWs (Bailey & van de Pol, 2016). For instance, in the context of global warming, it is widely recognised that temperature fluctuations within a given environment can affect biological systems through mechanisms that differ from those operating in constant environments (Gerhard et al., 2023). The challenge is that many studies still tend to focus on average temperature conditions and conduct experiments where variables remain constant over time (i.e., static designs), raising concerns about the accuracy of predicting biological responses to MHWs. For instance, predictable fluctuations can favour phenotypic plasticity, a trait that would not be selected for in a constant environment (Kroeker et al., 2020).

Second, it is widely acknowledged that the complexity of environmental changes makes single-stressor experiments insufficient for accurately assessing and predicting the effects of global change on biological systems (Gunderson et al., 2016; Todgham & Stillman, 2013; Wernberg et al., 2012). Multi-stressor experiments are now widely used to generate more realistic inferences about global change effects on a biological system (Gunderson et al., 2016). An organism subjected to multiple stressors can show three different kinds of responses (Todgham & Stillman, 2013). Multiple stressors can have additive effects, where the combined response is equal to the sum of the individual responses to each factor, making them independent of one another. However, in reality, environmental stressors often interact in more complex ways, leading to either synergistic (where the combined impact is greater than the sum of individual effects) or antagonistic effects (where the combined impact is less than the sum) (Koussoroplis et al., 2017). These interactions can lead to different outcomes than those observed in single-factor experiments. Similarly, to how multiple stressors are essential for understanding biological responses to global changes, it is equally important to study MHWs by manipulating multiple components, such as timing, duration, frequency, and magnitude (Fig. 2.1) (Gerhard et al., 2023). Nevertheless, such approach is still not widely used. A recent review found that only 7 % of studies considered the role of MHW duration, and none conducted fully orthogonal experiments to investigate interactions between different components (Joyce et al., 2023). Focusing on just one aspect of MHWs provides an incomplete understanding of their full impact on biological systems. Therefore, new experimental designs that explore the interactive effects of various MHW components are urgently needed.

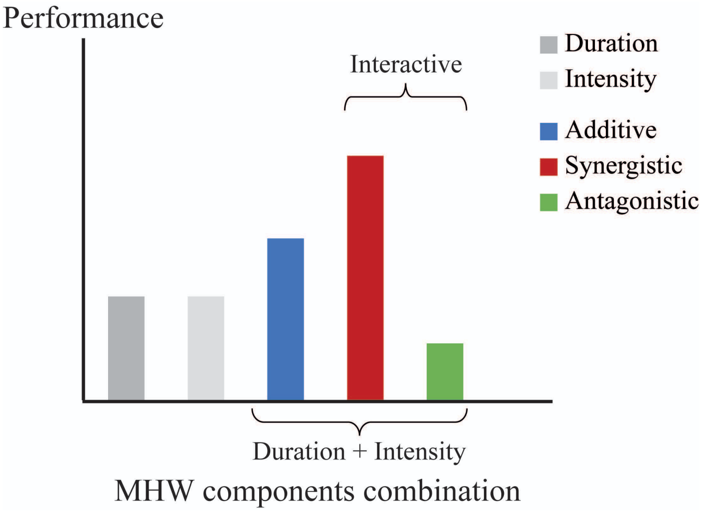

Figure 2.1. Possible effects of MHW components (here duration and intensity) on the performance of an organism.

Last, a critical factor that influences how biological systems respond to MHWs is the time-dependent nature of the event (Rezende et al., 2014). MHW impacts on biological systems will depend heavily on the time frame over which these changes occur (Gunderson et al., 2016). Moreover, the interactive effects of multiple components, such as intensity and duration, may vary depending on when they occur. For instance, increasing the duration of a MHW at the same time as increasing its intensity, or at a later point, could lead to different outcomes (Gunderson et al., 2016). Additionally, since an organism's biological traits dictate its response to MHWs, it is crucial to match the temporal scale of the MHW with the biological system under study (Giménez, 2023). For instance, the timing of a MHW in relation to key life events, such as reproduction, growth, and recruitment, may have a much greater impact on a population than if the MHW occurred outside these critical periods (Bertocci et al., 2005; Smith et al., 2023).

Therefore, experiments studying MHWs (1) under dynamic conditions, rather than static ones, (2) manipulating multiple components and (3) including variation in the MHW timing, are crucial for developing a mechanistic understanding of their effects on biological systems. In addition, field observations are crucial for understanding how these fluctuations affect organisms in real world. When used together, these approaches will allow for a more realistic assessment of how MHWs influence biological responses in natural ecosystems.

2. The need for new methods

In order to provide a wider framework and global understanding of MHW impacts on biological systems, this thesis relies on both field observations (Block I) and laboratory experiments (Block II).

2.1. Block I: Field observations

As explained in section 1, a key limitation of field observations is the uncertainty regarding which environmental parameters or disturbances, such as MHWs, impact biological systems, due to natural variability. Even when a change can be identified and is correlated with a disturbance, it is not always clear that the relationship between the disturbance and the response of the biological system is causal (Underwood, 1991). Additionally, the unpredictable nature of MHWs poses challenges in accurately quantifying their effects on communities. Most studies in this field have been opportunistic, focusing on a single large-scale event and examining community dynamics before, during, and after the event. However, these studies typically lack replication over time and often fail to fully assess MHW impacts, as only one impacted period is available for comparison. Such designs make it difficult to determine whether the observed changes are specific to the MHW event or part of an unrelated disturbance (Underwood, 1992).

Chapter 3 addresses this crucial point by employing a new method based on a robust design with multiple temporal replicates, as well as control and impact units to properly assess MHW impacts on the mesozooplankton community dynamics in the North Sea. This method is grounded in a Before-After-Control-Impact (BACI) design, a well-established and powerful statistical tool in environmental impact studies (Seger et al., 2021). The BACI design is particularly effective in distinguishing between pulse and press disturbances, and allows the comparison between the state of a community affected by a disturbance (impact treatment) and an undisturbed control (Underwood, 1991). It helps to account for natural or existing differences between a control and impact treatment, allowing a better estimation of the actual impact of a disturbance (Seger et al., 2021). In traditional BACI designs, control and impacted sites are defined as spatial units and are sampled simultaneously (Conner et al., 2016). However, as discussed in Section 2.1 of the introduction, long-term time series with high temporal resolution often compromise spatial resolution, limiting data collection to a single location. In **Chapter 3**, the BACI approach was modified by defining control and impact units based on time, rather than space.

Another limitation in current studies on MHW impacts using field observations is the omission of the event's timing (see section 1). To date, most studies on the effects of MHWs on marine communities have focused on single long-term events lasting months to years. However, seasonality, or seasonal variations, is a fundamental characteristic of nearly all ecosystems and plays a crucial role in shaping communities worldwide. In marine ecosystems, seasonal patterns significantly influence organisms, populations, and communities. Organisms rely on environmental cues, such as changes in photoperiod and temperature, to adjust their biochemical and physiological processes (Mackas et al., 2012). Typically, organisms with short life cycles may respond to MHWs on much shorter timescales, with responses varying depending on the season in which the MHW occurs. **Chapter 3** addresses this gap by differentiating the effects of MHWs depending on the season in which they occur.

Moreover, depending on when a MHW occurs, the phenological timing of organisms might be impacted. While MHW effects on zooplankton communities have been well described (Beltrán-Castro et al., 2020; Brodeur et al., 2019; McKinstry et al., 2022; Suryan et al., 2021), these studies primarily focus on changes in abundance and community structure. To date, most reported changes in phenology have been observed in terrestrial plants (Cremonese et al., 2017; Jentsch et al., 2009; Orsenigo et al., 2015), leaving a gap in our understanding of phenological responses to MHWs in marine ecosystems. **Chapter 4** addresses this knowledge gap by employing a semi-quantitative method to classify copepod blooms through algorithmic estimation of bloom traits. It investigates whether MHWs occurring before and during a bloom can influence phenological timing and bloom duration.

2.2. Block II: Laboratory experiments

As highlighted in section 1, most of the studies using laboratory experiments to address the effect of MHWs on species performance concentrate on a single component of the MHWs, overlooking the cumulative effects of various components such as duration and timing. In the **second block**, this problem was addressed by conducting a complex heat experiment, where three components of the MHWs, namely the duration, the magnitude, and the timing, were manipulated to investigate MHW effects on larval performance.

Another limitations arises from the common practice of measuring MHW impacts against a constant baseline temperature. As highlighted in section 1, this approach does not adequately separate the effect of the fluctuation inherent to the heatwaves from the effect of an increased average (but constant) temperature. As there is a growing body of literature showing that biological responses to fluctuating environments differ from those occurring under constant conditions (Gerhard et al., 2023; Kingsolver et al., 2015; Niehaus et al., 2012), there is a need to properly disentangle the effect of a MHW from those attributed to global warming. **Block II** of this thesis also adresses this concern.

3. Model systems

The following sections outline the different model systems used in this thesis to address the main objectives and bridge existing gaps in knowledge and methodology. In **Block I**, the mesozooplankton community of the North Sea was used as a model system to investigate the impact of MHW on community dynamics using field observations. In **Block II**, the larvae of two decapod crustacean species were studied to assess the effects of MHW on larval performance using laboratory experiments.

3.1.1. Model community: mesozooplankton

In marine ecosystems, plankton form the base of the food web, and any changes in the composition and abundance of primary (i.e., phytoplankton) and secondary (i.e., zooplankton) producers can have direct effects on the entire food web and associated ecosystem services. Within the zooplankton community, mesozooplankton comprises organisms ranging in size from 0.2 to 20 mm (Sieburth et al., 1978) and primarily consists of small gelatinous zooplankton, pelagic larval stages (i.e., meroplankton) and crustacean plankton such as copepods and cladocerans. Mesozooplankton feed on detritus, graze on phytoplankton, and are a key predator of microzooplankton and other mesozooplankton (Buitenhuis et al., 2006). They are a major food source for zooplanktivorous organisms, including jellyfish, fish larvae, and small pelagic fish (Sommer et al., 2002). Consequently, mesozooplankton are crucial for linking the microbial loop to the classic food web, playing a significant role in transferring energy from primary producers to higher trophic levels (Helaouët & Beaugrand, 2007). Therefore, changes in mesozooplankton communities can have profound impacts on ecosystems.

More than their ecological importance, mesozooplankton, as ectothermic organisms with short lifespans, have a metabolism and development closely tied to abiotic conditions (Richardson, 2008), making them particularly sensitive to environmental changes, including temperature. Consequently, global warming and MHWs can have drastic repercussions on mesozooplankton communities, potentially leading to shifts in community composition (Alvarez-Fernandez et al., 2012; Di Pane et al., 2023), species distribution (Beaugrand, 2002), and phenology (Edwards & Richardson, 2004), which could, in turn, impact the entire food web and associated ecosystem services.

As for many communities in marine ecosystems, seasonal variation plays a crucial role in shaping mesozooplankton communities. The North Sea exhibits a clear seasonal production cycle (Quante et al., 2016). The spring season brings higher concentrations of dissolved inorganic nutrients, increased temperatures, and more sunlight, all of which promote phytoplankton growth and result in a large phytoplankton bloom (Wiltshire et al., 2008). This surge in food availability triggers a subsequent rise in zooplankton production, leading to a zooplankton bloom that follows the phytoplankton bloom. In contrast, during winter, reduced light and lower temperatures cause a decline in phytoplankton levels, which in turn reduces zooplankton populations. While the spring mesozooplankton bloom is considered the most important in the North Sea, seasonal bloom timing can vary depending on the species studied. For instance, the calanoid copepod *Temora longicornis* typically blooms in spring, whereas the cyclopoid copepod *Oithona* spp., tends to peak in the beginning of summer, and copepods from the Harpacticoida order are more likely to bloom in autumn (Deschamps et al., 2023).

Their position at the base of the food web, as well as their sensitivity to temperature changes, raises important questions about how the mesozooplankton community will respond to MHWs. Cold-adapted species may struggle during MHWs, while warm-adapted species could benefit from it, potentially driving shifts in community structure. But will these effects differ depending on the season in which the MHW occurs? If this is the case, zooplankton responses to winter MHWs may be less severe than those in spring and autumn, where MHWs could have direct impacts on the growth or decline phase. The timing of MHWs during growth periods could also disrupt their phenology, leading to mismatches with higher trophic levels and triggering far-reaching consequences for the entire ecosystem. **Chapters 3** and **4** explore these questions, offering new insights into how seasonal MHWs influence shifts in mesozooplankton community structure and phenology, and how these changes may ripple through marine ecosystems.

3.1.2. The decapod crustaceans *Carcinus maenas* & *Hemigrapsus sanguineus*: life history and the larval phase

While the impact of warming on decapod crustaceans is well-documented, a proper understanding of MHW effects on larval performance is currently missing (see **Chapter 1** section 1.2.3). In this thesis, larvae from two decapod crustacean species commonly found in the North Sea were used as model organisms.

The first species studied was *Carcinus maenas*. *C. maenas* is widely distributed along most of the European coastline, its native habitat (Carlton & Cohen, 2003). It is an important species, playing a central role in the benthic ecosystem, but also commercially fished for use as bait or food in Europe (Klassen & Locke, 2007; Young & Elliott, 2020). *C. maenas* is also known as a global invader (Klassen & Locke, 2007) and one of the 100 worst invaders in the world (Simberloff & Rejmanek, 2019).

Like many decapod crustaceans, *C. maenas* exhibits a biphasic life cycle that consists of a pelagic larval phase and a benthic adult phase (Klassen & Locke, 2007). After hatching, the larvae progress through four stages known as zoea, before undergoing metamorphosis into the megalopa stage (Dawirs, 1985; Spitzner et al., 2018). At this point, the megalopa are semi-benthic. Following a second metamorphosis, they transition into the juvenile stage, settling into the benthic habitat (Fig. 2.2). In the North Sea, as in much of Europe, reproduction typically occurs from April to November (d'Acoz, 1993), with the main hatching activity from the end of May to mid-July (Dawirs, 1985) when intertidal temperatures reach 15 °C, allowing for embryo development. Indeed, embryonic and larval development of *C. maenas* are primarily influenced by temperature, which causes larval abundance to often peak in spring rather than late summer or early autumn (Dawirs, 1985). Although larvae can tolerate a wide range of temperatures, their survival sharply decreases below 12.5 °C, with no larvae reaching the megalopa stage below 10 °C (deRivera et al., 2007). Similarly, larvae cannot successfully develop to the megalopa stage above 25 °C (deRivera et al., 2007).

The second species used in **Block II** was the Asian shore crab, *H. sanguineus*. *H. sanguineus* is native to the east coast of Asia and has successfully established non-native populations along the coasts of North America (McDermott, 1991) and Northern Europe (Dauvin, 2009; Jungblut et al., 2017). In the European coast, larvae of *H. sanguineus* appear to thrive at high temperatures where those of *C. maenas* struggle to grow (Espinosa-Novo et al., 2023; Giménez et al., 2021). In North America, *H. sanguineus* has led to important changes in the benthic community (Gerard et al., 1999), displacing native species such as the mud crab and the other invader *C. maenas* (Epifanio, 2013). The success of *H. sanguineus* in non-native habitats can be attributed to an extended spawning season and high fecundity, as well as superior competition for space and food (Epifanio, 2013). Moreover, direct predation by *H. sanguineus* on newly settled *C. maenas* was discovered on the east coast of North America, which was probably linked to the recruitment failure of *C. maenas* in shared areas (Lohrer & Whitlatch, 2002).

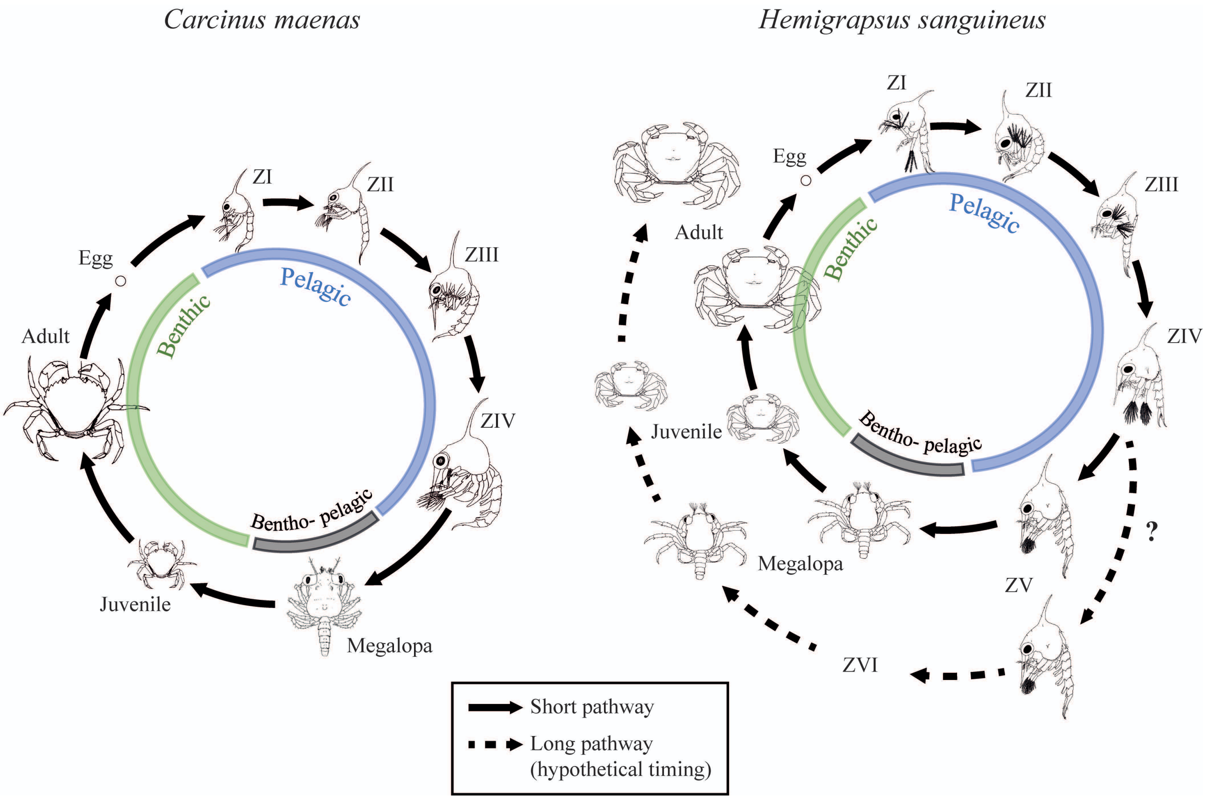

Figure 2.2. Life cycle of *C. maenas* (left) and *H. sanguineus* (right). Embryos are carried by the females, followed by pelagic zoeal stages, then the semi benthic megalopa, and benthic juvenile and adult stages. *H. sanguineus* can develop through two distinct pathways: a longer pathway and a shorter one. The timing that triggers the longer developmental pathway is currently unknown, and the position of the arrow indicating this process is hypothetical. Z: zoea, I-VI: zoeal stages. Drawings of the different stages were adapted from Torres et al. (2021) for *C. maenas* and Kornienko et al. (2008) for *H. sanguineus*.

In contrast to *C. maenas*, *H. sanguineus* thrives at temperatures higher than 15 °C (Epifanio, 2013; Espinosa-Novo et al., 2023). While no data currently exist on the upper thermal tolerance of *H. sanguineus*, it is likely above 27 °C, as larvae have been observed to successfully develop and reach the megalopa stage at this temperature (Deschamps, *pers. obs.*). While its distribution is currently limited to regions where summer temperatures are above 12-

13 °C (Stephenson et al., 2009), limiting further poleward expansion (Giménez et al., 2020), there seems to be no barrier preventing the species from eventually expanding into southern Europe, including the Mediterranean Sea.

H. sanguineus exhibits a biphasic life cycle, developing though five zoea stages before undergoing metamorphosis into the megalopa stage (Hwang et al., 1993). In contrast to *C. maenas*, *H. sanguineus* larvae have the ability to develop through two different pathways: a short pathway when environmental conditions are suitable and a longer pathway with one extra zoea stage (Zoea VI) under stressful environmental conditions (Espinosa-Novo et al., 2023) (Fig. 2.2). In the North Sea, reproduction generally begins in the spring (April-May) and continues until early autumn, with the summer months being the most productive season (Dauvin & Dufossé, 2011).

The coexistence of *C. maenas* and *H. sanguineus* along the coasts of Europe and North America raises important questions about how these species will respond to MHWs. *C. maenas* larvae are constrained by warmer temperatures, while *H. sanguineus* benefits from such conditions, potentially giving the latter a competitive advantage during a MHW. This difference in thermal tolerance could drive shifts in community dynamics as MHWs become more frequent and severe. Furthermore, the distinct developmental strategies of the two species, *C. maenas* following a traditional larval development, while *H. sanguineus* is able to switch between developmental pathways, adds another layer of complexity.

These differences in both thermal tolerance and plasticity raise a key question: Will MHWs benefit both species? Or will they disproportionately favour *H. sanguineus*, potentially opening new windows of thermal opportunity (Giménez et al., 2020), leading to competitive exclusion of *C. maenas*? In the case where one species benefits over the other, one of the main hypotheses is that intense MHWs could promote the success of warm-adapted species like *H. sanguineus*, while negatively impacting native species such as *C. maenas*. Furthermore, due to stage sensitivity in decapod crustaceans, the timing of these events may be critical, as MHWs occurring during vulnerable developmental stages could exacerbate these effects. These are some of the critical questions and hypotheses that the **Chapters 5** and **6** aim to explore, offering insights into the role of MHWs in facilitating biological invasions.

BLOCK I: Field observations

Mesozooplankton community dynamics under marine heatwaves

CHAPTER

3

Responses of the mesozooplankton community to marine heatwaves: challenges and solutions based on a long-term time series

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RESEARCH ARTICLE

Responses of the mesozooplankton community to marine heatwaves: Challenges and solutions based on a long-term time series

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Abstract

1. Marine heatwaves (MHWs) are extreme weather events that have major impacts on the structure and functioning of marine ecosystems worldwide. Due to anthropogenic climate change, the occurrence of MHWs is predicted to increase in future. There is already evidence linking MHWs with reductions in biodiversity and incidence of mass mortality events in coastal ecosystems. However, because MHWs are unpredictable, the quantification of their effects on communities is challenging.
2. Here, we use the Helgoland Roads long-term time series (German Bight, North Sea), one of the richest marine time series in the world, and implement a modified before-after control-impact (BACI) design to evaluate MHW effect on mesozooplankton communities. Mesozooplankton play an essential role in connecting primary producers to higher trophic levels, and any changes in their community structure could have far-reaching impacts on the entire ecosystem.
3. The responses of mesozooplankton community to MHWs in terms of community structure and densities occurred mainly in spring and autumn. Abundances of seven taxa, including some of the most abundant groups (e.g., copepods), were affected either positively or negatively in response to MHWs. In contrast, we observed no clear evidence of an impact of summer and winter MHWs; instead, the density of the most common taxa remained unchanged.
4. Our results highlight the seasonally dependent impacts of MHWs on mesozooplankton communities and the challenges in evaluating those impacts. Long-term monitoring is an important contributor to the quantification of effects of MHWs on natural populations.

Keywords: BACI design – community structure – Helgoland Roads – marine ecosystems – marine heatwaves – North Sea – zooplankton

INTRODUCTION

As consequence of anthropogenic climate change, the frequency and magnitude of extreme weather events such as droughts, storms, and floods are expected to increase in the coming decades (IPCC, 2022). This predicted increasing frequency of extreme events, including marine heatwaves (MHWs) is currently causing ecological and socio-economic concern (Holbrook et al., 2020; Oliver et al., 2021). Mass mortalities, habitat loss, shift in species distributions and reduction in biodiversity in all living compartments (Smith et al., 2023), including plankton (Arteaga & Rousseaux, 2023; Brodeur et al., 2019; Nielsen et al., 2021), macroalgae (Weitzman et al., 2021), and sea birds (Jones et al., 2018) have been attributed to intense and long MHWs. These effects of MHWs on biological systems may have profound socioeconomic implications on a global scale, as MHWs compromise essential ecosystem services, including provisioning (i.e., fisheries), cultural (i.e., loss of iconic species) and regulating (i.e., carbon sequestration) (Smith et al., 2021).

A critical point in the quantification of MHWs effect on marine ecosystems is their lack of predictability, although some forecasting methods have been developed recently (Jacox et al., 2022). Therefore, most studies in this area have been opportunistic, concentrating on a single large-scale event (Table S3.1). Indeed, most studies are based on individual MHW events, examining the differences in processes or the density of species of interest before, during, and after events. Some studies also compare conditions during the MHW to those in the same season but in a year without recorded heatwaves. In both cases, the control condition is restricted to a single period, which is used as a reference to quantify MHW impacts. Given the unpredictability of MHWs, such designs have been one of the most effective options and have provided the first warnings about the effects of MHWs on organisms. As longer time series become available, there is the opportunity of applying stronger designs, based on several controls and impacted years, which essentially means that one obtains a higher level of replication.

Another important point is that most studies on MHWs are limited to specific regions that have experienced one single intense event (Table S3.1). For instance, approximately 75 % of the studies we identified (Table S3.1) exploring MHW impacts on communities using time series data, were carried out either in the North Pacific Ocean, during the 2013-2016 MHW ("the Blob") or in the Indian Ocean during the 2010-2011 MHW (see also Joyce et al., 2023). Other regions, such as the North Sea, have been overlooked. Despite experiencing numerous heatwaves ranging from normal to severe over the past decades (Giménez et al., 2024), a comprehensive understanding of community changes in response to MHWs in the North Sea is still missing.

Here, we quantify the effect of MHWs on a coastal mesozooplankton community, using a modified BACI design, based on a high sampling frequency long-term time series (Helgoland Roads, North Sea). The Helgoland Roads (HR) time series (Wiltshire et al., 2010, Boersma et al., 2017, Amorim et al., 2023) is a unique data set and one of the richest marine time series in the world. Located near the island of Helgoland in the German Bight (54°11'18 "N 7°54' E), HR started in 1962 with daily measurements of sea surface temperature, nutrients and phytoplankton. In 1975, the dataset was expanded to include zooplankton samples taken three times a week. At HR, multiple MHW events were recorded from 1962 to 2018 (Giménez et al., 2024). Here, MHWs are defined as periods of time ≥ 5 days during which seawater temperatures exceed the 90th quantile (i.e., Q90th percentile) of a baseline temperature time series (Hobday et al., 2016). We used the long MHW events (i.e., all MHWs of a duration ≥ 14 days to meet the conditions required for our design) occurring at specific seasons as replicate units. We then compared mesozooplankton densities, diversity, and community structure during periods of MHWs with those observed in the same times and seasons of "control" years where MHWs did not occur. This comparison aimed to understand the specific effect of MHWs on the mesozooplankton community structure, diversity and density depending on the season in which the event occurred. This design enabled us to (i) achieve replication at the level of MHW events, (ii) compare responses in terms of community structure against replicate controls of season response, and (iii) quantify season-specific effects of MHWs on key taxa in terms of density and diversity.

The quantification of MHWs effects on mesozooplankton (i.e., zooplankton from 0.2 to 20 mm) is central to understand their impact on the entire marine food web and associated ecosystem services. Mesozooplankton play a central role in the trophodynamics of pelagic ecosystems, as well as in nutrient recycling and export of nutrients and carbon to depths (Helaouët & Beaugrand, 2007; Steinberg & Landry, 2017). In addition, because of their short generation time, mesozooplankton, including copepods, respond rapidly to temperature increases (Richardson, 2008) and are therefore likely to respond to MHWs.

During MHWs, zooplankton are subjected to rapid and extreme temperature increases over short periods. This sudden thermal stress can exceed their thermal tolerance limits, leading to significant changes in physiological and life history traits, such as altered metabolic rates, accelerated development, and potentially mortality if temperatures surpass survival thresholds (Smith et al., 2023). Species with narrow thermal tolerance ranges are particularly vulnerable to MHWs compared to those with broader tolerances (Smith et al., 2023). Furthermore, invasive species, smaller species, and warm-adapted species may thrive during intense MHWs at the expense of native, larger, and cold-adapted species (Evans et al., 2020; Gubanova et al., 2022). The timing of MHWs is also critical; if they coincide with key biological events such as reproduction, they can shift species phenology, potentially causing mismatch situations with predators (Cushing, 1990) which could then have strong repercussions on higher trophic levels. While MHWs can have similar effects to long-term warming, the latter involves a gradual increase in average temperatures over decades, allowing more time for mesozooplankton to adapt or shift their distribution. In contrast, the rapid onset of MHWs leaves insufficient time for adaptation or migration, leading to abrupt and sometimes irreversible changes in community composition and ecosystem dynamics. For instance, in the Tasman Sea, a shift in the zooplankton community was recorded in response to the 2015-2016 MHW (Evans et al., 2020): smaller warm-water copepods dominated the community and gelatinous zooplankton increased in density, replacing large temperate or cold-water zooplankton, including copepods, Cladocera, and Appendicularia. Likewise, the 2014-2016 Pacific MHW resulted in an increase in warm-water copepod density in autumn, which persisted through the winter months (McKinstry et al., 2022). In the Gulf of Alaska, the 2014-2016 MHW resulted in increased zooplankton densities, particularly copepods (Batten et al., 2022). The studies mentioned above focus on single long-term events with durations of months to years. However, because zooplankton organisms have short life cycles, we expect responses to MHWs occurring at shorter time scales. Indeed, seasonal variations play a crucial role in shaping many communities in the world, including zooplankton, due to the annual cycle of environmental conditions such as temperature, light, and nutrients (Mackas et al., 2012). These factors influence primary production, which in turn affects food availability for zooplankton. For example, in spring, increased sunlight and warmer temperatures typically lead to phytoplankton blooms (Wiltshire et al., 2008). In response to this increase in food availability, zooplankton also increase in density. Conversely, during autumn and winter, reduced light and lower temperatures can decrease phytoplankton levels, leading to a decline in zooplankton. These seasonal fluctuations not only impact the density and composition of the community but also affect the broader marine ecosystem. Changes in mesozooplankton populations can influence the distribution and density of higher trophic levels, including fish (Beaugrand et al., 2003).

Therefore, we hypothesise that the mesozooplankton response to MHWs should vary among seasons. For instance, planktonic responses to winter MHWs may be less severe than those in other seasons as biological activity is lower during this time (van Beusekom & Diel-Christiansen, 2009). Moreover, temperature alone is not the sole driver of mesozooplankton changes. Other factors, such as light availability, turbidity, and phytoplankton, play equally significant roles alongside temperature. We hypothesise that spring and autumn MHWs could influence community structure and densities of mesozooplankton taxa, especially those undergoing growth or decline phases. In the North Sea, spring and autumn MHWs are unlikely to exceed the thermal tolerance of mesozooplankton taxa. For instance, *T. longicornis*, a cold-temperate species, has an upper thermal limit of around 22.5 °C (Halsband-Lenk et al., 2002). Given that spring and autumn temperatures are usually around 6 °C and 13 °C respectively (Amorim et al., 2023), it is improbable for temperatures to reach such high levels during these seasons even in the case of MHW events. Consequently, heatwave events could promote an earlier and faster growth period for taxa peaking in spring. Similarly, for taxa that peak in late summer or early autumn, MHWs could lead to an extended and slower decline phase, up to a point where temperatures fall below the lower thermal limits. In contrast, summer MHWs are more intense than those in other seasons, often far exceeding the intensity threshold, with most of the top 10 events (intensity larger than three times the difference between the threshold and the climatology) identified in summer (Giménez et al., 2024). Therefore, we anticipate a shift in the community structure of mesozooplankton, favouring warm-water assemblage over cooler-water ones.

MATERIALS & METHODS

The Helgoland Road Time series

Mesozooplankton counts (density: ind.m^3) from the HR dataset (Boersma et al., 2017; AWI et al., 2023; Wiltshire et al., 2010) were used in this study. From 1975 onwards, monitoring of mesozooplankton has been conducted near the island of Helgoland in the German Bight (54°11'18 "N 7°54' E). Mesozooplankton are sampled three times a week using a Nansen net (aperture 17 cm, net length 100 cm) fitted with a 150 µm mesh net coupled with a flowmeter. The complete monitoring method was described by Greve et al. (2004). The current analysis of the mesozooplankton response to MHWs was carried out for the period 1975-2018. Mesozooplankton taxa identified over the complete time period and with a mean relative density higher than 3 % were extracted from the HR dataset (PANGAEA doi:

10.1594/PANGAEA.872023) (Table 3.1). This threshold was applied to exclude very rare (zero-inflated) taxa while still preserving a significant portion of the overall mesozooplankton community. This approach ensures that the analysis maintains sensitivity and minimises the potential influence of rare taxa, thereby enhancing the reliability and interpretability of the results.

Table 3.1. Mesozooplankton identified at HR and used in the study. Most abundant (i.e., relative density < 3 %) are represented in bold. For copepods, other taxa were only used to calculates density at order level and diversity indices. For non-copepods, other orders were only used to calculates diversity indices.

	Order	Taxa
Copepods	**Calanoida**	*Calanus* spp., ***Acartia* spp.**, *Centropages* spp. ***Pseudo/Paracalanus* spp.**, ***Temora longicornis***
	Cyclopoida	***Oithona* spp.**, *Corycaeus anglicus,* other non-identified
	Harpacticoida	*Euterpina acutifrons*, other non-identified
		Copepoda nauplii
Non-Copepods	Amphipoda, **Cladocera**, Cumacea, Decapoda, Isopoda, Mysida, Pantopoda	**Annelida larvae**, **Appendicularia**, **Chaetognatha**, **Cirripedia larvae, Echimodermata larvae**

To assess the impacts of MHWs on the mesozooplankton community, the timing and duration of MHWs detected at HR between 1975 and 2018 were used and obtained from Giménez et al. (2024, see their supplemental information, Table S3.1). Sea surface temperature data (°C) used for MHW detection are measured on a work daily basis directly from the research vessel using a thermometer at the same sampling site as the mesozooplankton. Due to strong tidal currents and shallow depth, the water column at the sampling site is well mixed, ensuring that depth does not affect temperature. At HR, MHWs show a positive correlation with atmospheric heatwaves across the German Bight (Giménez et al., 2024). Additionally, sea surface temperature anomalies are positively correlated with those at Sylt Roads in the Wadden

Sea and the wider North Sea (Amorim et al., 2023). This suggests that MHWs recorded at HR occur on a wider spatial scale, encompassing the German Bight. Therefore, the observed correlations with broader regional data underscore the relevance of using MHWs recorded at HR to understand the general MHW pattern in the German Bight.

All analyses are based on the detection of MHW events using a fixed 30-year baseline period set between the 1st January 1962 and the 31st December 1991 (Giménez et al., 2024) to calculate the climatology and identify deviations from this baseline (Hobday et al., 2016; Oliver et al., 2021). For each specific day, all temperature values within a specific window, over all the baseline, are pooled together and organised into a frequency distribution. From this distribution, the 90th quantile (Q90) is calculated, identifying the temperature below which 90 % of the observations fall (See Giménez et al., 2024 for more information). An event of unusually warm sea temperature will be then identified as a MHW if the temperature exceeds this Q90 for more than five days (Hobday et al., 2016). From this MHW dataset, only the longest events (i.e., $\geq$ 14 days) were selected to meet the conditions required for our design.

Giménez et al. (2024) provided both a fixed and a 30-years shifting baselines and comparing the response to MHW using both baselines will be insightful. However, here, we will focus solely on the fixed baseline for two reasons. First, the comparison between both baselines is valid only for the second part of the time series as it assumes that organisms experienced the MHW according to the previous 30 years of temperature. As a result, the shifting baseline produced a shorter time series with fewer number of MHW and, consequently, fewer replicate units, directly reducing the power of the test. Second, it would be more informative to create species-specific shifting baselines calibrated with the time scale of mesozooplankton adaptive responses to temperature, rather than using a fixed 30-year duration. However, we lack information about the time scale of adaptation of mesozooplankton in the German Bight. Interestingly, MHW effects observed in this study (see results) might not be detected using a shifting baseline, as some replicate units currently classified under the MHW treatment would be reassigned to the control years. This could potentially mask the effects of thermal fluctuations on organisms.

BACI design

One approach that helps to understand the effect of natural or anthropogenic disturbance on a community is the use of a Before-After-Control-Impact (BACI) design (Underwood, 1991). BACI allows the comparison of the state of a community when a disturbance occurs, defined as impact treatment (**I**) with a control treatment (**C**) in which no disturbance was recorded (Underwood, 1991). Both, the impact and the control treatment are sampled before (**B**) and after (**A**) the disturbance. The BACI design typically defines control and impacted conditions as spatial units, with both control and impacted sites sampled simultaneously (Conner et al., 2016). Because our variation was temporal rather than spatial, we modified the design (Fig. 3.1) by defining replicate units in time, with each unit representing a different year. Thus, in our study, the before and after periods refer to the week preceding and following the MHW, respectively. The control refers to a period of a year (defined by week of year) without MHW, while impact refers to a period of a different year (same week in the year as the control, ± three days), when a MHW occurred. To mitigate any potential lagged temporal responses of zooplankton to heatwaves, control treatments were carefully assigned to minimise the likelihood of residual effects from MHW. Specifically, control periods were chosen to be as distant as possible from any MHWs included in this study. As a result, the average duration between a MHW and the following control period for another MHW was approximately 172 days.

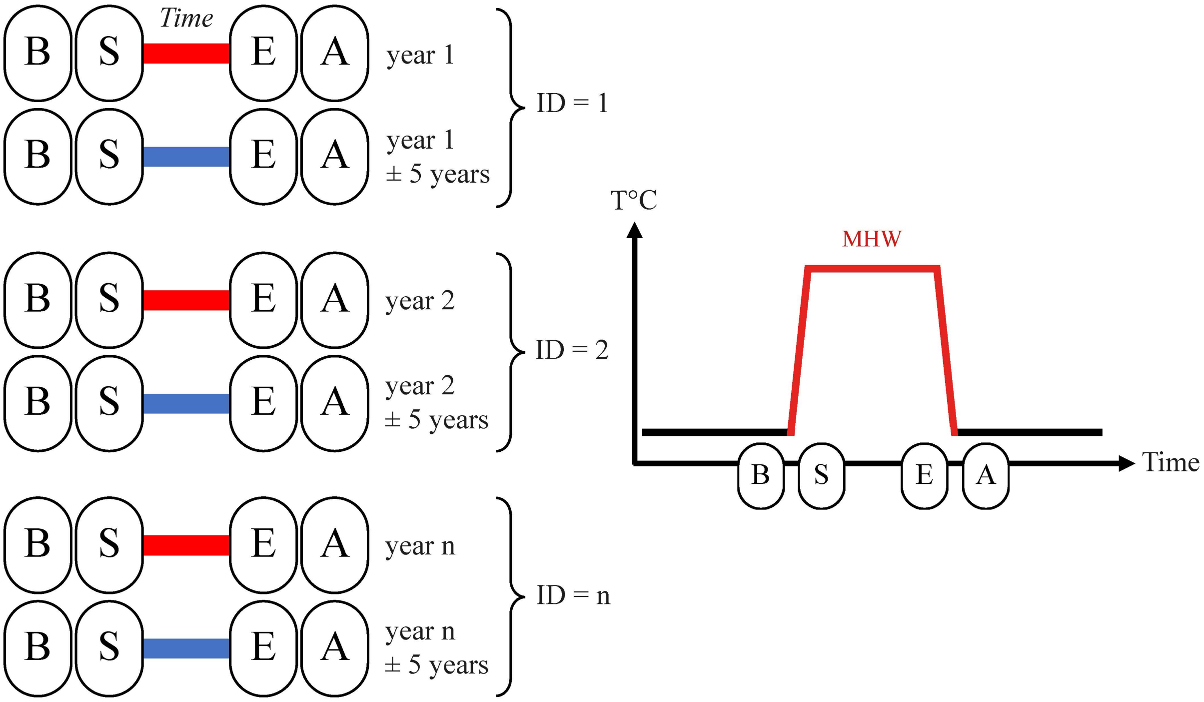

Figure 3.1. Modified BACI design. Red line represents the impact treatment (i.e., MHW). Blue line represents the control treatment (i.e., no MHW). The control is assigned in the five-year window around the impact year. The oval shape indicates the sampling period with two periods outside the MHW (B: before treatment; defined as one week preceding the MHW. A: after treatment; defined as the week following the MHW) and two periods inside the MHW (S: start of treatment; defined as the first week of the MHW and E: end of treatment; defined as the last week on the MHW). A period of one week ensures that at least three samplings took place in

each period. An ID number is assigned to each pair of treatments. The design is repeated for each season where a MHW occurred.

An important aspect of the spatial BACI, is that both control and impacted sites should be defined in similar habitats to avoid sampling different communities. We applied the same logic for our modified BACI design considering that both the pelagic habitat (e.g., temperature) and the mesozooplankton community sampled at HR have changed over the past 50 years (Amorim et al., 2023; Di Pane et al., 2023). Hence, to consider comparable years, we used a paired design (identification: **ID**) where the control was assigned within five years preceding or following the impacted year. In cases where several controls were eligible for a given impact, the one closest to the impact was chosen.

For each impacted or control unit, we defined two other periods per treatment, within the MHW, i.e., start (**S**) defined by the first week of MHW and end (**E**) defined as the last week of MHW. By including these periods, we aimed to capture the immediate impact of MHWs but also observe the trajectory of the response over time. This allows for a better understanding of how a community adapts or recovers after the MHWs and gives more credibility to the statistical output. Each period was composed of three replicates, which is equivalent to one week of data per period (Fig. 3.1). Analysis focused exclusively on extended MHWs (i.e., ≥ 14 days, Table 3.2), and shorter MHWs were discarded due to insufficient data to include the start and end treatments. In the same way, MHWs separated by < 14 days were considered as one MHW event as there would be an overlap between the period following the first MHW and the period preceding the second one. We categorised each MHW based on the season during which it occurred. When a MHW extended across two seasons, we attributed it to the season that

Table 3.2. MHW events used in this study and associated traits. Temperature intensity (difference between the Q90 and the temperature observed), maximum temperature intensity and Δ Temperature between Control *vs*. Impact are given in °C; Duration is given in days. Range is given in days and corresponds to the minimal and maximal number of MHW days in a season. Values shown are the mean ± standard error. Note that duration and range do not correspond to the average length of individual MHW, but rather to the average length of events, which can include several MHWs.

Season of occurrence	Number of MHW	Temperature intensity	Maximum temperature intensity	Duration	Range	ΔT°C Control *vs.* Impact
Spring	11	0.48 ± 0.02	1.27 ± 0.24	50 ± 11	[16-149]	2.48 ± 0.14
Summer	7	0.76 ± 0.04	1.78 ± 0.21	34 ± 11	[17-103]	1.85 ± 0.09
Autumn	8	0.61 ± 0.03	1.40 ± 0.30	44 ± 9	[14-90]	1.75 ± 0.13
Winter	7	0.37 ± 0.02	0.92 ± 0.15	34 ± 9	[14-83]	2.20 ± 0.17

included the majority of its duration as well as the peak of intensity (i.e., day of maximum temperature intensity recorded during the MHW). MHWs that extended across more than two seasons were discarded from the analysis. Overall, our design contained 33 MHW events (Table 3.2) including four of the ten most severe MHWs identified since 1975 (Giménez et al., 2024). The remaining six severe MHWs could not be incorporated due to the lack of comparable control periods or their spanning of multiple seasons (e.g., the 2006−2007 event comprised two consecutive MHWs affecting all seasons, Giménez et al., 2024).

Data analysis

All analyses were conducted under R environment (R Core Team, 2020) with a threshold of significance set at 5 %.

To assess the response of mesozooplankton community structure to MHWs, a permutational-based ANOVA (PERMANOVA) was performed. The first step was to quantify dissimilarities between taxa by using a Bray-Curtis dissimilarity index, previously standardised with the Hellinger method. Through PERMANOVA (999 permutations), we tested the interaction between treatments (**CI**, two levels: Control C; Impact I) and periods (**P**, two levels: Before B; After A) for each season to evaluate mesozooplankton community response to MHWs. Multivariate homogeneity of groups dispersion was tested, followed by a permutation test with 999 permutations. Start and End periods showed significant heterogeneity of group dispersion in spring, summer and winter and were therefore excluded from the analysis to ensure the validity of the assumptions. When a significant interaction was observed, multilevel pairwise comparisons were carried out posteriori. To integrate the dependencies in the data, the control/impact pairs (**ID**) were considered as a random factor in the models.

A Canonical Analysis of Principal Coordinates (CAP, 999 permutations) was used to visualise the community structure in response to MHWs. CAP is a flexible constrained ordination method that allows any dissimilarity measures to be used (Anderson & Willis, 2003). It is particularly useful when there is a prior hypothesis regarding the possible dissimilarities between the groups being analysed. By identifying the axis that best separates the groups, CAP enabled the detection of differences that might not be apparent through other ordination methods such as Principal Coordinates Analysis (PCoA) or Non-Metric Multidimensional Scaling (NMDS). To identify taxa responsible for the differences among groups, correlation coefficients (r^2) and associated *p*-value between taxa and canonical axes were calculated. A significance threshold was then applied to select taxa significantly correlated with canonical axes. Additionally, the distance between each control/impact pair for both before and after treatment was quantified to provide a clear quantitative measure of community dynamics in response to MHWs. This involved calculating the difference for each axis by comparing the coordinates of the impacted year against those of its corresponding control. Data points centred around zero indicate no divergence between the impact and control, i.e., stability in community structure. Conversely, a deviation from zero indicates a shift in the community structure.

Our second objective was to examine densities of single taxa as well as two alpha diversity indices (i.e., Shannon diversity and Pielou's evenness). The indices were calculated for the whole mesozooplankton community and, at a finer scale, for the copepod community. This separation ensures a consistent measure of diversity, as these two communities are identified at different taxonomic resolutions (see Table 3.1). Additionally, maintaining taxonomic resolution allows for a better understanding of the specific contributions of copepods and other mesozooplankton to overall biodiversity. Gamma Generalized Linear Mixed Effects models (GLMMs: Zuur et al., 2009) with a log link function were then performed seasonally by using the *lme4* R package (Bates et al., 2015). The fixed factor period (**P**, four levels: Before B; Start S, End E, After A) was included in the model, in interaction with treatment (**CI**, two levels: Impact I, Control C). The ID was used as a random factor. Here, all model assumptions were verified by checking residuals and overdispersion using the *DHARMa* package (Hartig & Lohse, 2022). The family function was replaced by a negative binomial (*glmmTMB* package) in case of violation of model assumptions. To assess model fit, model selection procedures (Zuur et al., 2009) were used based on the corrected Akaike Information Criterion (AICc). Specifically, the best-fitting model was determined by identifying the one with the lowest AICc value, with an exception made when the ΔAICc (i.e., difference between a candidate model and the model with the lowest AICc) was ≤ 2. Accordingly, we considered these models to represent a similar fit (Burnham et al., 2011; Zuur et al., 2009).

We used monotonic non-linear link functions, and hence we must pay attention to the type of interaction being detected. An important point is to recognise that some types of interaction among factors (here, BA:CI effect) are defined according to the scale where the variable is analysed and visualised (Spake et al., 2023). There is a subset of interactions, called "non-interpretable" or "quantitative" (Loftus, 1978; Spake et al., 2023), thereafter called "quantitative", where the scale determines whether they are removed (i.e., not detected in plots, considered significant) or retained through model selection procedures by a monotonic non-linear transformation. For example, interactions among two factors measured in a response variable (e.g., density) in the raw scale, will result in additive contributions in the log scale if the underlying process is multiplicative and if all treatments differ in density. However, there is an important subset of interactions, here referred to as "qualitative", where the statistical detection and visualisation is robust to a monotonic non-linear transformation. In the context of the BACI design used here, the latter group includes two subgroups: G1, characterised a lack of a "before effect" (i.e., density does not differ between control and impact before the MHW but it does, during or after the MHW); G2, characterised by a "before effect" and where the temporal trend in density differs between the control and impact before the MHW. Therefore, G1 is the one providing the evidence of MHW effects as the change in density between control and impact is restricted to the period when the MHW is experienced or immediately after it. We will point to the type of interaction in the results section.

RESULTS

Changes in mesozooplankton community structure

PERMANOVA analysis revealed a significant CI × P interaction for spring and autumn seasons (Table 3.3). Multilevel pairwise comparison tests between treatments highlighted no significant differences in the community structure between control and impact before the treatment. Significant differences in community structure were observed for the after periods (Table S3.2). Mesozooplankton community data dispersion did not differ significantly across P and CI for spring (*betadisper,* $F_{(3,126)} = 2.14$; $p = 0.10$) and autumn (*betadisper*, $F_{(3,90)} = 2.15$; $p = 0.12$) indicating homogeneous dispersion of the data. The CAP conducted on the spring and autumn seasons for the CI × P interaction showed strong evidence of separation among factor groups (Fig. 3.2a–c). Specifically, while there was no significant difference in the community structure between the before control and the before impact, significant multivariate dispersion was observed between the after periods. This suggests that the combined effect CI and P resulted in distinct changes in community composition during these seasons. Temporal dissimilarities between before and after were represented along the first axis while dissimilarities between the control and impact treatments were represented along the second axis. Further analysis of the coordinate distances between paired control/impact treatments reinforces these findings; the coordinate distances before treatment clustered around zero, indicating minimal initial disparity. In contrast, after treatment revealed a deviation from zero, suggesting a significant shift. For example, in spring, *T. longicornis* and Echinodermata larvae dominated the community structure after the control treatment while *Acartia* spp., and Appendicularia were dominant after the MHW (Fig. 3.2a). In autumn, Cyclopoida dominated the community structure of the after-control treatment while Harpacticoida were dominant after MHW (Fig. 3.2c).

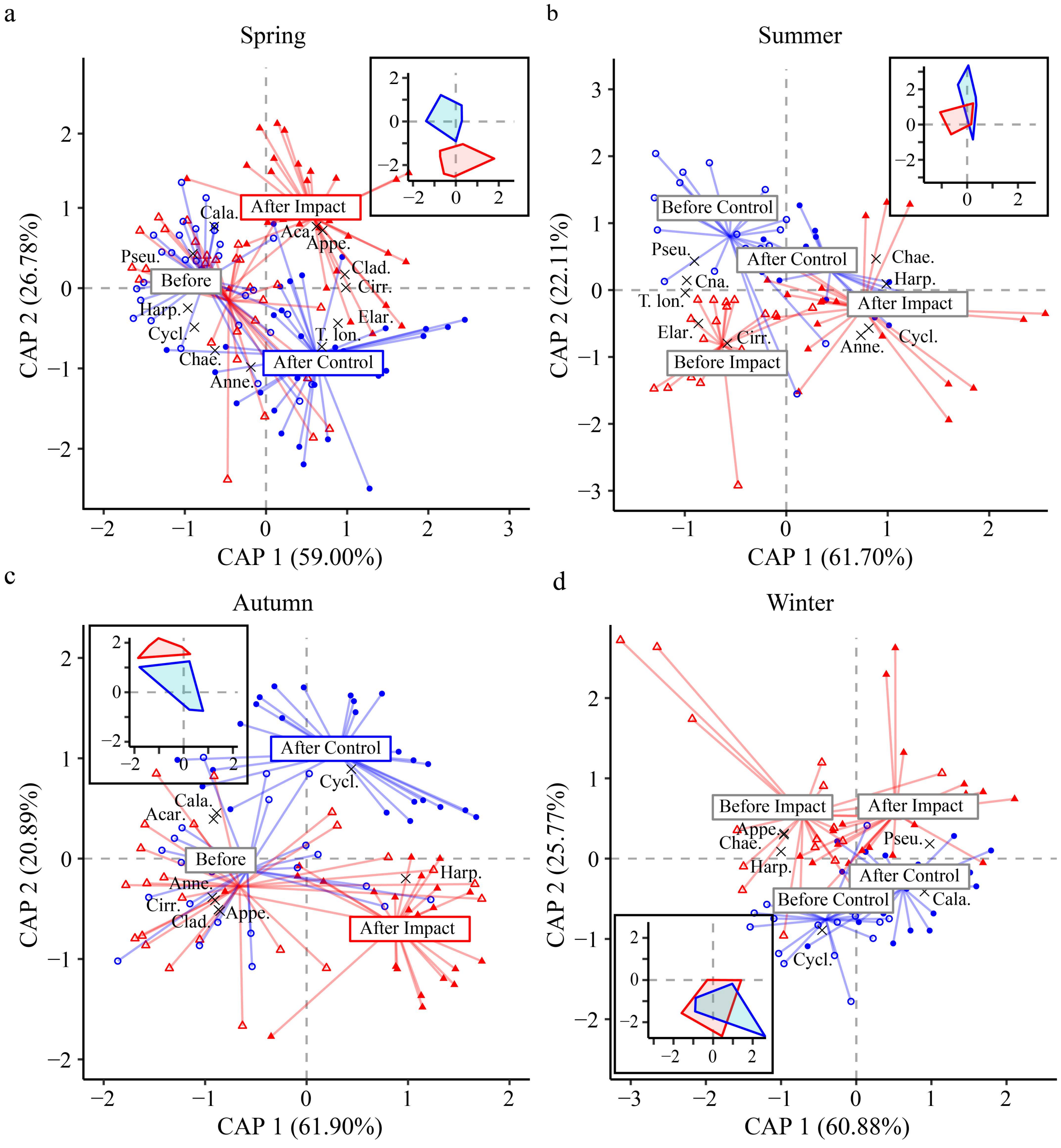

Figure 3.2. CAP on Bray–Curtis dissimilarity matrix of Hellinger transformed densities. Results of the CAP in **a.** spring, **b.** summer, **c.** autumn and **d.** winter showing canonical axes that best discriminate the structure from treatment-period interaction term with: control-before (○) control-after (●) impact-before (△), impact-after (▲). The grey label indicates no significant difference between treatments while red and blue indicate significant differences. Taxa significantly correlated with the canonical axes are represented by the vectors (Scaling type I). Acar: *Acartia* spp., Anne: Annelida larvae, Appe: Appendicularia, Cala: Calanoida., Chae: Chaetognatha, Cirr: Cirripedia larvae, Clad: Cladocera, Cna: Copepoda nauplii, Cycl:

Cyclopoida, E.lar: Echinodermata larvae, Harp: Harpacticoida, Pseu: *Pseudo/Paracalanus* spp., T.lon; *T. longicornis*. Distances between the control/impact pairs before (blue) and after (red) are displayed in the inset for each panel. X and Y axes correspond to the ΔCAP2 and ΔCAP1 coordinates, respectively (Impact−Control).

PERMANOVA test showed no significant interaction between CI and P in the mesozooplankton communities for summer ($F_{(1,80)} = 1.36$; $p = 0.14$, Table 3.3) and winter ($F_{(1,79)} = 0.26$; $p = 0.91$, Table 3.3) and no clear separation can be observed in the CAP ordination plot (Fig. 3.2b−d). Both the coordinate distances before and after treatments clustered around zero, indicating minimal disparity.

Table 3.3. PERMANOVA results for spring, summer, autumn, and winter. P: period, CI: Control/Impact treatment, Res: Residuals, Df: Degrees of freedom, SS: Sum of squares. PERMANOVA were performed on a Bray-Curtis dissimilarity matrix with 999 permutations. ID was used as a random factor. Significant interactions are indicated in bold.

	Spring					**Summer**					**Autumn**					**Winter**				
	Df	**SS**	**R²**	**F**	***p***	**Df**	**SS**	**R²**	**F**	***p***	**Df**	**SS**	**R²**	**F**	***p***	**Df**	**SS**	**R²**	**F**	***p***
P	1	0.49	0.09	12.52	<0.001	1	0.39	0.1	8.97	<0.001	1	0.4	0.09	9.26	<0. 01	1	0.28	0.09	8.03	<0.001
CI	1	0.09	0.02	2.42	<0.01	1	0.08	0.02	1.88	<0.05	1	0.0	0.01	1.49	0.10	1	0.08	0.03	2.38	<0.05
P × CI	1	0.14	0.02	3.47	**<0.001**	1	0.06	0.01	1.36	0.14	1	0.0	0.01	1.57	**<0.05**	1	0.01	0.003	0.26	0.91
Res	126	4.94	0.87			80	3.52	0.87			90	3.9	0.88			79	2.75	0.88		
Total	129	5.66	1.0			83	4.06	1.0			93	4.4	1.0			82	3.12	1.0		

Diversity and density responses to MHWs

We did not find any evidence of diversity and evenness response to MHWs. The interaction term (P × CI) for the Shannon diversity and Pielou's evenness was not retained in the model for copepods and for the complete mesozooplankton community, irrespective of season (Table S3.3, 3.4).

We found evidence of mesozooplankton response to spring MHWs for 8 out of 13 taxa, with all the interactive patterns being consistent with a qualitative interaction and most of them not showing evidence of differences in density between control and impact before the MHW. For copepods, the best model didn't include the interaction for Harpacticoida and Cyclopoida. The best model included the interaction for Calanoida (Table S3.5): Both treatments showed a significant increase in density throughout the periods (Fig. 3.3e) and higher density was observed at the end of MHW compared to the control (7.51 *vs.* 6.70; $p < 0.001$). The interaction was also retained in the model for three Calanoida taxa (*Acartia* spp., *Pseudo/Paracalanus* spp., and *T. longicornis*: Table S3.6). *Acartia* spp., density increased for both treatments throughout the periods (Fig. 3.3a) and higher density was observed at the beginning (4.25 *vs.* 4.97; $p < 0.05$) and end (4.91 *vs.* 6.09; $p < 0.001$) of the MHW compared to the control. Copepoda nauplii followed the exact same trend (Fig. 3.3d). *Pseudo/Paracalanus* spp., density increased during the impacted treatment (Fig. 3.4b) with higher densities at the end (5.40 *vs.* 6.66; $p < 0.001$) and after (6.04 *vs.* 6.58; $p < 0.05$) the MHW compared to the control. Density remained constant during the control treatment. These two taxa responded positively to spring MHW, in contrast to *T. longicornis.* While *T. longicornis* density increased for both treatments (Fig. 3.3c), smaller density was observed after the MHW (6.06 *vs.* 5.82; $p < 0.01$) compared to the control.

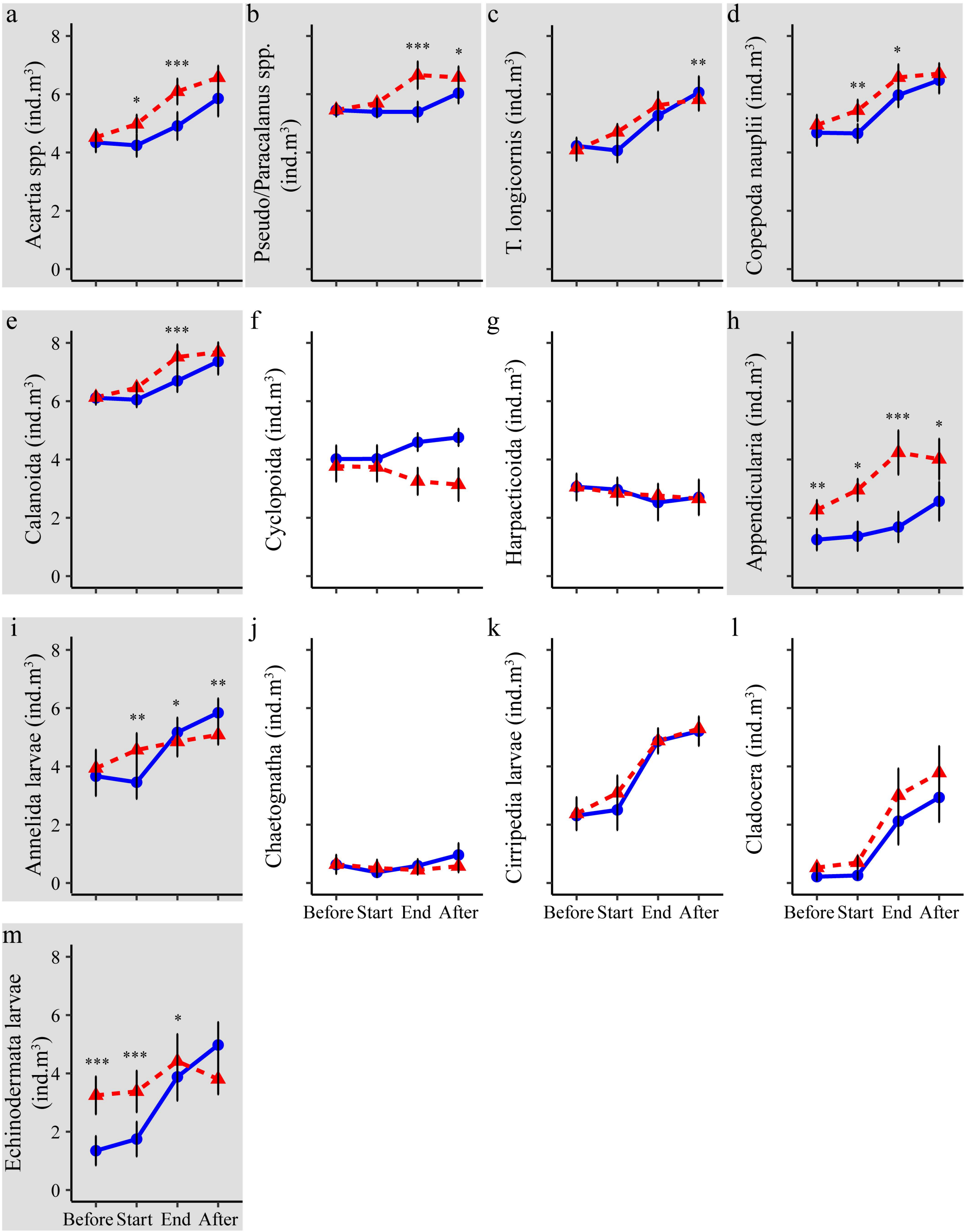

Figure 3.3. Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: impact) or absence (●: control) of spring MHWs. **a.** *Acartia* spp., **b.** *Pseudo/Paracalanus* spp., **c.** *T. longicornis*, **d.** Copepoda nauplii, **e.** Calanoida, **f.** Cyclopoida, **g.** Harpacticoida, **h.** Appendicularia, **i.** Annelida larvae, **j.** Chaetognatha, **k.** Cirripedia larvae, **l.** Cladocera, and **m.** Echinodermata larvae densities. Values shown are the means (log

transformed) ± standard error for each period per ID. Grey shape indicates significant interactions. Asterisks represent significant difference between control and impact for each period: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

For mesozooplankton taxa, the interaction effect was not included in the model for Chaetognatha, Cirripedia larvae and Cladocera. Only Appendicularia, Annelida larvae and Echinodermata larvae showed significant interactions (Table S3.6; Fig. 3.3h−i). A before effect was detected for Echinodermata larvae ($p < 0.001$) and Appendicularia ($p < 0.01$), indicating that the observed changes are not the result of a response to MHW. Therefore, only the changes observed for Annelida larvae could be associated with MHW; density increased throughout the control treatment but remained unchanged for the impacted treatment (Fig. 3.3i). The interaction showed higher density at the start of the MHW compared to the control treatment (3.46 *vs.* 4.56; $p < 0.01$). The trend reversed during the MHW with lower density at the end (5.17 *vs.* 4.85; $p < 0.05$) and after (5.84 *vs.* 5.08; $p < 0.01$) the event compared to the control.

In summer, most of the mesozooplankton taxa did not show any evidence of a response to MHWs, and the interaction effect was included in the model for only two taxa, namely Cladocera and Echinodermata larvae (Fig. 3.4l−m; Table S3.6). Interaction was qualitative and significant variations were observed between control and impact for both taxa at the end of the MHW. Specifically, Cladocera experienced an increase in density until the end of the MHW, after which their numbers decreased (Fig. 3.4l). The density at the end of the MHW was higher compared to the control (6.03 *vs.* 4.33; $p < 0.001$). In contrast, Echinodermata larvae showed a decrease in density in both treatments (Fig. 3.4m), with smaller density at the end of the MHW compared to the control (3.76 *vs.* 4.93; $p < 0.001$).

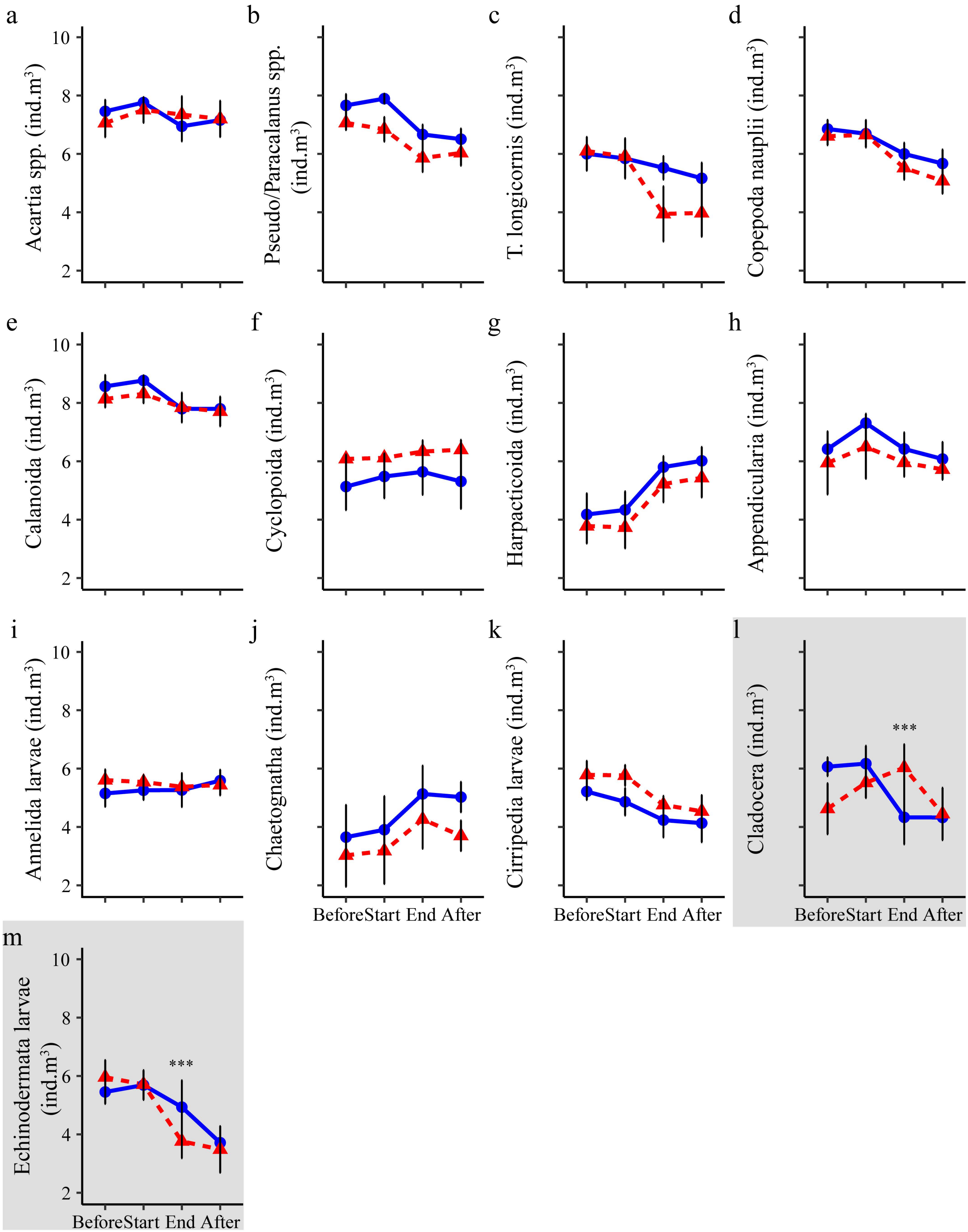

Figure 3.4. Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: impact) or absence (●: control) of summer MHWs. **a.** *Acartia* spp., **b.** *Pseudo/Paracalanus* spp., **c.** *T. longicornis*, **d.** Copepoda nauplii, **e.** Calanoida, **f.** Cyclopoida, **g.** Harpacticoida, **h.** Appendicularia, **i.** Annelida larvae, **j.** Chaetognatha, **k.** Cirripedia larvae, **l.** Cladocera, and **m.** Echinodermata larvae densities. Values shown are the means (log transformed) ± standard error for each period per ID. Grey shapes indicate significant interaction. Asterisks represent significant difference between control and impact for each

period: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

For the copepod community in autumn, the interaction term was retained in the model for Calanoida Harpacticoida and *Pseudo/Paracalanus spp.*, and these interactions were all of a qualitative type (Fig. 3.5). However, a before effect was detected for Calanoida ($p < 0.05$) and *Pseudo/Paracalanus spp.,* ($p < 0.01$), indicating that the observed changes are not a result of a response to MHW (Fig. 3.5b−e). Therefore, Harpacticoida was the only copepod taxa to respond to autumn MHW; density increased during the impact treatment while it stayed constant during the control (Fig. 3.5g). Pairwise comparisons showed higher density at the start (4.74 *vs.* 5.64; $p < 0.01$), end (4.81 *vs.* 6.19; $p < 0.001$), and after (4.98 *vs.* 6.25; $p < 0.001$) the MHW compared to the control.

For mesozooplankton taxa, Annelida larvae, Cirripedia larvae and Cladocera showed significant evidence of responses to autumn MHW. Annelida larvae density decreased for both treatments and was higher at the end of the MHW compared to the control (2.81 *vs.* 3.51; $p < 0.001$) (Fig. 3.5i). Cirripedia larvae density decreased for both treatments, and pairwise comparisons showed higher density after the MHW (1.33 *vs.* 2.00; $p < 0.01$) compared to the control (Fig. 3.5k). Cladocera density decreased for both treatments but to a much greater extent for the control (Fig. 3.5l). Pairwise comparisons showed higher density at the end (0.78 *vs.* 2.68; $p < 0.001$) and after (0.50 *vs.* 1.57; $p < 0.001$) the MHW compared to the control.

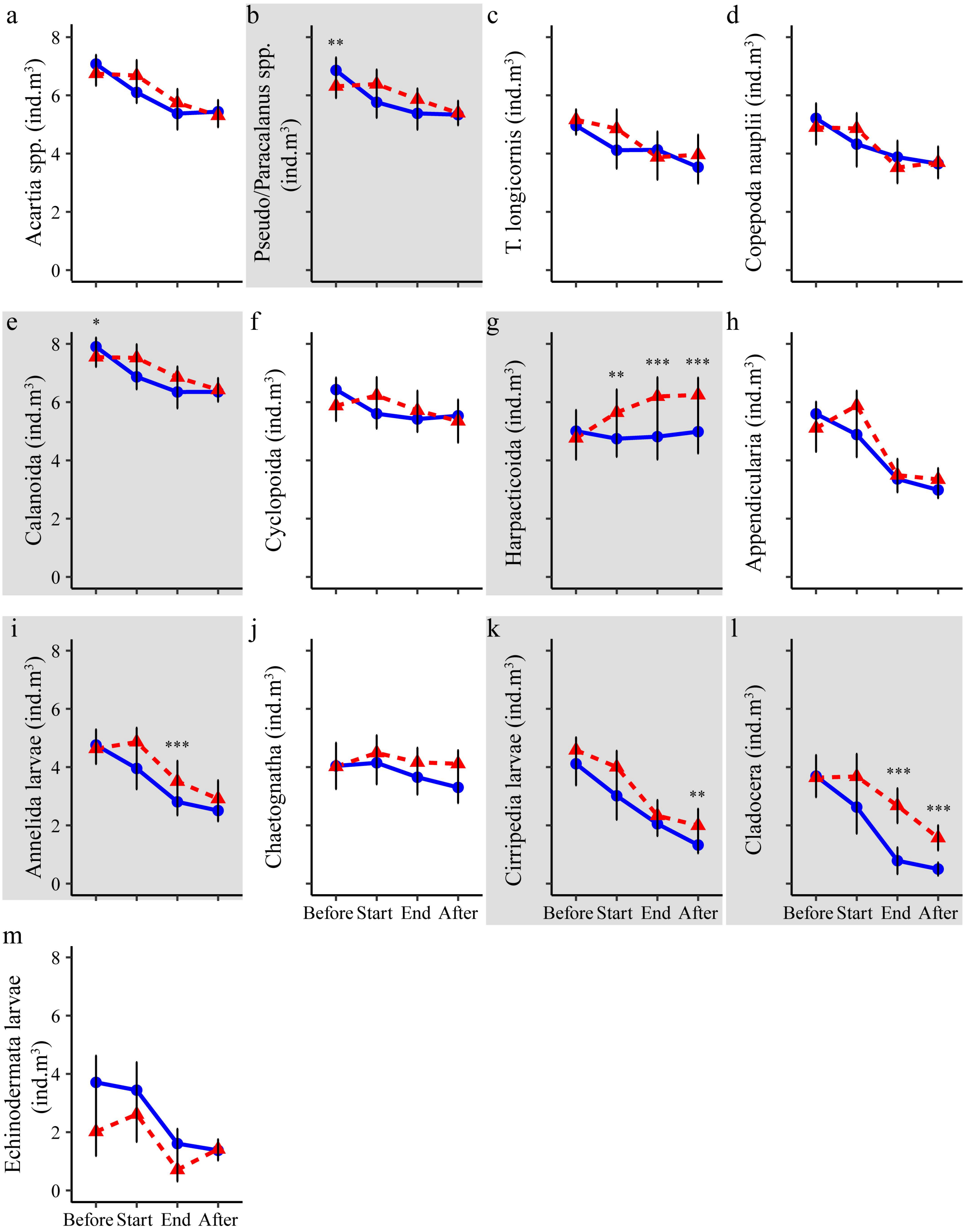

Figure 3.5. Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: impact) or absence (●: control) of autumn MHWs. **a.** *Acartia* spp., **b.** *Pseudo/Paracalanus* spp., **c.** *T. longicornis*, **d.** Copepoda nauplii, **e.** Calanoida, **f.** Cyclopoida, **g.** Harpacticoida, **h.** Appendicularia, **i.** Annelida larvae, **j.** Chaetognatha, **k.** Cirripedia larvae, **l.** Cladocera, and **m.** Echinodermata larvae densities. Values shown are the means (log transformed) ± standard error for each period per ID. Grey shapes indicate significant interaction. Asterisks represent significant difference between control and impact for each

period: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Models for each taxon were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

In winter, most of the mesozooplankton taxa did not show evidence of a response to MHWs (11 out of 13 groups) and the interaction effect was included in the model for only two taxa, namely the copepod Cyclopoida and Harpacticoida. Cyclopoida density stayed constant during the control treatment but decreased during the MHW with lower densities after the MHW (3.41 *vs.* 4.60; $p < 0.05$) (Fig. 3.6f). A before effect was detected for Harpacticoida ($p < 0.01$) indicating that the observed changes are not a result of a response to MHW (Fig. 3.6g).

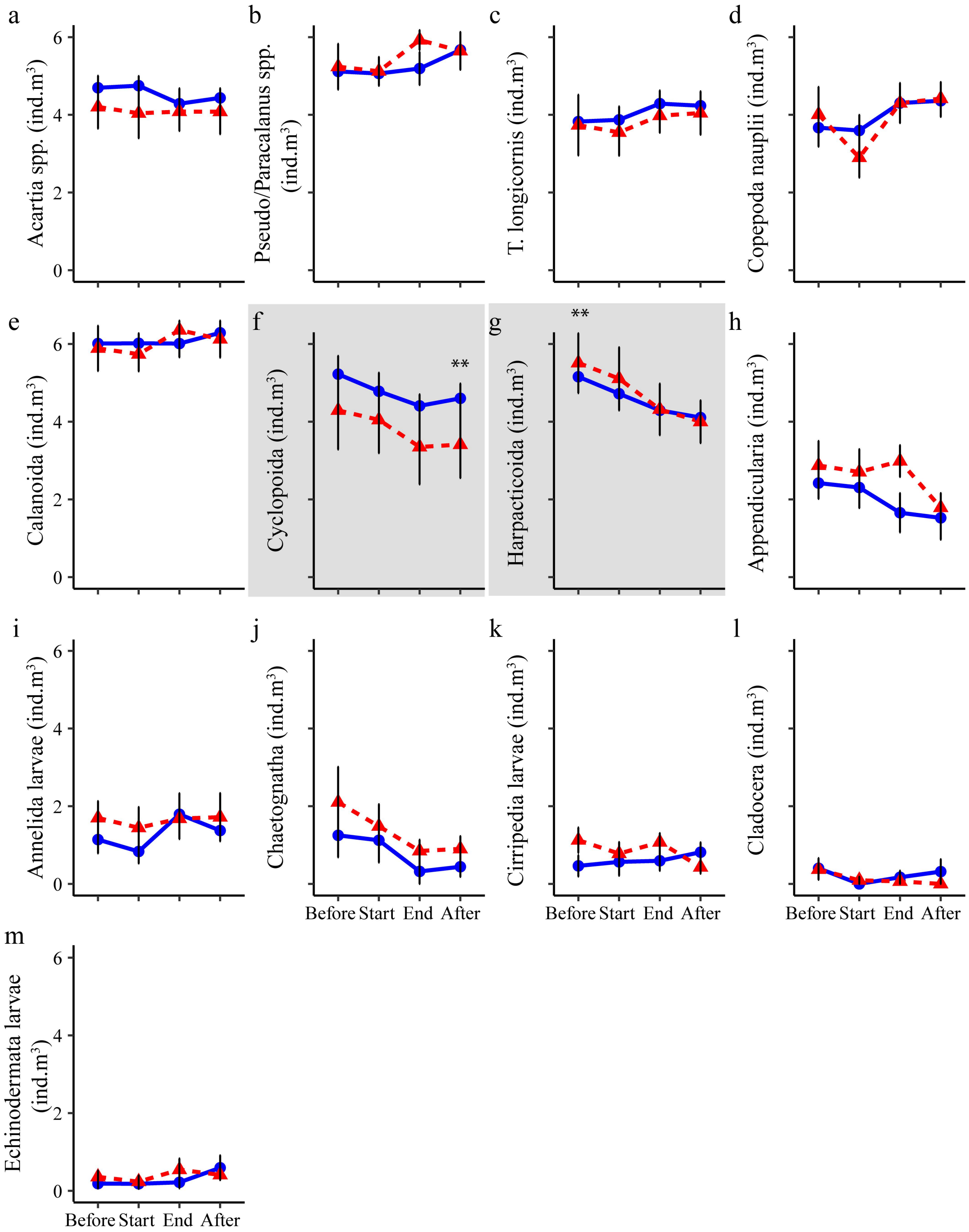

Figure 3.6. Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: impact) or absence (●: control) of winter MHWs. **a.** *Acartia* spp., **b.** *Pseudo/Paracalanus* spp., **c.** *T. longicornis*, **d.** Copepoda nauplii, **e.** Calanoida, **f.** Cyclopoida, **g.** Harpacticoida, **h.** Appendicularia, **i.** Annelida larvae, **j.** Chaetognatha, **k.** Cirripedia larvae, **l.** Cladocera, and **m.** Echinodermata larvae densities. Values shown are the means (log transformed) ± standard error for each period per ID. Grey shape indicate significant interaction. Asterisks represent significant difference between control and impact for each

period: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Models for each taxon were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

DISCUSSION

We examined the mesozooplankton community of the HR time series, during the most extensive seasonal MHWs recorded between 1975 and 2018. We found evidence of responses to MHWs in both the structure of the community and the density of single taxa, particularly in the seasons of strongest temperature change, spring and autumn. In support of the community level response in spring, 8 of the 13 taxa showed variations in density during the MHW, yet only 6 were directly linked to it. Indeed, two taxa displayed changes before the MHW, which could not be directly associated with the event. Five taxa exhibited no response to the spring MHW. Likewise, the community level response in autumn was supported by similar responses in four out of 13. Seven of the remaining taxa showed no evidence of response to MHWs. Additionally, in two taxa, temporal changes were independent of the MHWs, as they occurred during the period before the MHW. There was no indication of a change in community structure related to MHW during summer and winter, and few individual taxa were influenced. Because our study was based on intensive sampling of mesozooplankton organisms, which are characterised by short generation times (weeks to months), we were able to observe season-dependent responses to heatwave events.

Seasonal response to MHWs

For spring, we observed a divergence in the community composition between the post-MHW and post-control periods. Following a period without MHW, the community was primarily dominated by *T. longicornis* and Echinodermata larvae, and shifted after the MHW to a community dominated by *Acartia* spp., and Appendicularia, with less Cyclopoida, Chaetognatha, and Annelida larvae. Those results were supported by the positive response in density of the most important groups: Copepoda nauplii, Calanoida, *Acartia* spp., *Pseudo/Paracalanus* spp., and Appendicularia. The dominance of Appendicularia is consistent with the reported quick response to short-term increases in temperature (Winder et al., 2017) and the positive effect of warming on gelatinous zooplankton (Winder et al., 2017). As MHWs are expected to become more frequent in the coming decades (Hobday et al., 2016; Oliver, 2019), it is likely that Appendicularia will become more dominant in the German Bight. Unlike copepods, Appendicularia are able to feed on small particles, within the size range of the microbial loop (Acuña & Anadón, 1992). A shift to a dominance of Appendicularia could therefore significantly impact the microbial loop and subsequent energy transfer to higher trophic levels (Gorsky & Fenaux, 1998).

We hypothesised that spring MHWs would influence densities of mesozooplankton taxa that are undergoing growth phase. We found that copepods (including *Acartia* spp., a cold-temperate taxon; Alvarez-Fernandez et al., 2012) responded positively to MHWs. This response is logical given that spring MHWs may not reach the thermal tolerance limits but instead result in faster growth rates or forward shifts in phenology. Copepod nauplii reach their maximum density in May in the North Sea (Atkinson et al., 2015), while Calanoida species exhibit strong seasonality with a growth phase in spring, followed by a peak in June-July (Atkinson et al., 2015; Greve et al., 2004; O'Brien et al., 2013). The effects on phenology would explain why density of Calanoida, *Acartia* spp., and Copepoda nauplii were higher during but not after the MHW (similarly, *T. longicornis* decreased in density after the MHW). Thus, it appears that these taxa reached their respective density maxima earlier in the impact than would be expected in a normal season. Seasonal shifts may also explain why Annelida larvae decrease in density at the end of the MHW events. In our samples, Annelida larvae are mostly spionids (Deschamps *pers. obs.*), which appear to respond to warming with a delayed timing of occurrence (Mackas et al., 2012).

Similarly, we hypothesised that autumn MHWs could lead to an extension and slower decline phase for species peaking in late summer or early autumn. Like spring MHWs, the observed responses in autumn are also consistent with a phenological effect, with taxa exhibiting an extension of their seasonal peaks at the time when density typically decreases, except for Harpacticoida. For Harpacticoida, while the density remained stable throughout the control treatment, a sharp increase was observed during the MHW. In the North Sea, Harpacticoida reach their peak in late summer/autumn (Deschamps et al., 2023; Mortelmans et al., 2021). *Euterpina acutifrons* and *Microsetella* spp., two commonly found taxa in the HR time series, exhibit a seasonal peak in August (O'Brien et al., 2013). An autumn MHW may have therefore facilitated Harpacticoid copepods in the environment for a longer period than expected during a normal season. These responses are important as late summer and autumn MHWs characterised the seasonal pattern at HR, especially since the 1990s (Gimenez et al., 2024).

It is important to highlight that some mesozooplankton taxa did not exhibit changes in density during spring or autumn MHWs. In spring, Cyclopoida and Harpacticoida are notable examples. The lack of response could be linked to their phenological cycle. Indeed, at HR, Cyclopoida is predominantly composed of *Corycaeus anglicus* and *Oithona* spp. (mainly *O. similis* and *O. nana*). These species are known to reach their density peak towards late summer or early autumn, similar to Harpacticoida (Deschamps et al., 2023; Mortelmans et al., 2021; O'Brien et al., 2013). The same reason might account for the absence of a response to autumn MHWs for Copepoda nauplii, *Acartia* spp., and *T. longicornis*, as these taxa typically peak in summer (Deschamps et al., 2023). These observations suggest that the timing of copepod reproduction does not coincide with autumn MHW events, potentially minimising the impact on their populations.

We did not find clear evidence of mesozooplankton community responses to winter and summer MHWs; interactive effects were observed in only a small number of groups. The lack of responses in most groups is logical in winter because of very low biological activity (van Beusekom & Diel-Christiansen, 2009) and the low phytoplankton productivity (Townsend et al., 1994) limiting mesozooplankton density in the North Sea (van Beusekom & Diel-Christiansen, 2009). In summer, we expected a shift in the copepod community, with smaller taxa and warm water species becoming more abundant at the expense of large cold-water ones, driven by differences in thermal tolerance thresholds. However, the summer temperatures recorded at HR exceeded 20 °C only in August 1995, 2002, and 2006, which is still within the tolerance range known for most mesozooplankton species in the North Sea (e.g., *T. longicornis*: threshold temperature of 22.5 °C (Halsband-Lenk et al., 2002)). Therefore, we believe that the summer MHWs recorded from 1975 to 2018 may not have been sufficiently intense to adversely affect cold-water taxa or promote warm-water taxa. Given the projection that MHWs are expected to increase in intensity (Hobday et al., 2016; Oliver, 2019), our observations regarding the impact of summer MHWs on mesozooplankton communities could change in the upcoming decades.

Mechanisms driving mesozooplankton changes in response to MHWs

Different mechanisms may have driven the observed changes in density associated with MHWs. We cannot establish causal mechanisms but instead hypothesise about the potential drivers of the responses. For instance, temperature may have direct physiological impacts on metabolic, developmental and growth rates (e.g., copepod reproduction (Richardson, 2008)), but also indirect effects. Copepod density is positively correlated with temperature especially in spring when the effect of temperature is much larger (Mortelmans et al., 2021). In the North

Sea, copepod density peak occurs 11 to 52 days earlier for each 1 °C increase (Beaugrand, 2004) and *Acartia clausii* (present in the HR time series) experienced a shift in the phenology of 16 days ahead for every 1 °C increase (Atkinson et al., 2015). *A. clausii* always appears earlier in warm years in the English Channel (Plymouth L4 sampling site: Mackas et al., 2012) and both Copepoda nauplii and *A. clausii* experienced a forward shift in phenology in response to the 2016 MHW in Alaska (McKinstry et al., 2022). These studies strongly support the 'earlier when warmer' trend in copepods, that may also occur in response to short and acute temperature increases such as MHW. Likewise, favourable temperatures may explain the reduced rate of decline observed in autumn, as expected from the positive effects of temperature on the duration of the seasonal plankton peaks (Mackas et al., 2012; McKinstry et al., 2022). The case of Cladocera taxa provides a clear illustration (i.e., density remained stable throughout the entire MHW period, but declined in the control years). Indeed, our results are consistent with the known occurrence of the tropical/subtropical Cladocera *Penilia avirostris* in the North Sea, which increases during warm autumn (Johns et al., 2005). In September 1999, when a prolonged MHW was detected in HR (i.e., 42 days: Giménez et al., 2024, see Table S3.1), sea surface temperature was 2 to 4 °C higher than normal, leading to the rapid spatial expansion of *P. avirostris* (Johns et al., 2005).

In addition, mesozooplankton responses to MHWs may be mediated by changes in other trophic levels. In the North Sea, characterised by wind and well-mixed conditions in the water column, warming drives phytoplankton metabolic rates and densities, which subsequently enhance mesozooplankton (Richardson, 2008; Richardson & Schoeman, 2004). In high latitudes, MHWs can lead to elevated chlorophyll concentrations (Noh et al., 2022) and can trigger intense phytoplankton blooms in nutrient-rich areas (Hayashida et al., 2020). Moreover, during the "Blob", the MHW detected in the Pacific Ocean between 2013 and 2016, the phytoplankton community in the Gulf of Alaska transitioned from a dominance of diatoms to dinoflagellates (Arteaga & Rousseaux, 2023). In the North Sea, dinoflagellates are an important nutritional resource for copepods (Gentsch et al., 2009; Ianora et al., 2004). We could therefore hypothesise that MHWs would favour copepods through changes in the composition of planktonic prey. This shift in prey composition may have broader implications for the food web. Species that rely on planktonic prey less favoured by heatwaves may experience reduced food availability, potentially leading to shifts in their population dynamics. Conversely, species consuming copepods, such as fish larvae, might benefit from an increase in copepod abundance. Currently, it appears that MHWs primarily increase growth rates and shift the peak of abundance over small temporal scales. However, with the projected increase in the intensity, duration, and frequency of MHWs in the coming decades (Oliver et al., 2018), we can hypothesise that copepod abundance peaks could shift earlier in the season. This could lead to mismatches between the larvae of spring-spawning fish species and the peak abundance of their prey (Cushing, 1990), potentially impacting fish recruitment. For example, the temperature increases since the mid-1980s in the North Sea have altered the copepod community (e.g., abundance and timing) in ways that have reduced the survival of early life stages of cod (Beaugrand et al., 2003). Although these changes have been linked to long-term warming, prolonged heatwaves could have similar impacts. Therefore, understanding these changes is crucial for predicting the overall impact of marine heatwaves on marine biodiversity and food web structures.

Challenges and future research

One of the great challenges in studying responses to MHWs in plankton is the limited capacity to perform field experiments, which would require sustained spatial sampling over long periods. Additionally, the occurrence of large heatwaves over wide spatial scales demands important efforts to conduct such replicated experiments. The length of our time series, in combination with the high frequency sampling of HR (Amorim et al., 2023), has enabled us to use a modified BACI design and overcome several challenges. Firstly, we defined replicated control and heatwave-impacted years to test MHW effects. Secondly, we defined controls within 5 years distance from the impacted treatments, crucial for accounting for potential decadal changes in plankton communities (Reid et al., 2016). We were also able to compare the density of key organisms at similar times of the year and explore season-dependent responses. Finally, we noted that the type of interaction needed to establish clear evidence of a heatwave effect was robust to a change in measurement scale (Spake et al., 2023).

There are, however, some limitations and potential confounding factors that are relevant for the analysis. First, we did not include heatwaves running for more than two seasons because appropriate replicates within each season could not be established (e.g., 2006-2007 with two MHWs covering all seasons: Giménez et al., 2024). While such MHWs were rare, they may constitute the primary source of data elsewhere: in such cases one would have to find control years lacking MHWs over long time periods. This might be difficult if the pool of potential control years contains some with several short MHWs. A possible solution to increase the number of control years could be to compare the planktonic responses in years with short

MHWs against years without any event. Moreover, in a few cases, taxa showed significant differences in density between control and impact years during the “before” period, and we refrained from making conclusions about them. One may therefore restrict the application of BACI to periods of the year when the “before” produces non-significant effects. In seasonal habitats, spring is perhaps the best period because the “before” could be set at the end of winter when density is consistently low.

In summary, we found that planktonic communities can respond to MHWs of the scale of several weeks of duration, with average durations ranging from 30 to 50 days depending on the season. This was found through a BACI design applied over a time series of several decades. We also highlight the challenge of ascertaining whether the event is the sole cause of the observed changes. The HR time series helped us to implement a design to control the response to MHW and to replicate it over several events. In synthesis, applying such design to other time series, will help to quantify the effects of MHWs in other regions. This method could be challenging for organisms with long generation times, as their responses might take months rather than days or weeks. At these timescales, extensive replication is needed (due to additional environmental variables), and finding enough control replicates over several months without MHW events can be difficult. Nonetheless, our method can be applied for time series involving organisms with short generation times or life phases (i.e., larvae).

Acknowledgments

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SUPPLEMENTARY MATERIAL

To investigate the number of studies examining the effect of MHWs on marine communities using time series analysis, a comprehensive table was created. This table identifies all relevant articles on the topic. The Web of Science online database was searched to identify literature associated with marine heatwaves, marine communities, and long-term time series. The search string included “marine heatwave” OR “marine heat wave” AND “marine community” OR “marine communities” AND “time series.” The search encompassed all literature published before 2024.

The search yielded 1,294 studies. Only research articles were included; other document types such as review papers (n = 71) and meta-analyses (n = 3) were excluded. Duplicates were removed before screening (n = 7). During the initial screening, articles that did not include the terms “marine heatwaves,” “heatwave,” or “heat wave” in their title and/or abstract were removed (n = 292). Exceptions were made for studies using the term “extreme events” or referring to specific MHWs, such as “the blob,” if they provided a clear definition of MHW in the Materials & Methods section. Studies unrelated to MHWs (e.g., out of scope or other extreme events such as terrestrial or freshwater heatwaves and cold spells) were also removed (n = 63).

During the abstract screening process, we excluded studies that did not focus on communities nor considered biological effects to ensure our investigation remained centered on the impacts of MHWs on marine communities. Additionally, studies emphasising long-term trends and global warming were removed for the same reason. Articles related to experiments or simulations of MHWs and those not directly linked to time series analysis were also removed. From the time series papers studying the effect of MHWs on marine communities (n = 63), those with biological time series shorter than two years were excluded (n = 10).

The final database comprised 53 articles. For each retained article, information was collected regarding the time series duration, the communities studied, the location and timing of the heatwave, and the general methods used to investigate the MHW effects on the community (e.g., presence of control periods and/or before/after periods). This information was added to the final table.

Table S3.1. Studies of MHW effect on marine communities involving time series (> 2 years)

Communities	**MHW Location**	**MHWs Timing**	**Biological time series duration**	**Methods**	**References**
Megafauna	Indian	2001	18 years	Comparison before (1998-2010) and after (2012-2015)	(Nowicki et al., 2019)
Top predators	North Pacific	2014, 2015, 2019, 2020		Comparison of each MHW years	(Welch et al., 2023)
Fish	North Pacific	2014-2015	11 years	Comparison 5 years before *vs.* 5 years after MHW	(Olsen et al., 2022)
	North Pacific	2014-2016	13 years	Comparison before (2007-2013), during (2014-2016) and after (2017-2020) MHW	(Ziegler et al., 2023)
	North Pacific	2014-2016	17 years	Comparison before (2013), during (2014-2015) and after (2016) MHW at different impacted locations	(Freedman et al., 2020)
	Indian	2010-2011	8 years	Coincidence between changes and timing of MHW. Comparison before (2008-2010), MHW (2011-2012) and post-MHW (2013-2015)	(Day et al., 2018)
	Northern Hemisphere (18 regions)		Between 11 and 26 years	Change in biomass in response to MHW cumulative intensity	(Fredston et al., 2023)
	North Pacific	2013-2015	1981-2015	Comparison between MHWs *vs.* non MHW year	(Cheung & Frölicher, 2020)

	Barents Sea	2006; 2013; 2016	14 years	Coincidence between bottom temperature maxima and observed responses from the fish communities	(Husson et al., 2022)
	Indian	2010-2011	Several time series from 1 to 22 years	Comparison before, during and after MHW	(Lenanton et al., 2017)
	North Pacific	2015-2016	18 years	Comparison baseline (2004-2014), during (2015-2016) and post-MHW (2017-2021) at different regions	(Robinson et al., 2022)
Fish and benthic	Indian	2010-2011	3 spring/summer months for 5 years	Comparison Pre-MHW (2006), Post-MHW (2013), Post-cooling (2017 & 2019)	(Bosch et al., 2022)
Benthic	Indian	2011	2 time series of 3 years 15 years apart	2 groups comparison (1999-2001 *vs.* 2016-2019)	(Mulders & Wernberg, 2020)
	Indian	2010-2011	17 years	Comparison pre (1999-2006) vs post MHW (2013, 2014, 2015) at different impacted sites	(Smale et al., 2017)
	Indian	2010-2011	6 year (2010-2014 and 2017)	Comparison 2010-2011 (MHW) and 2010-latest survey at different impacted locations	(Giraldo-Ospina et al., 2020)
	Mediterranean Sea	Multiple events	5 years	Relationship between mass mortality event and heat exposure associated with MHW	(Garrabou et al., 2022)
(kelp forest associated)	Indian	2011	5 years (2005-2007, 2010, 2011)	Comparison before (November 2005-2007, 2010) vs after (November 2011) MHW	(Smale & Wernberg, 2013)
(kelp forest associated)	North Pacific	2014-2016	15 years	Comparison before (2001-2013) and during (2014-2015) MHW	(Reed et al., 2016)

Communities	**MHW Location**	**MHWs Timing**	**Biological time series duration**	**Methods**	**References**
Intertidal	North Pacific	2014-2016	8 years	Coincidence between changes and rising temperature	(Whalen et al., 2023)
	North Atlantic	2018 & 2020	40 years	Frequency of events per year (winter and summer MHW) linked to change	(Mieszkowska et al., 2021)
	Pacific	All summer 2012-2016	15 years	MHW effect calculated using abundance data from multiple pre- and post-MHW surveys	(Ishida et al., 2023)
	North Pacific	2014-2016	Summer 2012-2019	Comparison before (2012-2014), during/after (2012-2014) MHW among impacted regions	(Weitzman et al., 2021)
	North Pacific	2014-2016	3years Spring/Summer	Yearly comparison (2016-2017 and 2018)	(Spiecker & Menge, 2022)
Coastal	North Pacific	2014-2016	Several time series from 4 to 5 years	Yearly comparison	(Sanford et al., 2019)
Invertebrates	Indian	2010-2011	35 years	Comparison before (2006-2010) and after (2011-2018) MHW	(Caputi et al., 2019)
Kelp forest	North Pacific	2014-2015	34 years	Temporal coincidence between shift in structure and MHW timing	(McPherson et al., 2021)
	North Pacific	2014-2016	Last autumn for 2 years	Comparison before (autumn 2013) and after MHW (autumn 2017) at different impacted locations	(Arafeh-Dalmau et al., 2019)

Communities	MHW Location	MHWs Timing	Biological time series duration	Methods	References
	North Pacific	2014-2015	14 years (once or twice seasonally)	Comparison before (2008-2013), during (2014-2015) and after (2016-2012) MHW at different impacted sites	(Michaud et al., 2022)
	North Pacific	2014-2016	6 years	Qualitative analysis of trends Comparison during (2014-2016) and after (2017-2018,2020-2021) MHW	(Tolimieri et al., 2023)
	North Atlantic	2018	< 1 year	Norway: Comparison before (April), during (July-August) and after (October-November) MHW Eastern US: before (June), during (August) and after (November) the MHW	(Filbee-Dexter et al., 2020)
	North Pacific	2014-2018	10 years	Comparison before (2009-2013), during (2014-2015, 2015-2016) and after (2016-2017, 2017-2018) MHW	(Cavanaugh et al., 2019)
Kelp forest, seaweed	Indian	2010-2011	16 years	Coincidence between MHW and change in reef cover	(Wernberg et al., 2016)
Seaweed	Tasman Sea	2017-2018	6 years	Comparison before (2017) and after MHW (2018-2022)	(Montie & Thomsen, 2023)

Communities	MHW Location	MHWs Timing	Biological time series duration	Methods	References
Seaweeds, sessile invertebrates, demersal fish	Indian	2010-2011	6 years	Comparison before (2006-2010) vs after MHW (2011) Yearly comparison	(Wernberg et al., 2013)
Seagrass	Indian	2010-2011	14 years	Comparison before (2002-2010) and after MHW (2014-2016)	(Strydom et al., 2020)
	Indian	2010-2011	12 years	Comparison before (2002) and after (2014)	(Arias-Ortiz et al., 2018)
Coral reef	Central equatorial Pacific	2002-2003 2009-2010 2015-2016	7 years (2000, 2002, 2005, 2009, 2012, 2015, 2018)	Yearly comparison and coincidence with MHWs	(Fox et al., 2021)
	Red sea	2015	2014-2015 & 2017-2019	Comparison before (2014-2015) and after (2017-2019)	(Anton et al., 2020)
	Indian	Multiple MHW from 2010 to 2012	3 years	Comparison before (2005-2006) and after (2013) MHWs at different locations	(Tuckett et al., 2017)
Phytoplankton	North Pacific	2013-2016	18 years	Detection of anomalies from monthly data	(Arteaga & Rousseaux, 2023)
Copepod	North Pacific	2014	2 years	Comparison MHW (Jan-Aug 2014) and El Niño (Nov 2014-Dec 2015)	(Beltrán-Castro et al., 2020)

Communities	**MHW Location**	**MHWs Timing**	**Biological time series duration**	**Methods**	**References**
Phytoplankton, zooplankton, intertidal, fish, marine birds, marine mammals	North Pacific	2014-2016	9 years	Trend Analysis over 5 years	(Suryan et al., 2021)
Ichthyoplankton	North Pacific	2015-2016	31 years	Comparison years before (1981-2014), during (2015-2016) and after (2017)	(Nielsen et al., 2021)
	North Pacific	2014-2016	66 years	Comparison before (1951-2013) and during (2014-2016) MHW	(Thompson et al., 2022)
Micronekton and Macrozooplankton	North Pacific	2015-2016	~ 2 summer months for 5 years	Temporal coincidence between changes in diversity, richness, evenness, densities and MHW year Yearly comparison	(Brodeur et al., 2019)
Meroplankton & embryos	North Pacific	2015-2016	3 winter months for 3 years	Temporal coincidence between concentration of embryos and MHW timing	(Shanks et al., 2020)
Nekton	East China Sea	2016-2017	4 years	Comparison before (2014-2015) and during (2016-2017) MHW	(Liu et al., 2022)
Zooplankton	North Pacific	2014-2016	7 years	Change in seasonal abundance trends co-occur with MHW Co-occurrence of variation in timing and duration of indicator species analysis groups and MHW	(McKinstry et al., 2022)

Communities	**MHW Location**	**MHWs Timing**	**Biological time series duration**	**Methods**	**References**
(Foraminifera)	Tasman Sea	2015-2016	~ 2 years	Temporal coincidence between abundance and community composition and MHW timing	(Evans et al., 2020)
	North Pacific	2014-2016	8 years	Occurrence of MHW with distinct foraminiferal assemblages	(Lane et al., 2023)
	Black Sea	2010	12 years	Yearly comparison and coincidence with MHW	(Gubanova et al., 2022)
	North Pacific	2014-2016	18 years	Comparison before (200-2013) during (2014-2016) and after (2017-2018) MHW	(Batten et al., 2022)
	Salish Sea	2015-2016	7 years	Comparison MHW (2015-2016) and non-MHW years (2014, 2017-2020) at different locations	(Winans et al., 2023)

Table S3.2. Multilevel pairwise comparison results table for spring and autumn. P: period, CI: Control/Impact treatment. Df: Degree of freedom. SS: Sum of squares. Res: Residual. *P*-value are adjusted using fdr correction. Method. ID was used as a random factor. Significant *P*-values are indicated in bold.

Source	**Before**					**After**			
	Df	**SS**	**F**	**R²**	**p-adj**	**SS**	**F**	**R²**	**p-adj**
Spring									
Control *vs*. Impact	1	0.06	1.71	0.03	0.16	0.17	3.97	0.06	**<0.01**
Autumn									
Control *vs*. Impact	1	0.03	0.71	0.01	0.58	0.10	2.44	0.05	**<0.05**

Table S3.3. Model selection results (AICc values) for zooplankton and copepod Shannon diversity index in response to treatment (CI), period (P) and pair identity (ID). ID is a random factor. CI and P are fixed. Model selection was carried out through maximum likelihood (ML) fitting. Best models are indicated in bold.

Model selection	Zooplankton Shannon diversity				Copepod Shannon diversity			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
CI × P + (1|ID)	100	85	46	61	63	58	−36	87
CI + P + (1|ID)	95	72	36	48	59	71	−42	74
P + (1|ID)	105	**65**	**30**	**46**	53	71	**−46**	89
CI + (1|ID)	**87**	73	34	55	**49**	**54**	−25	**70**

Table S3.4. Model selection results (AICc values) for zooplankton and copepod Pielou's evenness in response to treatment (CI), period (P) and pair identity (ID). ID is a random factor. CI and P are fixed. Model selection was carried out through maximum likelihood (ML) fitting. Best models are indicated in bold.

Model selection	Zooplankton Pielou's evenness				Copepod Pielou's evenness			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
CI × P + (1|ID)	−322	−182	−252	−198	−308	−176	−298	−140
CI + P + (1|ID)	−333	−200	−267	−215	−317	−167	−308	−157
P + (1|ID)	−324	**−208**	**−275**	**−219**	−324	−169	**−314**	−144
CI + (1|ID)	**−347**	−204	−274	−214	**−331**	**−189**	−296	**−166**

Table S3.5. Model selection results (AICc values) for Cyclopoida, Harpacticoida and Calanoida densities in response to treatment (CI), period (P) and pair identity (ID). ID is a random factor. CI and P are fixed. Model selection was carried out through maximum likelihood (ML) fitting. Best models are indicated in bold. Italic corresponds to model that didn't validate the assumptions and were changed to negative binomial

Taxa	Model selection	Spring	Summer	Autumn	Winter
Calanoida	CI × P + (1|ID)	**4330**	3237	**3216**	2440
	CI + P + (1|ID)	4334	3233	3220	2436
	P + (1|ID)	4337	**3231**	3218	**2435**
	CI + (1|ID)	4429	3244	3262	2437
Cyclopoida	CI × P + (1|ID)	*3029*	*2517*	2811	***2034***
	CI + P + (1|ID)	*3030*	***2511***	2811	*2036*
	P + (1|ID)	*3042*	*2513*	**2809**	*2041*
	CI + (1|ID)	***3025***	*2512*	2817	*2035*
Harpacticoida	CI × P + (1|ID)	*2503*	*2276*	**2674**	**2102**
	CI + P + (1|ID)	*2499*	***2273***	2693	2106
	P + (1|ID)	***2498***	*2278*	2709	2108
	CI + (1|ID)	*2500*	*2281*	2694	2124

Table S3.6. Model selection results (AICc values) for taxa densities in response to treatment (CI), period (P) and pair identity (ID). ID is a random factor. CI and P are fixed. Model selection was carried out through maximum likelihood (ML) fitting. Best models are indicated in bold. Italic corresponds to model that didn't validate the assumptions and were changed to negative binomial. X indicated that no model could be fitted to the data.

Taxa	Model selection	Spring	Summer	Autumn	Winter
Acartia spp.	CI × P + (1|ID)	***3594***	3032	***2898***	1935
	CI + P + (1|ID)	*3600*	3027	*2901*	1930
	P + (1|ID)	*3613*	3027	*2899*	1931
	CI + (1|ID)	*3714*	**3025**	*2943*	**1927**
Pseudo-Paracalanus spp.	CI × P + (1|ID)	***3892***	2805	***2842***	2269
	CI + P + (1|ID)	*3902*	**2799**	*2845*	**2266**
	P + (1|ID)	*3934*	2839	*2882*	2269
	CI + (1|ID)	*3908*	2814	*2843*	2269
T. longicornis	CI × P + (1|ID)	***3548***	*2411*	*2322*	1826
	CI + P + (1|ID)	*3551*	*2409*	*2319*	1824

	P + (1|ID)	*3549*	***2409***	***2317***	**1822**
	CI + (1|ID)	*3637*	*2432*	*2333*	1828
Copepoda nauplii	CI × P + (1|ID)	**3855**	2604	*2312*	*1901*
	CI + P + (1|ID)	**3855**	**2599**	***2309***	*1902*
	P + (1|ID)	3865	2605	*2309*	***1900***
	CI + (1|ID)	3979	2623	*2335*	*1914*
Appendicularia	CI × P + (1|ID)	***2484***	*2733*	2272	*1368*
	CI + P + (1|ID)	*2492*	***2729***	**2268**	***1365***
	P + (1|ID)	*2528*	*2729*	2269	*1373*
	CI + (1|ID)	*2572*	*2742*	2379	*1371*
Annelida larvae larvae	CI × P + (1|ID)	***3486***	2345	***2078***	*1093*
	CI + P + (1|ID)	*3504*	2340	*2079*	*1087*
	P + (1|ID)	*3503*	2338	*2089*	*1095*
	CI + (1|ID)	*3527*	**2336**	*2127*	***1085***
Cirripedia larvae larvea	CI × P + (1|ID)	*2976*	2240	***1824***	X
	CI + P + (1|ID)	*2975*	**2236**	*1823*	X
	P + (1|ID)	***2974***	2241	*1828*	X
	CI + (1|ID)	*3094*	2245	*1889*	X
Cladocera	CI × P + (1|ID)	X	***2457***	***1653***	X
	CI + P + (1|ID)	X	*2472*	*1672*	X
	P + (1|ID)	X	*2471*	*1686*	X
	CI + (1|ID)	X	*2481*	*1721*	X
Chaetognatha	CI × P + (1|ID)	X	*2009*	*2244*	X
	CI + P + (1|ID)	X	***2002***	*2244*	X
	P + (1|ID)	X	*2012*	*2242*	X
	CI + (1|ID)	X	*2030*	***2241***	X
Echinodermata larvae	CI × P + (1|ID)	2941	***2330***	X	X
	CI + P + (1|ID)	2949	*2340*	X	X
	P + (1|ID)	2981	*2338*	X	X
	CI + (1|ID)	3061	*2357*	X	X

CHAPTER

4

Beyond warming: copepods face marine heatwaves during blooms due to unchanged phenological timing

Beyond warming: copepods face marine heatwaves during blooms due to unchanged phenological timing

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Abstract

In marine ecosystems, copepods play an essential role in linking primary producers to higher trophic levels. As ectothermic organisms with short life cycles, they are particularly sensitive to environmental changes, as their metabolism and development are closely tied to abiotic conditions. Consequently, changes in environmental conditions, including temperature, can affect copepods, potentially leading to phenological shifts that may disrupt entire food webs. While such shifts have been linked to global warming, the specific impact of marine heatwaves (MHWs) on copepod phenology remains unclear. In this study, we used the Helgoland Roads long-term time series (German Bight, North Sea), one of the world's richest marine datasets, to examine changes in the phenological timing of key copepod taxa in response to MHWs. We computed yearly bloom traits using an algorithm adapted from phytoplankton bloom and assessed their relationship with MHW conditions, both before and during the bloom. With the exception of the calanoid copepod *Acartia* spp., we found no evidence of a consistent phenological shifts in response to MHW conditions (i.e., mean intensity and proportion of MHW days) occurring before the bloom. However, MHWs during copepod blooms led to significant changes in bloom duration. The bloom duration of nearly all taxa was correlated with several MHW components, including the proportion of MHW days and temperature increase rates within the bloom. Overall, a higher proportion of MHW days and rapid temperature rise resulted in a bloom contraction. Interestingly, copepods experienced an increase in the mean and variance of MHW conditions during their blooms, suggesting a shift in selective pressure linked to MHW exposure patterns. These findings highlight the complex interactions between MHWs and copepod phenology and the potential consequences for marine food webs, including mismatches with fish larvae, potentially affecting fish recruitment. Understanding these dynamics is crucial, as MHWs are expected to intensify in duration, frequency, and magnitude under future climate scenarios.

Keywords: Copepod – Helgoland Roads Time Series – marine heatwaves – North Sea – Phenology

INTRODUCTION

Mesozooplankton play a vital role in plankton communities, serving as a critical link between primary producers and higher trophic levels (Mackas & Tsuda, 1999). This key trophic group plays a central role in the trophodynamics of pelagic ecosystems (Helaouët & Beaugrand, 2007). Within the mesozooplankton community, copepods dominate, comprising over 80 % of the mesozooplankton biomass in oceans (Kiørboe, 1997). They represent the majority of secondary production and serve as a major food source for zooplanktivorous fish, fish larvae, and other organisms like jellyfish and chaetognaths (Kiørboe, 2011). As ectothermic organisms with short life cycles, copepods are particularly sensitive to temperature fluctuations, as their metabolism and development are closely linked to abiotic factors (Richardson, 2008). Consequently, global warming can affect copepod populations, potentially leading to shifts in community composition and changes in species distribution, which may, in turn, disrupt entire food webs and the ecosystem services they support.

Over the past decades, the North Sea copepod community has undergone considerable change primarily due to environmental shifts, with rising temperatures being the most prominent factor (Amorim et al., 2023; Edwards et al., 2002). Authors have observed a decline in the proportion of cold-adapted copepods relative to warm-adapted ones (Alvarez-Fernandez et al., 2012). Additionally, Boersma et al. (2015) reported a significant decrease in the calanoid copepods such as *Temora longicornis, Acartia* spp., and *Pseudo/Paracalanus* spp., while cyclopoids like *Oithona* spp., showed the opposite trend. Copepod functional community changes in response to warming have also been documented, with smaller copepod with a short development time and a higher abundance in autumn becoming more abundant at the expense of larger copepods with longer development time, peaking in summer (Deschamps et al., 2023). Along with these community shifts, warming has also induced geographic redistributions (Beaugrand, 2002), as well as shifts in phenology of key copepod taxa (Corona et al., 2024).

Among all mechanisms, phenological shifts can allow species to remain in an environment with optimal conditions (Beaugrand & Kirby, 2018). As temperature can explain most of the variability in the timing of copepod abundance (Atkinson et al., 2015; Mackas et al., 2012), a phenological shift can enable a species to maintain its thermal niche (Corona et al., 2024). As copepods are an important main food source for many organisms, phenological shifts can have dramatic impacts on community functioning if the synchrony between copepod cycles and those of their predators is disrupted. Indeed, according to the match-mismatch hypothesis, interannual variations in larval fish recruitment are directly linked to the overlap between their annual peak and the peak in prey (Beaugrand et al., 2003; Cushing, 1990). Consequently, shifts in copepod phenology in response to warming and the potential resulting mismatch with higher trophic levels can have consequences for the entire food web.

The study of phenological shifts in response to warming generally involves analysing long-term time series. However, beyond changes in mean conditions, climate change is also linked to increased variability (IPCC, 2022), which is typically filtered out at annual and shorter time scales before analysis. This variability is just as important to study as changes in mean temperature, since organisms respond differently to fluctuating environments compared to constant conditions (Gerhard et al., 2023; Kingsolver et al., 2015; Niehaus et al., 2012).

In the context of temperature change, marine heatwaves (MHWs) are extreme weather events that can directly impact marine communities (Smith et al., 2023; Suryan et al., 2021). MHWs are becoming increasingly frequent and intense (Frölicher et al., 2018; Meehl & Tebaldi, 2004; Oliver et al., 2018; Perkins et al., 2012), raising ecological and socioeconomic concerns (Smith et al., 2023). The effect of MHWs is especially important if they coincide with critical phenological events, such as migration (Woehler & Hobday, 2024), growth (Atkinson et al., 2020) and reproduction (Leach et al., 2021). Therefore, it is crucial to understand how organisms, particularly those representing a crucial link with higher trophic levels, respond to MHWs in terms of phenology (Arteaga & Rousseaux, 2023; Ma et al., 2015; Vad et al., 2023).

MHWs can lead to a complete reorganisation of plankton communities. For instance, in the Tasman Sea, a shift in the zooplankton community was recorded in response to the 2015-2016 MHW (Evans et al., 2020) with smaller warm-water copepods dominating the community and replacing larger temperate or cold-water copepods. Another MHW occurring in 2014-2016 in the Northeast Pacific Ocean, also called "The Blob", resulted in an increase in warm-water copepod in autumn, which persisted through the winter months (McKinstry et al., 2022) as well as an increase in copepod abundances in the Gulf of Alaska (Batten et al., 2022).

While MHW effects on zooplankton community compositions have been relatively well described (Beltrán-Castro et al., 2020; Brodeur et al., 2019; McKinstry et al., 2022; Suryan et al., 2021; **Chapter 3** of this thesis), these studies primarily focus on changes in abundance and community structure. However, MHWs also have the potential to disrupt phenological timing by exceeding threshold temperatures and triggering growth and reproduction (Atkinson et al., 2020). While changes in phenology were mainly reported for plants in terrestrial ecosystems

(Cremonese et al., 2017; Jentsch et al., 2009; Orsenigo et al., 2015), phenological shift in response to MHWs have also been observed in the ichthyoplankton community (Auth et al., 2018; Thompson et al., 2022). Since biological factors such as prey availability can influence fish spawning timing it is crucial to understand MHW effects on the phenological timing of copepods.

In this study, we quantified the phenological response of copepod taxa in the North Sea to MHWs. Here, we used the term “phenology” or “phenological timing” to denote seasonal timing of adult copepod density. We used the density of key copepods from the Helgoland Roads times series (54°11'18 "N 7°54' E), a unique dataset and one of the world’ richest marine time series (Wiltshire et al., 2010) as well as all the MHWs recorded at Helgoland Roads from 1975 to 2018 (Giménez et al., 2024). Here, MHWs, are defined as periods of time ≥ 5 days during which seawater temperature exceeds the 90th quantile of a baseline temperature time series (Hobday et al., 2016). This study is structured into four sections. First, we characterised the seasonal pattern of copepod density, determining if one or more peaks existed within each year, and if blooms could be easily defined using a set of phenological descriptors (hereafter, bloom traits). Second, we investigated changes in copepod phenology in response to the MHWs experienced within a fixed period of time before a bloom (i.e., fixed window). The pre-bloom period encompasses the time when copepods transition from either diapause stages or a state of reduced activity, to hatching and active reproduction. Therefore, changes in MHW conditions during this phase could have a direct influence on bloom timing. For this purpose, we computed yearly bloom traits using an algorithmic method adapted from phytoplankton blooms (Mieruch et al., 2010) and assessed the relationship between bloom traits and two keys MHW components, the mean intensity and proportion of MHW days experienced within a fixed window. Third, as demonstrated in **Chapter 3** of this thesis, copepod densities responded to MHWs only after the onset of the latter. Therefore, to understand the immediate effect of the MHW, we analysed MHW conditions during each bloom, focusing on changes in the mean and variance of the intensity and the proportion of MHW days occurring within each bloom. We then assessed changes in the copepod bloom duration in response to other MHW components experienced during the bloom, such as the temperature increase and decrease rate. We hypothesise that shifts in timing will be specific to each taxon, with some consistent patterns emerging among taxa from the same season. In high or mid-latitude regions, species from spring and early summer often exhibit an "earlier when warmer" response (Mackas et al., 2012) as well as a phenological contraction (Beaugrand & Kirby, 2018) in response to global warming. Therefore, we anticipate that MHW occurring before a bloom will lead to earlier and faster blooms in copepod taxa associated with these seasons. Conversely, late summer/autumn taxa will respond to warming with a phenological expansion (Beaugrand & Kirby, 2018). If no shift in timing is observed in response to MHW occurring before a bloom, we believe that changes in bloom traits in response to MHW occurring during the bloom might occur.

MATERIALS & METHODS

Data sources and software

All analyses were conducted under R environment (R Core Team, 2020) with a threshold of significance set at 5 %.

Copepod densities (ind.m^3) from the Helgoland Roads (HR) time series (Boersma et al., 2017; Wiltshire et al., 2010) were used in this study. Since 1975, mesozooplankton have been sampled near the island of Helgoland in the German Bight (54°11'18"N, 7°54'E) using a Nansen net (150 µm, aperture 17 cm, and net length 100 cm) fitted with a flowmeter. The complete monitoring method is described by Greve et al. (2004). Only copepods identified over the period 1975-2018 and with a mean relative density ≥ 3 % were selected for analysis. The complete table included two taxa peaking in spring (*T. longicornis* and Copepoda nauplii), three peaking in summer (The Cyclopoid *Oithona* spp., composed by *O. similis* and *O. nana*, the Calanoids *Acartia* spp., composed by *A. tonsa* and *A. clausi* and *Pseudo/Paracalanus* spp., composed by *Pseudocalanus elongatus* and *Paracalanus parvus*), and one taxon peaking in autumn (Harpacticoida). At HR, sampling is carried out three times a week. Therefore, prior to analysis, density data were interpolated and smoothed to reduce noise (Fig. 4.1). Several smoothing methods (i.e., simple moving average, loess, bin smoothing, GAM) were tested. After comparison, a cubic smoothing spline was fitted to the data as it maintained an optimal balance between smoothness and fidelity to the original data (Reinsch, 1967).

All MHWs events recorded at HR from 1975 to 2018 were obtained from Giménez et al. (2024). At HR, sea surface temperature is recorded on a workday basis at 1 m depth using a thermometer. A 30-year fixed baseline (form the 1st January 1962 to the 31st December 1991) was then applied to these temperatures in order to compute the threshold temperature (90th quantile) above which anomalously warm sea temperature will be considered as a MHW if the event lasts for more than five days (Hobday et al., 2016).

Copepod periodicity

The first objective was to characterise the variability in the annual periodicity of copepod blooms (Fig. 4.1). Temporal patterns in taxa densities were visualised using wavelet analysis (Cazelles et al., 2008). In ecology, spectral or correlation analyses are usually used to detect periodicities in time series. These methods assume that the statistical properties of the time series are stationary (i.e., constant through time) However, this assumption is often violated, specifically when studying populations, including zooplankton (Molinero et al., 2013) or phytoplankton (Alcocer et al., 2022) where dynamics can change over time in response to environmental variables. Wavelet analysis deals with non-stationarity (Cazelles et al., 2008); it decomposes the variable of interest (here taxa densities) as a function of period (here days) and time (here years) in order to determine the dominant scales of variability. Wavelet analysis can therefore be used to identify statistically significant periods at a certain time such as seasonal cycles. Here, the R package *WaveletComp* (Roesch & Schmidbauer, 2014) was used to perform wavelet analysis with 999 simulations on both the linear and logarithmic scales of the taxa densities. As densities were interpolated prior to analysis, a time resolution of one day was used. The wavelet power spectrum (heatmap, see Fig. 4.1) was then used to assess the periodicities of the density time series.

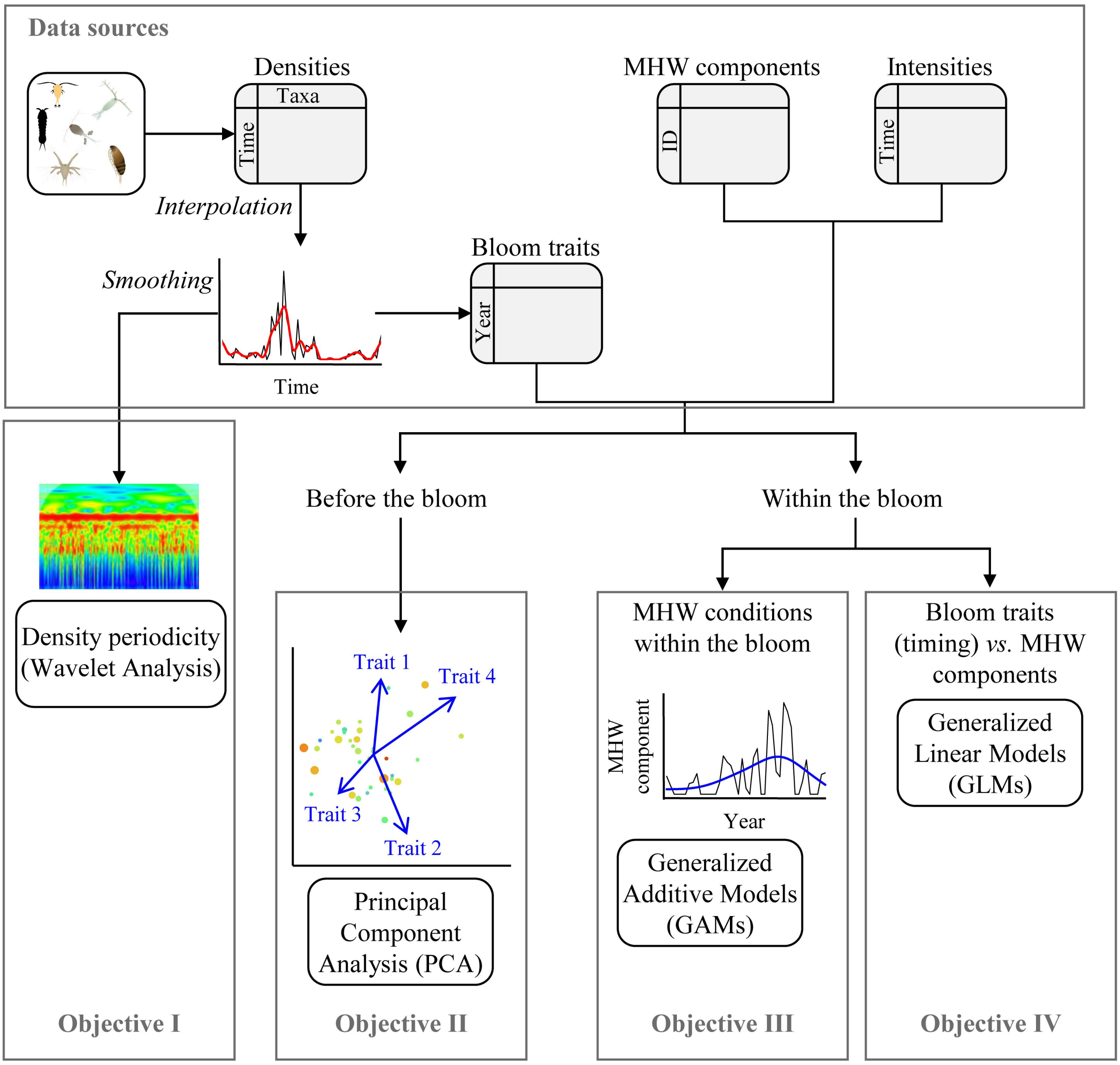


Figure 4.1. Workflow diagram for the different analyses of this study. In objective I, copepod densities (ind.m³) were interpolated and smoothed to assess periodicity. Densities were then combined with MHW data. MHW data were extracted from the MHW component table from Giménez et al., (2024) and the intensity (°C above or below the climatology) to address the three other objectives. Objective II: Association between MHW components pre-bloom and copepod bloom traits. Objective III: Quantification of MHW conditions experienced during the blooms. Objective IV: Association between bloom traits and MHW components exhibited during the bloom.

Copepod phenological traits

Objectives II-IV (Fig. 4.1) required the quantification of phenological traits. In order to describe copepod phenology, a semi-quantitative method of classification of copepod blooms based on an algorithmic estimation of several bloom traits was used (Table 4.1). First, the maximum density as well as its assigned Julian day were retrieved from the time series for each year and taxon. Second, in order to compute the start and end of the bloom, a method adapted from Mieruch et al. (2010) was applied. Several methods exist (Fig. 4.2) and selecting an appropriate bloom metric is challenging as no strict guidelines exist that recommend one metric over the other. The first method consists of using a fixed threshold in abundance that, when reached, will be considered as the start and/or end of the bloom (e.g., Fleming & Kaitala, 2006). However, such methods can only work when the bloom intensity (i.e., seasonal pattern of density and its peak abundance) varies little from year to year, except for shifts in timing. In years with seasonal patterns characterised by low density, a bloom may go undetected even if it is occurring. This is the case at Helgoland Roads, where densities of copepods taxa have changed dramatically over the past decades (Boersma et al., 2015; Di Pane et al., 2023). A second approach would be to define the start (and end) of the bloom based on when densities cease to be, or become undetected (= zero in the data set) (Mieruch et al., 2010). However, this method often results in excessively long bloom periods, sometimes extending throughout the entire year: in many situations abundance can remain at very low levels for long time before it undergoes the exponential phase towards the peak. The third method would be based on quantiles of the distribution of abundance (e.g., Racault et al., 2015; Siegel et al., 2023) (e.g., first and third quartiles). However, because these indicators respond to the overall properties of the distribution, and abundance is distributed over time, such method results in the reversal of apparent causation where the start of the bloom is affected by the event occurring thereafter (i.e., during the bloom). The method employed here (see below; full description in Mieruch et al. 2010) accounts for yearly variations in bloom intensity, long periods of low abundance and reversal causation.

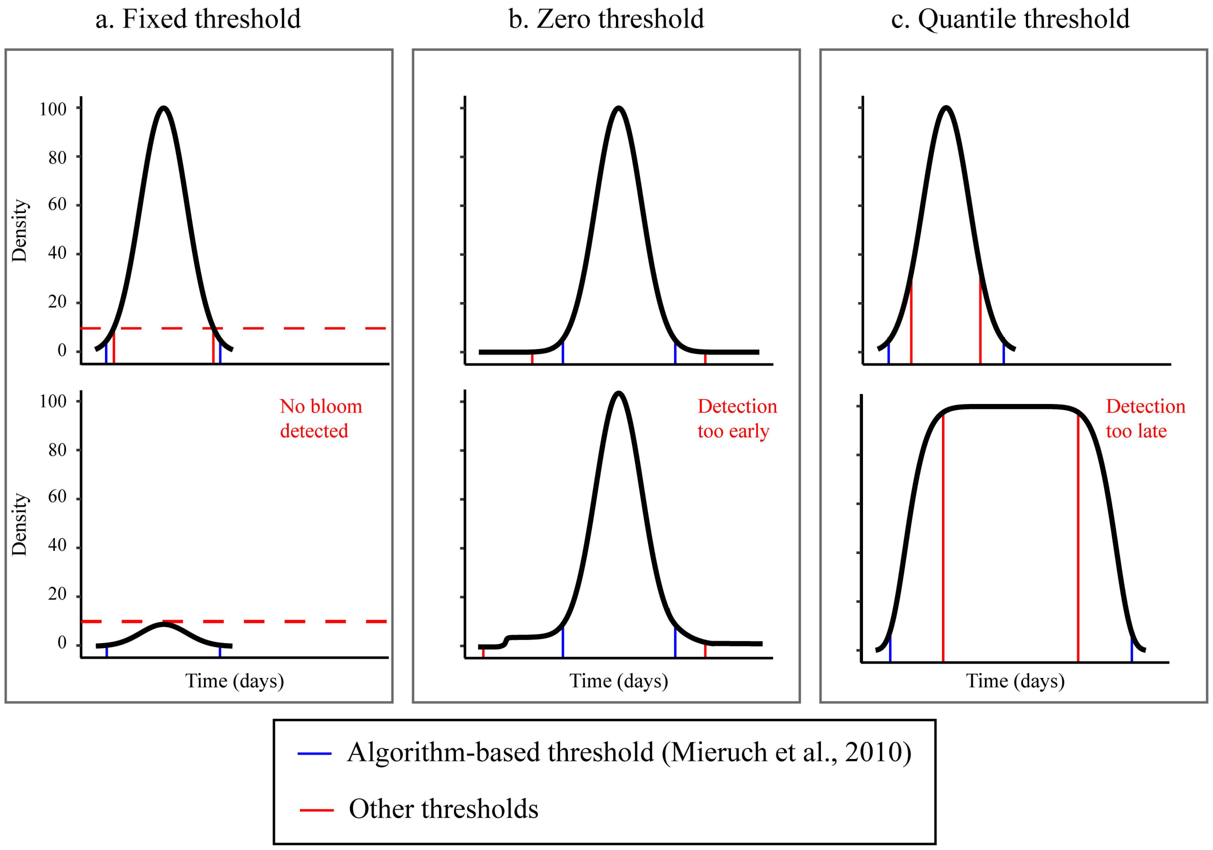


Figure 4.2. Bloom start and end detection methods as described by Mieruch et al. (2010) are shown in blue, alongside three alternative methods: **a.** fixed, **b.** zero, and **c.** quantile, displayed in red. The algorithm-based threshold is calculated using interpolated, smoothed, and log-transformed density data. While the algorithm consistently produces the same bloom start date, the alternative methods either shifted the timing or failed to detect the bloom when the overall shape of the bloom distribution changed.

To identify the start and end of the yearly bloom, an initial search interval was defined. This interval began on the day of maximum density and extended both backwards and forwards, respectively. The beginning and end points of the interval search were established when the copepod taxa density was ≤ 5 % of the maximum yearly density. Hence, in this method, the abundance peak of all blooms is normalised, (to 100 %) accounting for year-to-year variations in bloom intensity, and the searching pattern avoids long periods where abundance is overly low. In some instances, the Julian day for the search interval could not be found within the same year as the maximum density. In such cases, the search was extended into the previous or following year until the threshold was reached. For these scenarios, the beginning and end of the interval search were calculated as 1 - the number of days from the threshold to January 1st, and 365 + the number of days from December 31st to the threshold, respectively. For some taxa, such as *Pseudo/Paracalanus* spp., the maximum density was generally too low to identify points where the density was ≤ 5 % of the yearly maximum. Since the primary goal of this study was to examine changes in phenology in response to MHW rather than to compare taxa, the threshold for the interval search was adjusted to 1 % of the maximum density on a case-by-case basis. Once the interval was identified, instantaneous growth rates for each bloom were calculated by applying a logarithmic transformation to the copepod densities. For each three-day window within the bloom period, linear regressions were performed on the log-transformed abundances, with the growth rate determined from the slope of the regression. These calculations were repeated for each day within the bloom period, ensuring that growth rates were computed for overlapping three-day intervals. The differences between consecutive growth rates were then calculated, with the bloom start and end defined as the points of maximum increment. Therefore, the bloom's start and end correspond to the days of maximum rate of changes (i.e., maximum acceleration/deceleration). Finally, the maximum growth and decline rates were also determined. It is important to note that this method does not account for multiple blooms within a year for a given species, but rather focuses on the bloom corresponding to the highest density observed during the year.

Table 4.1. Phenological traits and MHW components used in this study to describe copepod phenology. All descriptors were computed after pre-processing of the copepod density. Bloom duration: number of days between the bloom start and end. Onset duration: number of days between the start and the peak of the bloom. Decline duration: number of days between the peak and the end of the bloom. Bloom peak: day of the maximum density. Mean intensity: mean difference between the Q90 threshold and the temperature.

Phenological traits	**Unit**	**MHW components**	**Unit**
Bloom start	Julian day	**Within four-months window**	
Bloom end	Julian day	Mean intensity	°C
Bloom duration	Number of days	Proportion of MHW days	
Onset duration	Number of days	**Within the bloom**	
Decline duration	Number of days	Mean intensity	°C
Bloom peak	Julian day	Cumulative intensity	°C
Maximum peak of density	Ind.m^3	Proportion of MHW days	
Maximum growth rate	Day^{-1}	Maximum temperature increase rate	Day^{-1}
Maximum decline rate	Day^{-1}	Maximum temperature decrease rate	Day^{-1}

MHW conditions before the bloom

Our second objective was to understand the effect of MHWs occurring before the bloom on the phenology of copepod taxa (Fig. 4.1). Two key components were examined: the proportion of MHW days and the mean intensity (°C deviation from climatology) during a specific window preceding a bloom. The analysis included all blooms, even those that experienced no MHWs during this timeframe. As a result, the proportion of MHW days ranged from 0 to 1, and mean intensity varied from -2.33 °C to 3.18 °C. The pre-bloom window was set to end on the start date of the earliest bloom for each taxon, extending four-month prior to provide a sufficient time frame. This window was chosen to capture both pre-bloom environmental changes and key life cycle transitions in copepods (diapause, resting eggs, reduced activity). If MHWs started before the fixed four-months window, they were included in the analysis only if their peak intensity (i.e., day of MHW maximum intensity) occurred within this window. The proportion of days in MHW and mean intensity were then recalculated to consider only the days within the fixed window.

Prior to this, the temporal dynamics of each bloom trait was investigated to determine if it was consistent across all taxa. For this purpose, copepod bloom traits were standardised and centred scaled Principal Component Analysis (PCAs) were performed on the copepod community for each bloom traits separately. Since the temporal dynamics of copepod bloom traits were not consistent across taxa (see Results), the effect of MHW on copepod phenology was investigated individually for each copepod taxon. Centred-scaled PCAs were then performed for each taxon on the standardised bloom traits table, displaying the temporal (yearly) dynamics of the bloom traits. To identify a trend in the dynamic of bloom traits over time, Linear Models (LMs) were performed on the PC scores (Two first PCs separately) representing changes in bloom traits over time. The fixed factor Year was included in the model. All model assumptions were verified by checking residuals and overdispersion. The mean intensity as well as the proportion of MHW days within the four-month fixed window were added to the PCA to visualised any pattern in bloom traits related to MHW conditions. To examine the relationship between bloom traits and changes in MHW components over time, additional PCAs were conducted for each taxon based on the MHW components. Redundancy Analyses (RDAs) were subsequently performed for each taxon, using the PCA scores of bloom traits as the response matrix and the PCA scores of the MHW components as explanatory variables. The significance of each model was tested using an ANOVA-like procedure with 999 permutations (Legendre et al., 2011).

MHW conditions within the bloom

Our third objective was to investigate whether copepods experienced changes in MHW conditions during their bloom over time. Specifically, we examined variability in two key MHW components, the intensity and the proportion of MHW days occurring within each copepod bloom. All blooms experiencing at least one MHW were considered while years without MHWs were excluded (Fig. 4.1). In the German Bight, the mean intensity and the number of MHW days have been increasing since 1962, specifically after 1990 (Giménez et al., 2024). To determine whether this trend was also observed within the bloom of each copepod, the mean intensity and the proportion of MHW days within the bloom were also analysed. Overall, similar trends were found in the blooms of most taxa (See Supplementary Material Fig. S4.1-4.2).

The variance of the MHW components was computed through a moving variance (i.e., a method that calculates the variance of a subset of data points within a moving window across a larger dataset) with a window of three years. Based on the linearity of the data, either LMs or a Generalized Additive Models (GAMs) were performed for each taxon. The fixed factor Year (numerical) was included in the model with a smooth term applied in the case of GAMs. In case of violation of model assumptions, LMs were replaced by beta regression models. Since beta regression cannot handle values = 0 or 1, proportions were transformed before analysis using the following formula:

$$\mathbf{P} = \frac{\mathbf{p} \times (\mathbf{N} - \mathbf{1}) + \mathbf{0.5}}{\mathbf{N}}$$

Where p is the proportion of MHW days within the bloom and N the duration of the bloom.

MHW effect on bloom duration

Our fourth objective (Fig. 4.2) was to evaluate the effect of MHW components on the bloom duration of copepod taxa. LMs were performed on both the linear and logarithmic scales for each taxon and for three types of bloom duration: the start to peak duration, the peak to end duration and the full bloom duration. The fixed factors maximum decline rate (RD), maximum growth rate (GR), mean intensity (Im), cumulative intensity (Ic), and the proportion of days in MHW (HW days) were included in the model. Multicollinearity between MHW components was checked through a Variance Inflation Factor with a threshold value set at 10. Cumulative intensity showed multicollinearity and was removed from all models. To assess model fit, model selection procedures (Zuur et al., 2009) were used based on the corrected Akaike Information Criterion (AICc).

RESULTS

Copepod periodicity

Throughout the time series of all copepod taxa, the annual period (365 days) was the most dominant scale of variation in densities. This periodicity was significantly detected across the entire time series only for *Acartia* spp (spring bloomer; Fig. 4.3c). In contrast, for all other taxa, the annual pattern was not consistent over the full time series. The annual pattern disappeared from ~2009 to 2014 for *T. longicornis* (spring bloomers; Fig. 4.3b) and from ~2007 to 2011 for *Pseudo/Paracalanus* spp., (summer bloomer; Fig. 4.3e) and became weaker between ~2005 and 2015 for Copepoda nauplii (spring bloomer; Fig. 4.3a). While *Oithona* spp., also showed discontinuity in the annual periodicity around 2010, the longest period without an annual bloom occurred between ~1978 and 1985 (summer bloomer; Fig. 4.3d). The autumn bloomer Harpacticoida exhibited the most discontinuity, with no annual pattern observed before ~1983, between ~1986 and 1988, and between ~2006 and 2010 (autumn bloomer; Fig. 4.3f).

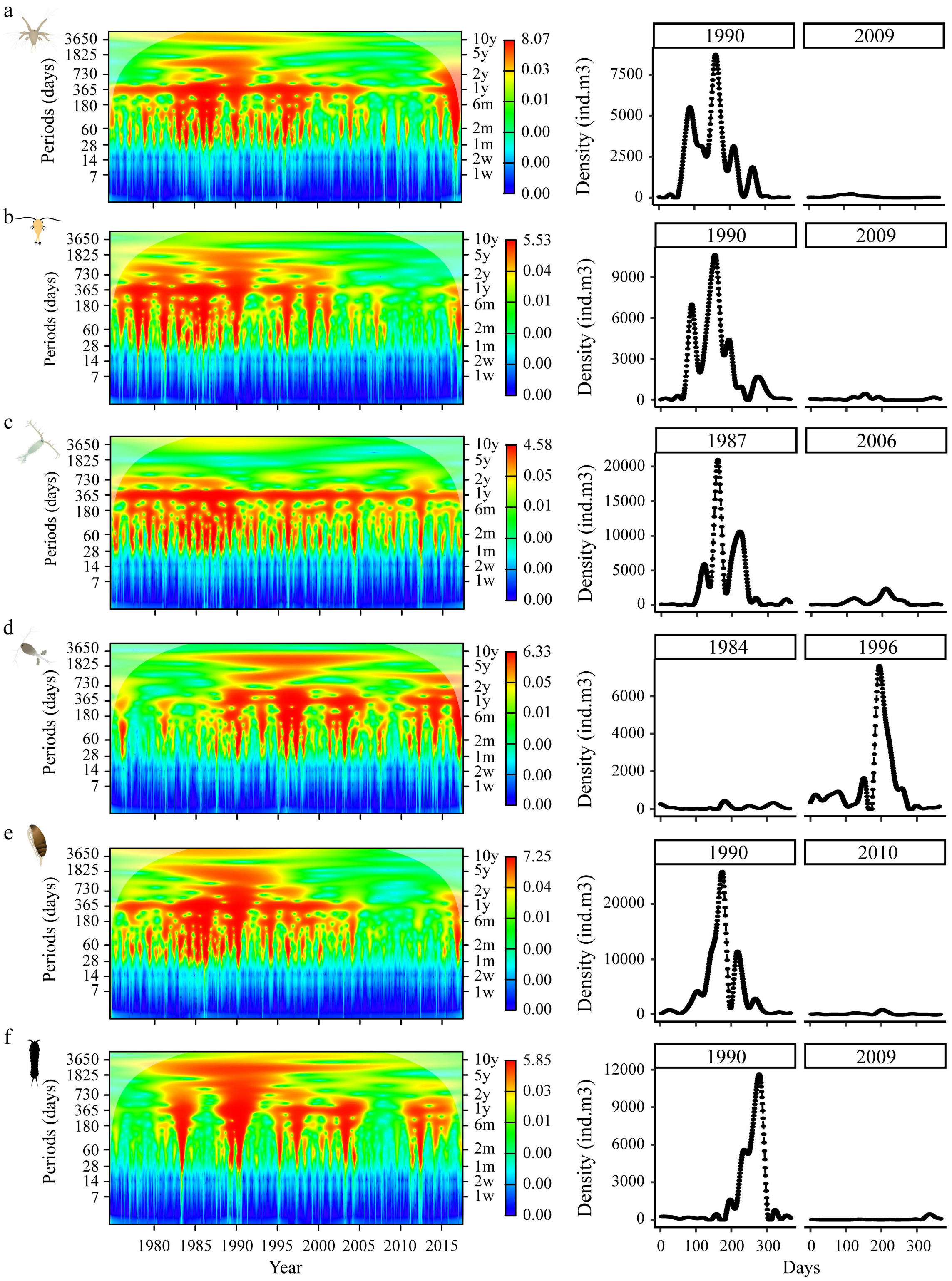


Figure 4.3. Spectrogram from wavelet analyses applied to the smoothed time series of **a.** Copepoda nauplii (spring bloomer), **b.** *T. longicornis* (spring bloomer) **c.** *Acartia* spp., (summer bloomer), and **d.** *Oithona* spp., (summer bloomer), **e.** *Pseudo/Paracalanus* spp., (summer bloomer) and **f.** Harpacticoida (autumn) densities and example years for comparison. The colour gradient represents wavelet power (σ^2), with red indicating a strong signal and blue indicating little to no signal. The shaded area in the top corners represents the edge effect.

The comparison of densities between two years (Fig. 4.3, right panels) highlights that changes in the magnitude of the annual periodicity are largely driven by changes in density. The logarithmic transformation is essential to recover the annual patterns and allows for consistently detecting significant periodicity across all taxa throughout the time series (Fig. S4.3), accounting for varying bloom intensities rather than a bloom *vs.* no bloom scenario.

Importantly, all taxa exhibited significant, though intermittent, sub-annual periodicity ranging from a month to a year. These periodicities, while less dominant than the annual one, underscore the temporal structure of copepod blooms. Rather than being described by a single annual peak of occurrence, copepod blooms consist of one major peak and several smaller peaks occurring on a sub-annual scale.

Changes in bloom traits in response to MHW occurring before the bloom

Our second objective was to examine the temporal dynamics of copepod bloom traits. An important point here was to determine if the temporal dynamics of copepod bloom traits were consistent across taxa. This assessment aimed to establish whether the impact of MHWs on copepod phenology could be analysed collectively for all taxa or if it required investigation at the taxa level. Overall, copepods did not show a community level change in phenological traits (Fig. S4.4) and therefore all analyses were performed at the taxa levels.

For all groups, the first two axes explained approximately 60 % of the total variability. Timing traits, such as the start, end, and peak of the bloom, were the main contributors to the formation of PC1, while bloom duration contributed significantly to PC2 formation (Fig. 4.4). Additionally, maximum density and growth rate contributed to PC2 for *T. longicornis*, Copepoda nauplii, and *Oithona* spp., while decline rate contributed to PC2 only for Copepoda nauplii and Harpacticoida.

For the summer bloomer *Acartia* spp., PC1 scores exhibited an increasing trend in bloom traits changes over time, while PC2 scores showed no clear temporal changes (Table 4.2). Both PC1 and PC2 responded positively to MHW intensity and the proportion of MHW days (ANOVA-like procedure comparing PC scores of bloom traits with PC scores of MHW components: $p < 0.05$), indicating that MHWs resulted in shorter and earlier blooms (Fig. 4.4c). Conversely, periods with little to no MHW activity were associated with later bloom timing.

For Copepoda nauplii, *T. longicornis*, *Oithona* spp., *Pseudo/Paracalanus* spp., and Harpacticoida, no trends in bloom traits over time were observed, and no clear patterns emerged in response to MHW conditions (Fig. 4.4a, b, d, e, f; Table 4.2).

Table 4. 2. Results of linear regression of bloom trait changes (PC1 and PC2) over time (Year) for each copepod taxon.

	PC1 ~ Year			**PC2 ~ Year**		
Species	**F-value**	**Adj-R2²**	***P*-value**	**F-value**	**Adj-R2²**	***P*-value**
Copepoda nauplii	0.11	−0.02	0.74	0.10	−0.02	0.75
T. longicornis	0.24	−0.01	0.62	0.49	−0.01	0.48
***Acartia* spp.**	16.92	0.27	**<0.001**	0.08	−0.02	0.78
***Oithona* spp.**	1.41	0.01	0.24	0.28	−0.02	0.59
***Pseudo/Paracalanus* spp.**	1.25	0.006	0.27	1.13	0.003	0.29
Harpacticoida	0.03	−0.02	0.85	1.63	0.01	0.21

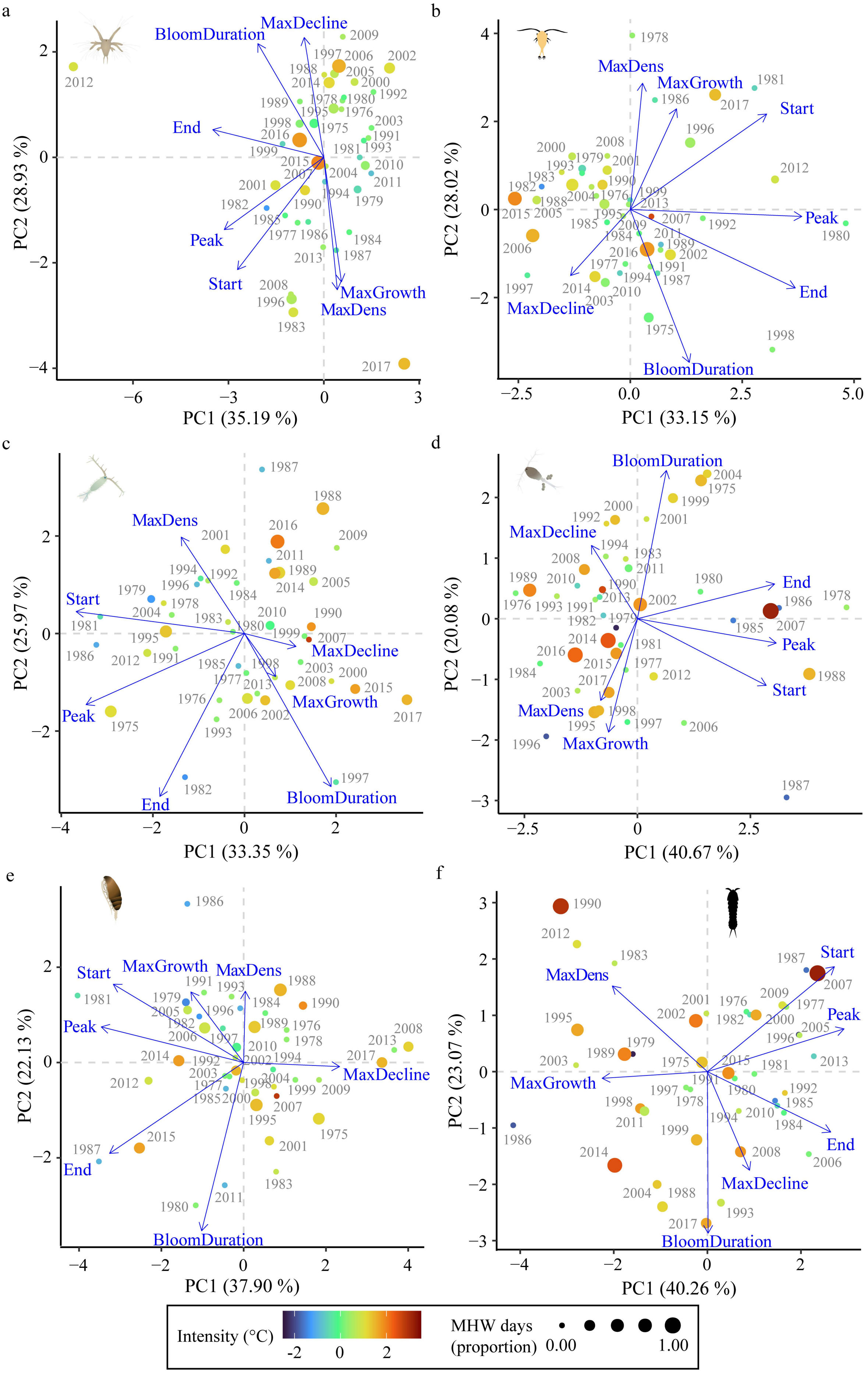

a
BloomDuration
MaxDecline
End
Peak
Start
MaxGrowth
MaxDens
PC2 (28.93 %)
PC1 (35.19 %)
b
MaxDens
MaxGrowth
Start
Peak
End
MaxDecline
BloomDuration
PC2 (28.02 %)
PC1 (33.15 %)
c
MaxDens
Start
Peak
End
MaxDecline
MaxGrowth
BloomDuration
PC2 (25.97 %)
PC1 (33.35 %)
d
BloomDuration
MaxDecline
End
Peak
Start
MaxDens
MaxGrowth
PC2 (20.08 %)
PC1 (40.67 %)
e
Start
MaxGrowth
MaxDens
Peak
MaxDecline
End
BloomDuration
PC2 (22.13 %)
PC1 (37.90 %)
f
MaxDens
Start
Peak
MaxGrowth
End
MaxDecline
BloomDuration
PC2 (23.07 %)
PC1 (40.26 %)
Intensity (°C)
-2
0
2
MHW days
(proportion)
0.00
1.00

Figure 4.4. Changes in bloom traits in response to MHWs components before the bloom of **a.** Copepoda nauplii (spring bloomer), **b.** *T. longicornis* (spring bloomer) **c.** *Acartia* spp., (summer bloomer), **d.** *Oithona* spp., (summer bloomer), **e.** *Pseudo/Paracalanus* spp., (summer bloomer) and **f.** Harpacticoida (autumn bloomer). PCAs were performed on the standardised bloom traits for each taxon. Colour gradient and dot size represent the mean intensity (°C) and the proportion of MHW days recorded respectively, during a fixed four-month window preceding the earliest bloom of each taxa. BloomDuration: bloom duration (Julian days), End: day of the bloom end (Julian days), MaxDens: Maximum densities (ind.m^3), MaxDecline: maximum bloom decline rate (day^{-1}), MaxGrowth: maximum bloom growth rate (day^{-1}), Peak: day of maximum density peak (Julian days), Start: day of the bloom start (Julian days).

MHW conditions within the bloom

The moving variance of the proportion of MHW days within the bloom showed significant temporal changes across all taxa. For Copepoda nauplii, the variance increased over time (Fig. 4.5a). In contrast, *T. longicornis* exhibited a constant variance at the beginning of the time series, followed by a sharp increase from 2000 onwards (Fig. 4.5b). *Oithona* spp. experienced an increase in variance earlier, in 1990 which then decreased after 2005 (Fig. 4.5d). *Acartia* spp., *Pseudo/Paracalanus* spp., and Harpacticoida showed high temporal variability (Fig. 4.5c, e, f). The variance for these three taxa was higher between 1990 and 2005, with *Pseudo/Paracalanus* spp., showing and additional increase from 2012 onward (Fig. 4.5e).

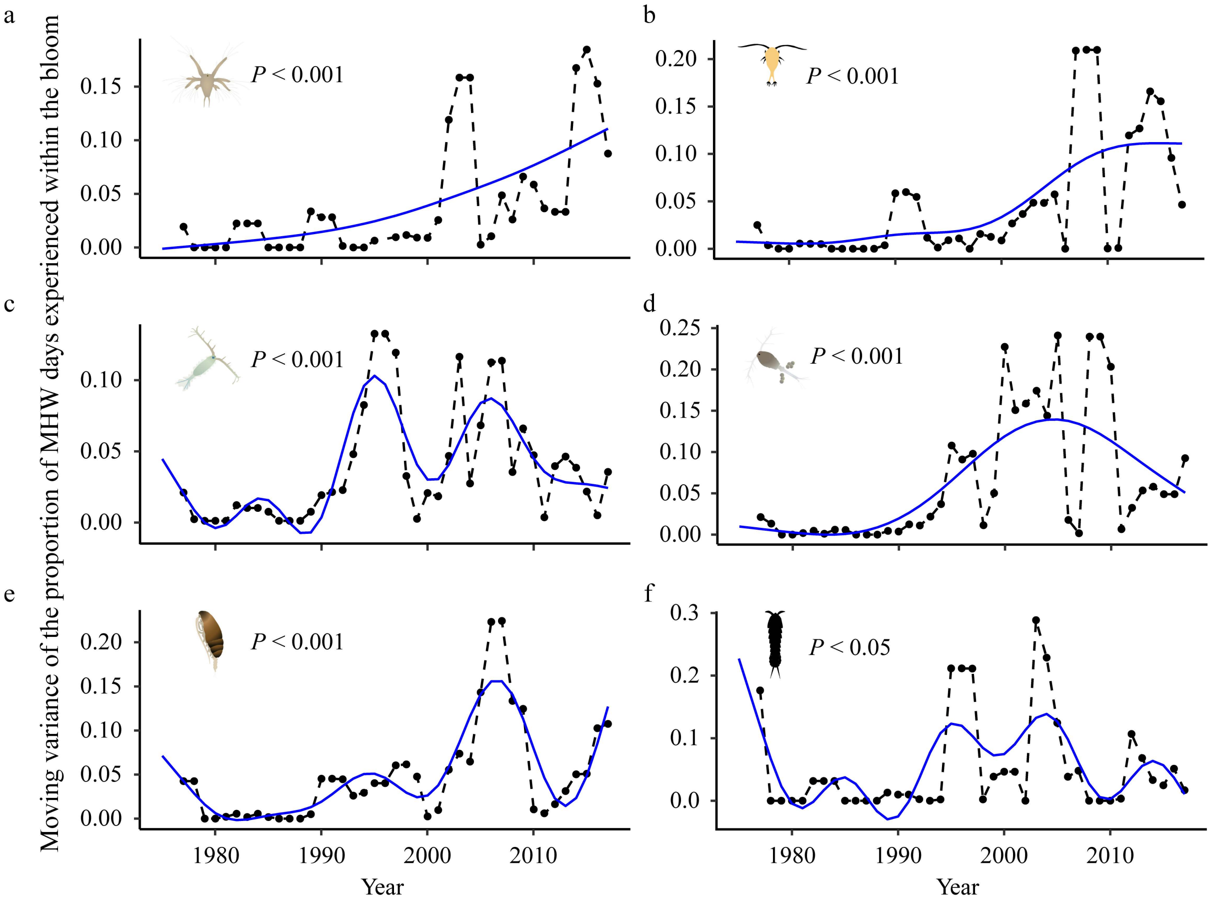


Figure 4.5. Time series of the moving variance of proportion of MHW days experienced within the bloom **a.** Copepoda nauplii, **b.** *T. longicornis*, **c.** *Acartia* spp., **d.** *Oithona* spp., **e.** *Pseudo/Paracalanus* spp., and **f**. Harpacticoida. The blue curves represent the model fit: GAMs were used for all species except for Copepoda nauplii (beta regression). The moving variance was computed using a three-year window.

In contrast, the variance in intensity remained unchanged for all taxa except for *Pseudo/Paracalanus* spp., where variance increased over time (Fig. 4.6).

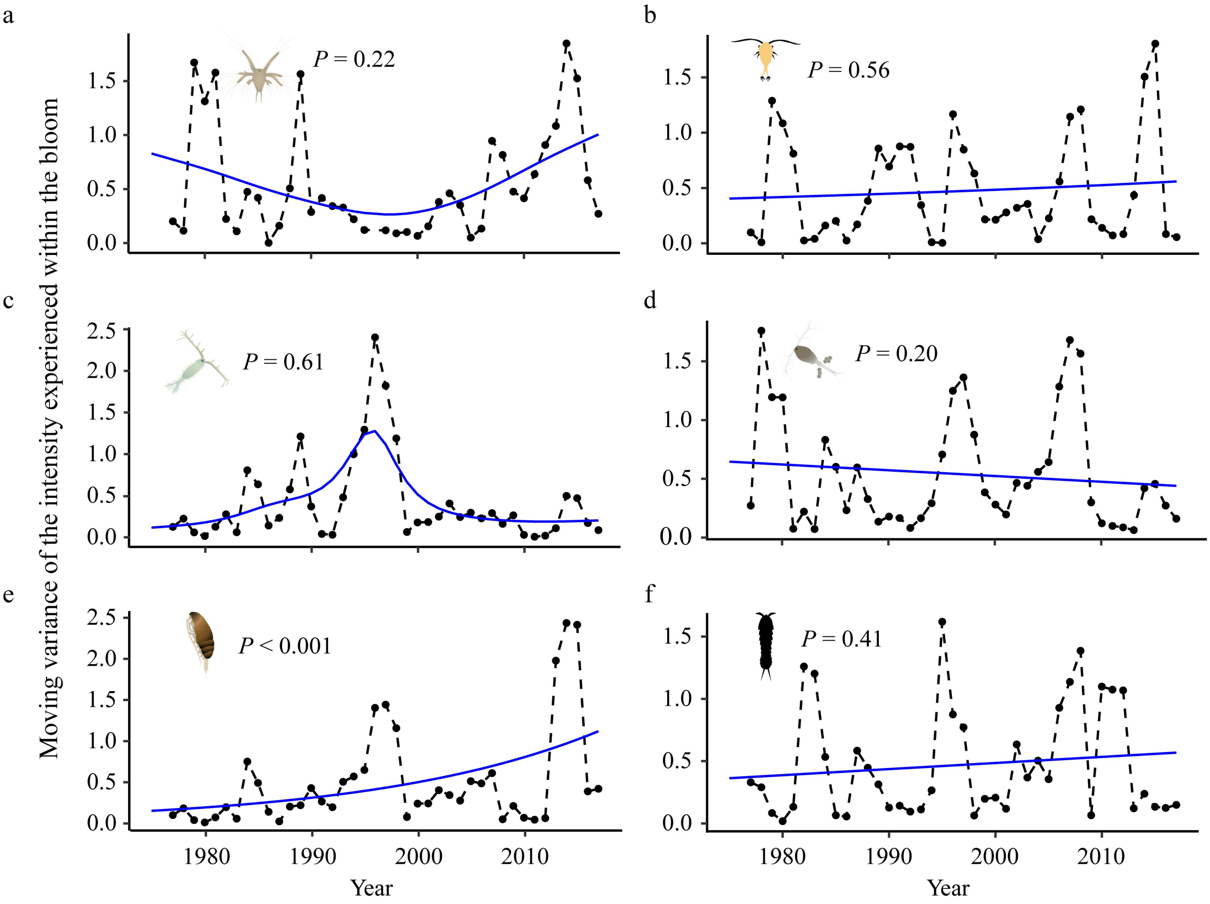


Figure 4.6. Time series of the moving variance of the intensity (°C, relative to the climatology) experienced within the bloom of **a.** Copepoda nauplii, **b.** *T. longicornis*, **c.** *Acartia* spp., **d.** *Oithona* spp., **e**. *Pseudo/Paracalanus* spp., and **f**. Harpacticoida. The blue curves represent the model fit: LMs were used for all species except for Copepoda nauplii and *Pseudo/Paracalanus* spp. (GAMs). The moving variance was computed using a three years window.

Changes in bloom duration in response to MHW conditions within the bloom

Compared to the MHWs occurring before the bloom, those occurring within the bloom significantly impacted the bloom duration of several taxa. The total duration of the bloom was the most impacted by MHW components, with four out of six taxa showing significant effects. The best fitting models included the additive effect of all four predictors (mean intensity, proportion of MHW days, maximum growth and decline rate) for *T. longicornis* and *Acartia* spp. (Table S4.2-S4.3) and the additive effect of three predictors (proportion of MHW days, maximum growth and decline rate) for Copepoda nauplii and *Pseudo/Paracalanus* spp. (Table S4.1-S4.5). For both *Acartia* spp., and *Pseudo/Paracalanus* spp., the total bloom duration was significantly shorter with higher maximum growth rate ($p < 0.05$ for both). *T. longicornis* bloom duration significantly decreased with increasing maximum growth rate and proportion of MHW days ($p < 0.01$ for both). For Copepoda nauplii bloom, duration was significantly shorter when the proportion of MHW days increased ($p < 0.001$). No evidence of an effect of MHW components was found for Harpacticoida.

Regarding the onset bloom duration, the best model for *Acartia* spp., included the additive effects of maximum growth and decline rates, while all four components were included for Harpacticoida (Tables S4.3-S4.6). For *Acartia* spp., onset duration significantly decreased when the maximum growth rate increased ($p < 0.05$). For Harpacticoida, the duration decreased when the maximum decline rate increased ($p < 0.05$) and the intensity decreased ($p < 0.05$). The remaining four taxa showed no evidence of any MHW component affecting onset bloom duration.

For the decline duration, the best model for *Acartia* spp., included all four predictors (Table S4.3). Duration significantly decreased with both increasing proportion of MHW days ($p < 0.01$) and intensity ($p < 0.05$). No evidence of an effect of any MHW component on the decline bloom duration was found for the remaining five taxa.

Oithona spp. showed no evidence of an effect of MHW components on any aspect of the bloom duration.

DISCUSSION

We examined the effects of MHWs on the phenology of key copepod taxa of the North Sea. Our study yields four main findings. First, although our focus was on the most dominant bloom within each year, our results indicated that sub-annual blooms can also occur suggesting complexity in copepod bloom patterns. Sub-annual blooms have been recorded at other stations in the North Sea, such as Plymouth and Stonehaven (Corona et al., 2024). Authors suggested that abundance may be a better proxy for species with a single wide peak, while species with several peaks could obscure the real phenological changes (Corona et al., 2024). Second, we expected to observe changes in the phenology of copepod taxa in response to MHW occurring before the bloom but found no clear evidence of changes in bloom traits for most taxa. Consequently, copepods did not exhibit a phenological shift in response to MHW event occurring within the four-month window preceding the bloom. Third, during the bloom period, copepods experienced changes in MHW variability over time with some taxa-specific trends observed. Last, nearly all taxa bloom durations were affected by MHW conditions within the bloom, particularly by the MHW maximum temperature increase rate and proportion of MHW day and, to a lesser extent, by the MHWs mean intensity. Our results are important, first to better understand the effects of MHWs on organism but also help to visualise current and future changes in selection pressure associated with the temporal pattern of exposure to MHW events.

Phenological response to MHW

In marine ecosystems, changes in phenology have been related to climate variability and climate changes (Sydeman & Bograd, 2009) with organisms showing advanced or delayed timing in response to warming. We hypothesised that if MHWs occurred before a given bloom for spring and summer taxa, the bloom would be advanced while it would be delayed for autumn taxa.

The only taxa that responded to increased MHW intensity and number of MHW days with an earlier bloom was the summer-blooming *Acartia* spp., suggesting that the early life stages of this taxon were impacted by changes in MHW conditions. Previous studies have already documented earlier bloom timings in response to warming for this species (Borkman et al., 2018; Corona et al., 2024). While this study cannot pinpoint the exact number of days the bloom shifted due to MHWs, it is highly likely that such shifts could have significant impacts on higher trophic levels. For example, at this latitude in the North Sea, herring (*Clupea harengus*) typically spawn between August and October (Hufnagl et al., 2015), relying on a peak in prey availability during this time. *Acartia* spp. is the most dominant taxon recorded at Helgoland Roads since 1975 (Boersma et al., 2015, 2017) and a key prey for *C. harengus* (Arrhenius, 1996). As a result, changes in its seasonal timing due to MHWs could create a mismatch between *Acartia* spp. availability and *C. harengus* larvae, potentially affecting herring recruitment (Alvarez-Fernandez et al., 2015). This problem is likely to be exacerbated by the observed contraction of *Acartia* spp., bloom duration in response to MHW components, which will be further discussed in a later section.

With the exception of *Acartia* spp., our findings provide no clear evidence of a systematic phenological shift for other taxa in spring, summer, or autumn when a MHW occurred pre-bloom. Indeed, the response of zooplankton to elevated temperatures during MHWs is influenced not only by the intensity and duration of the heatwave but also by its seasonal timing, as demonstrated in **Chapter 3** of this thesis. Although a winter MHW might provide favourable thermal conditions for copepod development, their growth remains constrained by limited food and light availability (van Beusekom & Diel-Christiansen, 2009). Consequently, a winter MHW is unlikely to significantly impact the copepod community, as the increase in temperature cannot overcome the limitations imposed by the photoperiod, which will continue to indirectly restrict their development (Beaugrand & Kirby, 2018). Supporting this hypothesis, **Chapter 3** showed no evidence of winter MHW affecting the mesozooplankton community, including copepods. Therefore, the lack of evidence in bloom responses to pre-bloom MHWs might be explained by unsuitable light and food conditions existing during winter. It is important to note, that MHWs may operate differently compared to long-term warming. While our findings indicate no effect of winter MHWs on copepod phenology, other studies have suggested that a gradual increase in winter temperatures could enhance the survival of herbivorous copepods, leading to higher densities (Sommer & Lewandowska, 2011; Wiltshire & Manly, 2004). We believe that, while this effect may occur with prolonged warming, a winter MHW is unlikely to promote copepod growth, as it is a short-term event, and temperatures will return to typical winter levels afterward. If spring bloomers are unable to shift their phenological timing in response to MHWs, they might experience drastic declines in the future as spring MHWs become more frequent, longer and intense. *T. longicornis* is already experiencing negative impacts from MHWs, with declining densities observed during spring MHWs (see **Chapter 3**). While some taxa currently respond positively to MHWs, this trend may be reversed in the coming decades as suggested by a recent experiment simulating heatwave in the late summer/beginning of autumn (Meunier et al., *in press*).

While the absence of a phenological shift for spring bloomers could be explained, the lack of any observed shift for summer and autumn bloomers was surprising. Indeed, McKinstry et al. (2022) observed the earlier appearances of both the summer and autumn zooplankton groups during the 2016 MHW in Alaska, with the summer group, typically seen from July to September, appearing in May, and autumn group appearing late August. The difference with our results may be attributed to several reasons. First, McKinstry et al. (2022) focused on a single large MHW event running for 711 days (Hobday et al., 2018). In comparison, the largest MHW in the North Sea was much smaller with a duration of 195 days (Giménez et al., 2024). Due to the extended duration of this event, McKinstry et al. (2022) were able to compare phenological timing across years before, during, and after the event. In contrast, our study focused on the proportion of MHW days and the average intensity of all events occurring during the four months before the annual bloom, spanning 43 years of copepod density data. Unlike their approach, which examined shifts in phenological timing within the MHW period, we analysed changes in phenology during the same season following a MHW event. Moreover, had we focused on a specific large event, we might have observed similar effects of MHW on phenology. For example, while we did not consistently find earlier blooms for any taxa, we did observe that intense MHWs and a high number of MHW days pre-bloom were often associated with earlier bloom timings for *Oithona* spp., a summer bloomer. In the North Sea, 2016 was also a year characterised by intense and long MHW (Giménez et al., 2024). The four-month period pre-bloom during this year was marked by high temperatures and a large number of MHW days, and was associated with earlier bloom for *Oithona* spp. Other years with intense MHWs during this four-month period, such as 1990 and 2014, showed similar patterns (see Results and Fig. 2 from Giménez et al., 2024).

Another reason why a phenological shift was not consistently observed could be the fact that the anticipated changes in timing in response to warming in the North Sea are not evident. Indeed, while earlier timings were observed over time at Helgoland Roads, Corona et al. (2024) demonstrated that there is no clear evidence that spring or summer species tend to emerge earlier in warmer years, or that autumn species appear later in response to increased seasonal temperatures. At Helgoland Roads, at least one timing index (bloom start or peak) of *Acartia* spp., and *Oithona* spp., was negatively correlated with increasing seasonal temperature highlighting a shift to earlier timing in response to warming but not significant relationship was observed for all other species studied (Corona et al., 2024). The results of this study, however, contrast with the findings of Wiltshire & Boersma, (2016) that observed a shift toward early timing in response to temperatures. This discrepancy suggests again that MHWs might influence bloom timing differently than long-term warming trends, but it is also important to emphasise that the different method of calculating bloom timing might explain the observed pattern. Wiltshire & Boersma (2016) used cumulative density to determine bloom timing. This approach, while common, can result in reversal causation, as it depends on the overall size and duration of the bloom. The cumulative nature of this method may cause shifts in the perceived start date based on the bloom event in itself rather than independent environmental cues triggering the bloom.

It is also important to note that while no evidence of a phenological shift in response to MHWs was found, the complexity of copepod blooms might conceal potential effects. This study revealed that copepod blooms at Helgoland Roads are more complex than they initially appear, exhibiting periodicity in density on both annual and sub-annual scales (from a month to a year). The presence of more than one density peak within a year significantly increases the complexity and challenges of analysing seasonal timing (Corona et al., 2024). Furthermore, these annual and sub-annual patterns, although observed across all taxa, were not consistent throughout the time series, sometimes disappearing during periods of very low densities, which complicates the analysis of bloom timing. For example, between 2005 and 2010 (and sometimes extending to 2015), most copepod taxa studied had very low densities. The mid-2000s have been documented as a period of regime shift associated with declining densities of nearly all mesozooplankton taxa in the North Sea, including copepods (Di Pane et al., 2023; Marques et al., 2023). This period was also characterised by a low number of MHW days and events in the North Sea (Giménez et al., 2024). While we do not claim a causal link between the observed regime shift and MHW activity, it is possible that the low number of MHW days and events contributed to the density decline, as most of the taxa studied responded positively to MHWs in spring and autumn (see **Chapter 3**).

Changes in selective pressures associated with temporal pattern of MHW exposure

Since copepod taxa did not consistently shift their phenology, it was logical to find that they encountered more intense and more frequent MHWs during their blooms throughout the year. Interestingly, these taxa also experienced significant variability in MHW conditions, particularly in the number of MHW days. The variance consistently increased around 1990 and 2000 but decreased around 2005 for all summer taxa, highlighting that the number of MHW days within the bloom is fluctuating and that this fluctuation is different depending on the taxa and season.

While in our case most groups appear to respond positively to heatwaves (see **Chapter 3**) quantifying the variability in MHW experienced during the peak abundance can help us to understand how organisms would respond adaptively to those heatwaves. Evolutionary theory predicts that environmental conditions and variability can drive different strategies (Scheiner, 2016). While stable environments favour a specialist strategy (Gilchrist, 1995), other strategies may emerge under fluctuating environments, depending on their predictability. While predictable fluctuations favour phenotypic plasticity, unpredictable fluctuations (e.g., MHW) select for bet-hedging or a generalist strategy (Gilchrist, 1995; Marshall et al., 2008; Simons, 2011). Given those predictions, we would expect that a shift in the environment, from low variability (see Fig. 4.5 pre-1990) to increased variability (e.g., post-1990), should result in a shift in the selective pressures, towards a generalist or bet-hedging strategy. Importantly, such pressure may not be permanent and instead a new shift may occur if a drop in MHW days occurs for many consecutive years. For instance, summer and autumn taxa have experienced high variability around 1995 and 2005 (Fig. 4.5), separated by a period of approximately 10 years characterised by MHWs in low frequency. Hence, over decadal timescales, the shift between high and low variability in MHW conditions suggests that organisms might experience shifts in the direction of selective pressures. How fast these organisms respond to those pressures depends on characteristics such as the generation time.

Changes in bloom duration in response to MHW conditions

With MHW conditions changing over time, and taxa not able to shift their bloom timing, it is likely that taxa will be strongly impacted (whether negatively or positively) by MHWs occurring within their bloom. Along with phenological timing, bloom duration is a crucial phenological parameter to monitor when studying the effects of warming on communities. Indeed, research in freshwater ecosystems has shown that the active phase of copepods can be extended in both spring and autumn during warmer years (Gerten & Adrian, 2002). Similarly, late summer species in marine ecosystems may exhibit a phenological expansion, with both earlier and later phenology (Beaugrand & Kirby, 2018). In agreement with this statement, our findings revealed that the onset duration of the autumn bloomer, Harpacticoida and the decline duration of the summer bloomer *Acartia* spp., were prolonged in response to the increasing intensity of MHWs occurring during their respective bloom periods. In contrast, the decline duration for the autumn bloomer was unaffected by MHW intensity, likely due to the unsuitable light and food conditions following the autumn bloom.

Interestingly, while the MHW intensity led to an extended bloom period, a higher proportion of MHW days or more rapid temperature increases led to bloom contractions for several spring and summer taxa, such as Copepoda nauplii and *Acartia* spp. A sharp rise in spring temperatures following a cold period can reduce the spread of events like moulting and hatching (Giménez, 2011). Similarly, we believe that MHWs characterised by rapid temperature increases may have a comparable effect. The contrasting effects of different MHW components on bloom duration found in this study emphasise the need to consider other MHW components such as timing and duration to properly understand MHW effects on organisms. Focusing solely on temperature intensity may overlook how MHWs impact phenology.

Although Copepoda nauplii density increased during spring events (see **Chapter 3**), the higher number of MHW days likely accelerated their growth, causing the nauplii to reach adult stage sooner than usual and therefore shortened their time spent in the water column. This bloom contraction could have significant repercussions for higher trophic levels, such as early stages of fish. In the North Sea fish larvae, primarily feed on copepod nauplii (Last, 1978a, 1978b), and a shorter nauplii bloom duration could reduce prey availability, potentially impacting fish larval survival. Such effect has already been observed during the 2014-2016 MHW in the North Pacific, where a decrease in zooplankton nauplii negatively affected the survival of walleye pollock larvae (Rogers et al., 2021).

CONCLUSION

In this study, we demonstrate that the bloom phenological timing of key copepod taxa in the North Sea remained largely unchanged in response to MHWs experienced within the four months preceding the bloom. Instead, copepods consistently encounter MHW during their bloom periods. MHW occuring within the bloom influenced bloom duration, with blooms being longer in response to higher intensity but shorter when the maximum temperature increase rate and the proportion of MHW days increased. While MHWs occuring pre-bloom did not lead to phenological shifts, we believe that their effects are likely more pronounced on a much shorter timescale, triggering changes immediately after the onset of the event. It is thus important to continue monitoring changes in marine ecosystems in response to MHW to properly understand their effect on the phenology of ecologically important groups such as copeopod.

SUPPLEMENTARY MATERIAL

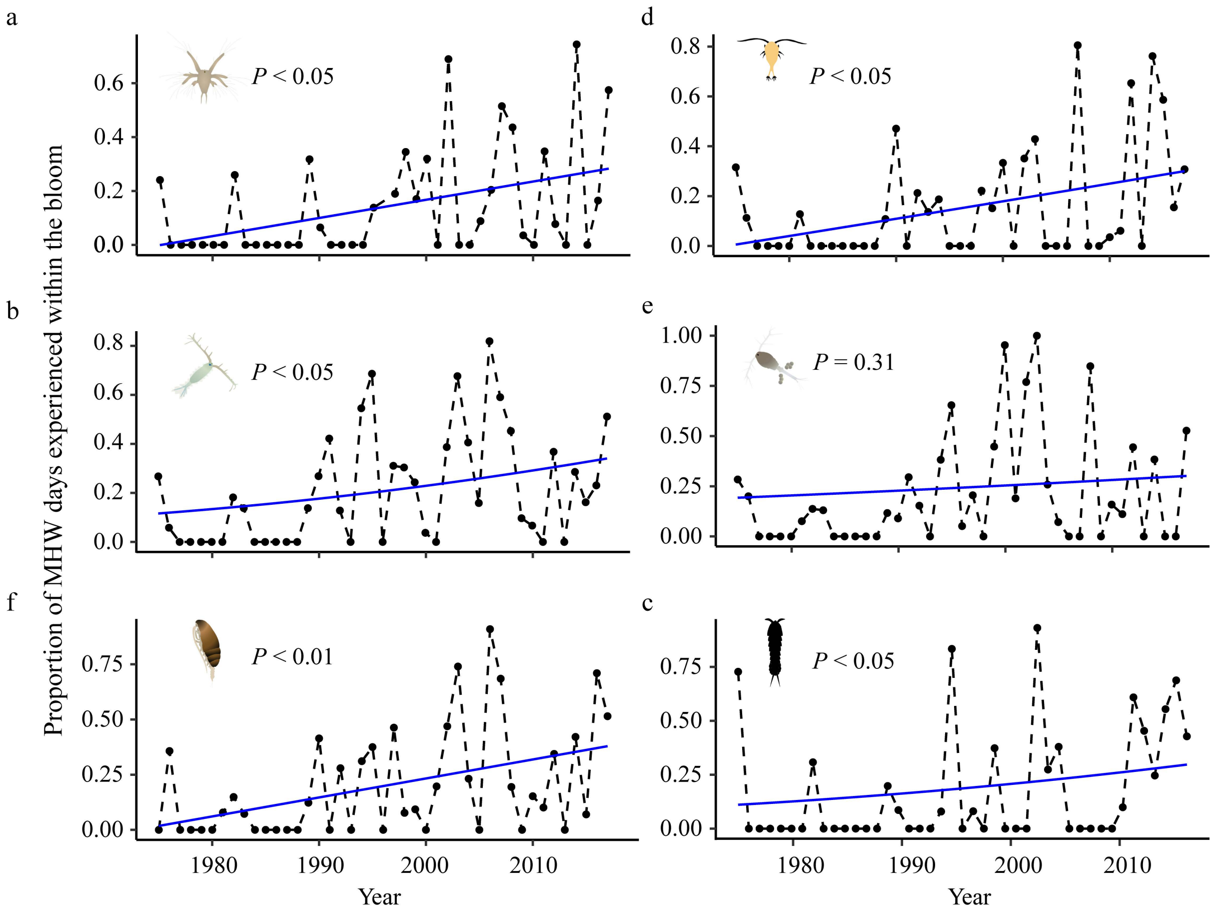


Figure S4.1. Time series of yearly proportion of MHW days experienced within the bloom of **a.** Copepoda nauplii, **b.** *T. longicornis*, **c.** *Acartia* spp., **d.** *Oithona* spp., **e**. *Pseudo/Paracalanus* spp., and **f**. Harpacticoida. The blue curves represent the model fit. Beta regressions were used for all species except for *Pseudo/Paracalanus* spp. (LM).

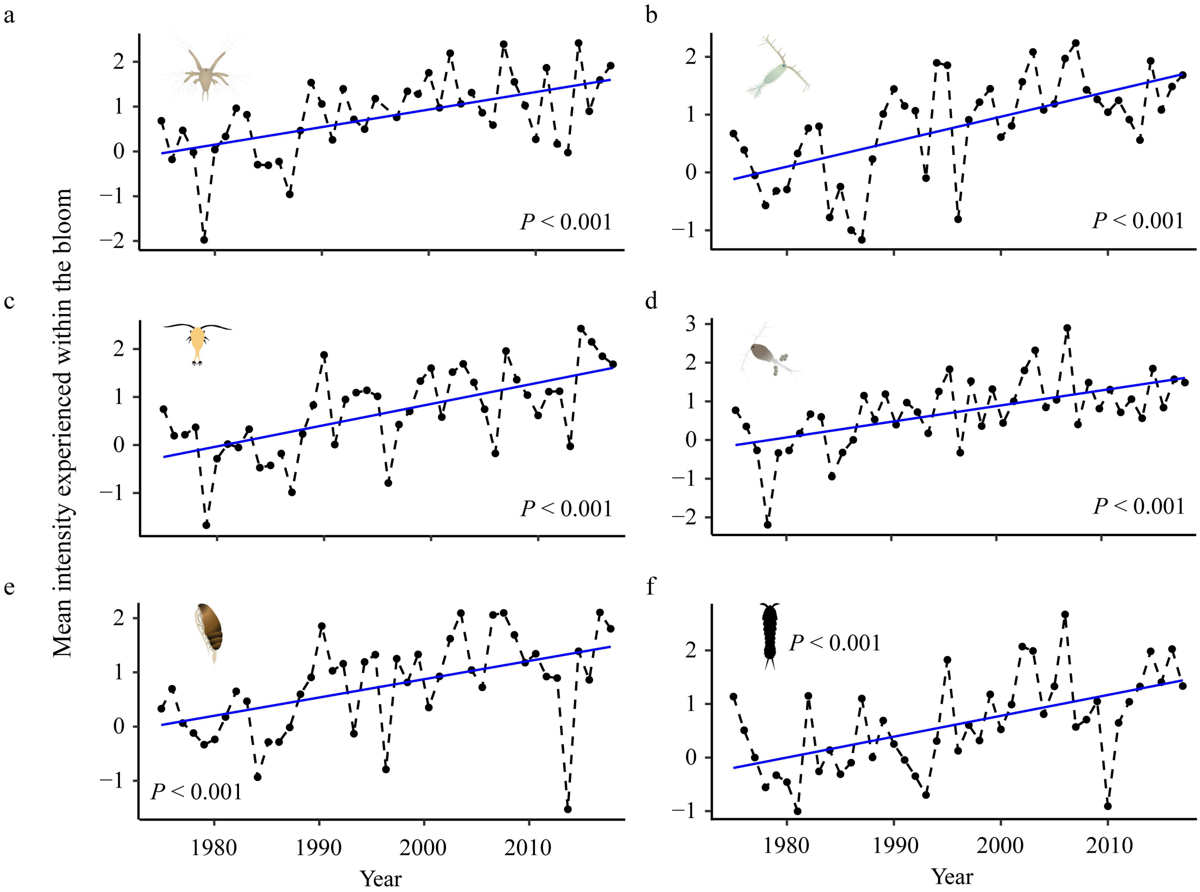


Figure S4.2. Time series of the mean intensity (°C relative to the climatology) experienced within the bloom **a.** Copepoda nauplii, **b.** *T. longicornis*, **c.** *Acartia* spp., **d.** *Oithona* spp., **e.** *Pseudo/Paracalanus* spp., and **f.** Harpacticoida. The blue curves represent the model fit. LMs were used for all species.

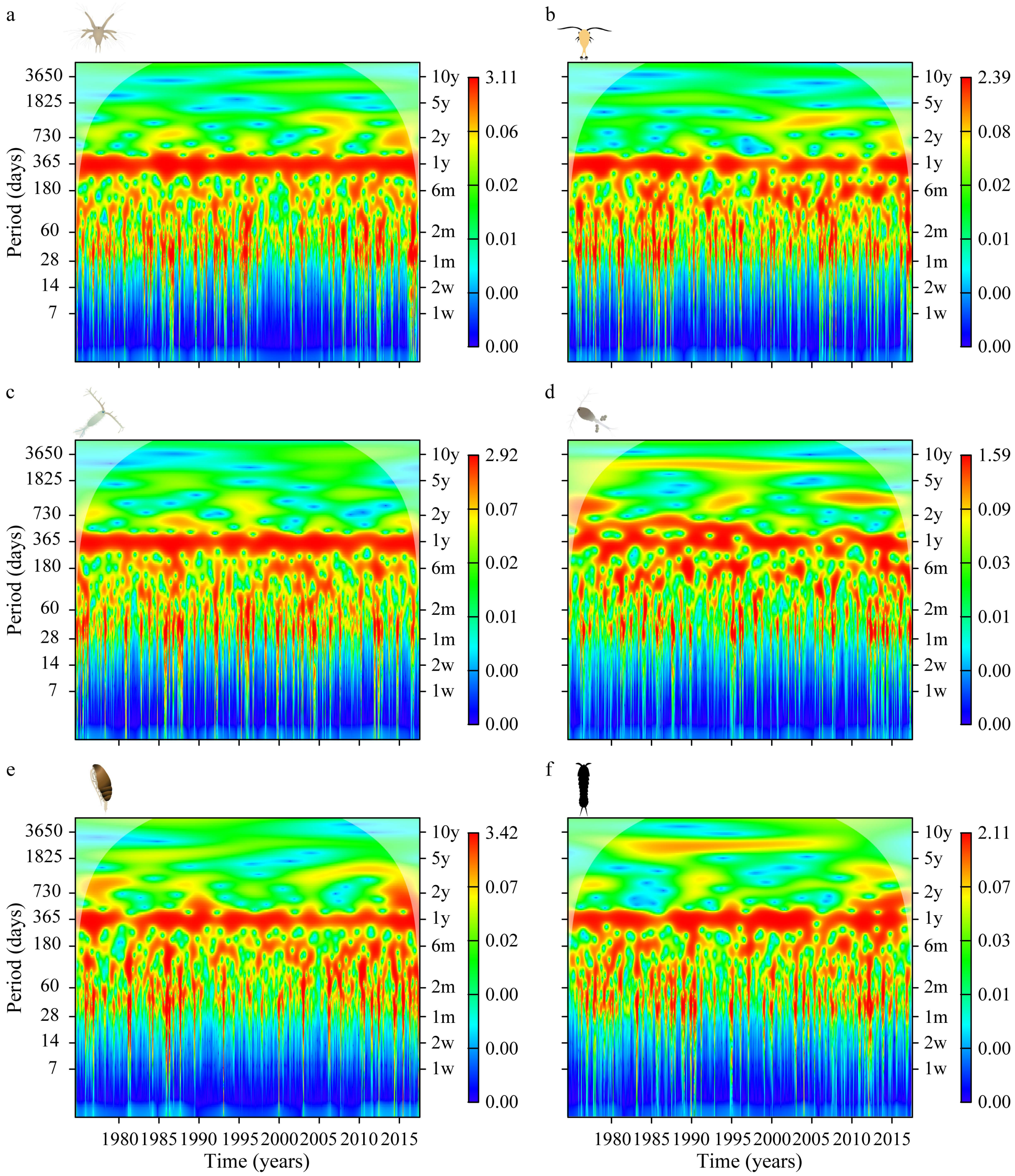
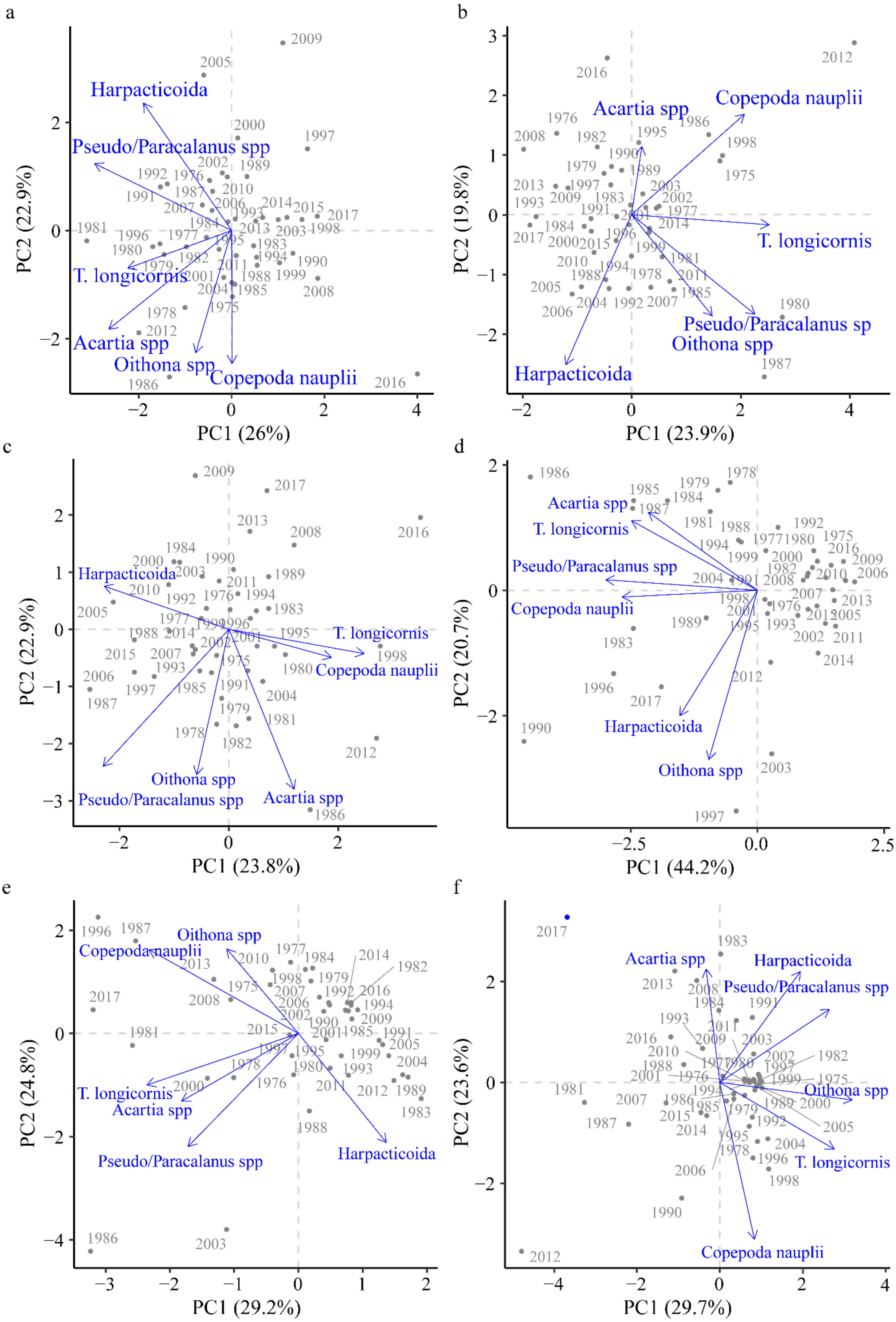


Figure S4.3. Spectrogram from wavelet analyses applied to the smoothed time series of **a.** Copepoda nauplii, **b.** *T. longicornis,* **c.** *Acartia* spp., **d.** *Oithona* spp., **e.** *Pseudo/Paracalanus* spp., and **f.** Harpacticoida densities and example years for comparison. Densities were log-transformed to mitigate the influence of extreme density and to emphasise the underlying periodic patterns in the data. The colour gradient represents the wavelet power (σ^2) and the shaded area in the top corners represents the edge effect.


a
PC1 (26%)
PC2 (22.9%)
Harpacticoida
Pseudo/Paracalanus spp
T. longicornis
Acartia spp
Oithona spp
Copepoda nauplii
2009
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2000
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1992
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1983
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1982
1979
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2004
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2008
1975
1978
2012
1986
2016
b
PC1 (23.9%)
PC2 (19.8%)
Acartia spp
Copepoda nauplii
T. longicornis
Pseudo/Paracalanus sp
Oithona spp
Harpacticoida
2012
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1987
c
PC1 (23.8%)
PC2 (22.9%)
Harpacticoida
T. longicornis
Copepoda nauplii
Oithona spp
Pseudo/Paracalanus spp
Acartia spp
2009
2017
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2016
1984
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PC1 (44.2%)
PC2 (20.7%)
Acartia spp
T. longicornis
Pseudo/Paracalanus spp
Copepoda nauplii
Harpacticoida
Oithona spp
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2007
2013
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2015
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1989
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2017
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2003
1997
e
PC1 (29.2%)
PC2 (24.8%)
Oithona spp
Copepoda nauplii
T. longicornis
Acartia spp
Pseudo/Paracalanus spp
Harpacticoida
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f
PC1 (29.7%)
PC2 (23.6%)
Acartia spp
Harpacticoida
Pseudo/Paracalanus spp
Oithona spp
T. longicornis
Copepoda nauplii
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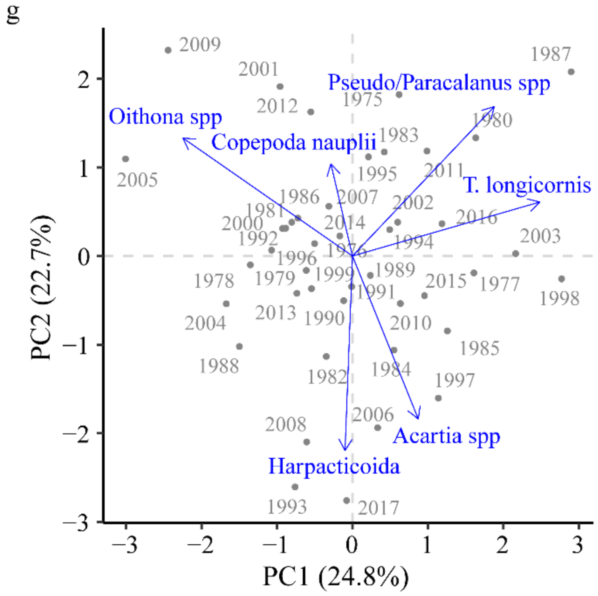


Figure S4.4. Temporal dynamic of copepod bloom traits. PCAs were performed on the copepod community for each bloom traits (standardised) separately. Changes in bloom **a.** starting day, **b.** ending day, **c.** day of maximum density, **d.** maximum density, **e.** maximum growth rate, **f.** maximum decline rate and **g.** total duration.

Table S4.1. Model selection results (AICc values) for Copepoda nauplii bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out using maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	279	57	320	105	311	43
3 predictors						
GR + DR + I	280	58	320	102	317	54
HW days + DR + I	309	60	350	113	342	47
HW days + GR + I	311	56	360	113	349	44
HW days + GR + DR	**276**	**54**	**318**	102	309	**40**
2 predictors						
GR + I	311	62	349	110	345	52
GR + I	313	59	361	111	358	58
GR + DR	277	55	**318**	**100**	**315**	51
HW days + I	344	61	391	121	382	50
HW days + DR	307	57	349	110	341	45
HW days + GR	309	54	358	110	348	41
1 predictor						
I	346	64	390	120	387	58
DR	308	60	347	108	343	50
GR	311	57	359	109	356	59
HW days	341	59	390	119	380	47

Table S4. 2. Model selection results (AICc values) for *T. longicornis* bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out using maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	290	58	276	89	**288**	43
3 predictors						
GR + DR + I	288	58	277	88	292	51
HW days + DR + I	346	70	323	108	342	58
HW days + GR + I	354	62	344	105	356	47
HW days + GR + DR	287	54	273	86	285	**40**
2 predictors						
GR + I	346	71	322	105	347	63
GR + I	355	66	345	106	362	60
GR + DR	**286**	**55**	**274**	**86**	289	48
HW days + I	414	78	393	127	418	73
HW days + DR	345	67	321	105	341	59
HW days + GR	352	60	342	103	353	44
1 predictor						
I	415	79	391	125	419	75
DR	344	69	319	103	344	62
GR	354	64	342	104	360	58
HW days	412	76	391	125	415	71

Table S4. 3. Model selection results (AICc values) for *Acartia* spp., bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out using maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	403	78	**391**	**58**	**407**	**41**
3 predictors						
GR + DR + I	403	77	394	68	416	50
HW days + DR + I	452	89	437	89	463	57
HW days + GR + I	487	90	484	85	505	59
HW days + GR + DR	400	75	394	62	408	42
2 predictors						
GR + I	452	88	444	99	472	67
GR + I	486	88	485	89	508	64
GR + DR	**400**	**74**	398	71	416	51
HW days + I	536	100	530	111	557	72
HW days + DR	451	87	439	88	461	55
HW days + GR	485	87	486	88	504	59
1 predictor						
I	535	98	533	116	563	78
DR	451	86	445	98	470	65
GR	484	86	487	90	508	63
HW days	535	98	531	110	555	70

Table S4. 4. Model selection results (AICc values) for *Oithona* spp., bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out using maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

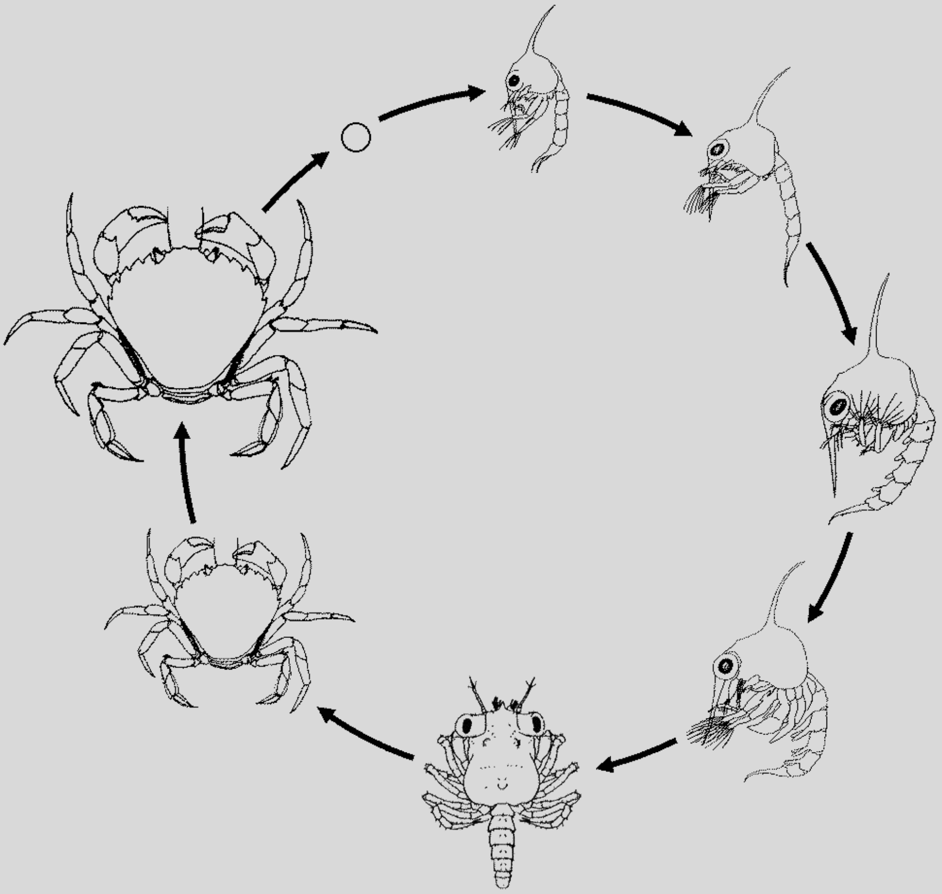
Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	358	76	333	71	368	54
3 predictors						
GR + DR + I	**355**	**73**	333	70	367	53
HW days + DR + I	385	78	358	71	395	53
HW days + GR + I	384	77	357	72	395	53
HW days + GR + DR	356	76	**330**	**67**	366	53
2 predictors						
GR + I	383	77	358	71	396	54
GR + I	381	75	360	74	395	53
GR + DR	354	73	331	**67**	**365**	**51**
HW days + I	420	81	392	84	433	57
HW days + DR	383	77	355	68	392	52
HW days + GR	382	76	355	70	393	**51**
1 predictor						
I	419	81	396	93	438	64
DR	381	75	356	68	394	53
GR	379	73	357	71	394	**51**
HW days	417	79	390	82	430	54

Table S4. 5. Model selection results (AICc values) for *Pseudo/Paracalanus* spp., bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out through maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	292	45	324	87	317	38
3 predictors						
GR + DR + I	289	42	324	85	318	38
HW days + DR + I	308	47	345	90	338	40
HW days + GR + I	353	45	399	109	389	48
HW days + GR + DR	289	42	**321**	84	**314**	**35**
2 predictors						
GR + I	305	44	343	88	337	38
GR + I	351	43	398	107	390	38
GR + DR	**287**	**39**	**321**	**82**	315	35
HW days + I	369	47	421	112	413	45
HW days + DR	305	44	342	87	335	37
HW days + GR	350	42	396	107	387	35
1 predictor						
I	367	45	419	110	412	44
DR	303	42	341	86	335	36
GR	348	40	395	105	388	36
HW days	367	46	419	111	411	42

Table S4. 6. Model selection results (AICc values) for Harpacticoida bloom durations in response to proportion of MHW days (HW days), GR (Growth rate) DR (Decline rate) and Intensity (I). Model selection was carried out using maximum likelihood (ML) fitting. Best models are indicated in bold. Models violating assumptions are indicated in red.

Model selection	**Start to Peak**		**Peak to End**		**Bloom duration**	
Fixed factors (ML)	**Linear**	**Log**	**Linear**	**Log**	**Linear**	**Log**
4 predictors						
HW days + GR + DR + I	223	**38**	257	81	252	41
3 predictors						
GR + DR + I	**222**	**38**	254	80	**251**	42
HW days + DR + I	258	44	303	94	299	43
HW days + GR + I	234	42	264	79	258	37
HW days + GR + DR	229	42	254	78	**251**	41
2 predictors						
GR + I	273	50	303	97	306	56
GR + I	231	39	264	80	259	39
GR + DR	226	39	**251**	77	248	40
HW days + I	279	49	311	93	305	43
HW days + DR	272	46	300	91	298	45
HW days + GR	232	42	261	77	257	38
1 predictor						
I	282	52	311	96	313	54
DR	272	48	300	94	303	53
GR	233	39	261	**77**	257	**38**
HW days	280	48	308	91	305	42



BLOCK II: Laboratory experiments

Performance of decapod larvae under marine heatwaves

Figure modified from Spitzner et al., (2018)

CHAPTER

5

Responses of larvae of the European shore crab *Carcinus maenas* to marine heatwaves: disentangling the effect of duration, intensity and timing.

Responses of larvae of the European shore crab *Carcinus maenas* to marine heatwaves: disentangling the effect of duration, intensity and timing.

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Submitted

Abstract

Marine heatwaves are causing significant disturbances to marine ecosystems worldwide, with concerning impacts on a multitude of different taxa. Especially, decapod crustaceans face an alarming threat from the increasing frequency and intensity of heatwaves as their early planktonic stages are particularly temperature sensitive. While marine heatwave effects on decapod crustaceans are well-documented, research often focuses on adult stages and a proper understanding of heatwaves effects on larvae is currently missing. The current study focuses on the effects of heatwaves on larvae of the European shore crab, *Carcinus maenas*. Through a factorial experiment, larvae, reared at an optimal temperature (15 °C), were exposed to a set of different laboratory marine heatwaves. We quantified the effects of warm events of varying onset timings, durations, and intensities including those of realistic heatwaves (18 °C, 21 °C: summer heatwaves in the German Bight) and higher temperatures (24 °C: expected for future heatwaves). Survival, development duration to the megalopa, and dry mass significantly decreased when larvae were subjected to intense warm events. The effect was more pronounced when the heatwave happened later in the larval development. We were able to disentangle the warm event effects (characterised by their components) from those attributed to the average temperature experienced during the experiments. We showed that larval performance was significantly affected during intense events compared to the performance expected under the average (constant) temperature. Our study suggests the presence of thresholds in intensity and timing beyond which larvae will be significantly impacted. These results highlight the need to consider changes in mean temperatures and the heatwaves timing relative to organism life cycles, to accurately predict how marine populations will respond in the context of climate change.

Key words: *Carcinus maenas* – Global warming – larval performance – Marine heatwaves –

INTRODUCTION

Anthropogenic climate change is a significant threat to biodiversity worldwide (IPCC, 2022). Alongside the ongoing trend of warming, discrete extreme weather events, such as heatwaves, are becoming more frequent and intense (Frölicher et al., 2018; Meehl & Tebaldi, 2004; Oliver et al., 2018; Perkins et al., 2012). Studies on the biological impacts of heatwaves on organisms have demonstrated that extreme events can impact biological processes at all levels, from the individual to the ecosystem (Harris et al., 2018; Smith et al., 2023; Woolway et al., 2021). Consequently, it is crucial to understand and predict how organisms, particularly those with short generation times and high sensitivity to temperature changes, respond to specific events (Arteaga & Rousseaux, 2023; Ma et al., 2015; Vad et al., 2023).

In marine ecosystems, extreme seawater temperature events have been documented around the world, sometimes exhibiting temperature 3–4 °C higher than the temperature typically observed on those dates (Bond et al., 2015; Oliver et al., 2017; Pearce & Feng, 2013; Sparnocchia et al., 2006). Following the definition by Hobday et al. (2016), there is a consensus that when these events exceed the 90th percentile of a climatological baseline and last more than five days, they are classified as marine heatwaves. In recent years, growing ecological and socioeconomic concerns about impacts of marine heatwaves have led to increased research efforts aiming at defining, categorising, and exploring their consequences across different levels of biological organisation (Smith et al., 2023). These impacts can vary widely, ranging from positive to negative, depending on the organism studied but also on the seasonal timing of the heatwave. At the individual level, increased basal metabolic rates and energy demands induced by marine heatwaves can influence the growth and reproduction of marine organisms (Spinks et al., 2019; Stubbs et al., 2020; Truong et al., 2020). In spring, when heatwave temperatures generally fall within the species thermal ranges, the effects will be mostly positive. However, these effects may become negative if temperatures exceed that range (Smith et al., 2023), as is more likely with summer heatwaves (Oliver et al., 2021). Population-wise, response to marine heatwaves can range from recruitment failure due to reproductive failures or mass mortality events, ultimately threatening species persistence (Chandrapavan et al., 2019; Shanks et al., 2020), to range expansion, increased abundance and reproduction (Smith et al., 2023). Lastly, heatwaves might trigger shifts in marine community structure, favouring warm-water species over those adapted to cooler waters (Evans et al., 2020; Wernberg et al., 2016).

The predicted increase in frequency and magnitude of heatwaves (Frölicher et al., 2018; Oliver et al., 2018) has become particularly alarming for marine organisms with complex life cycles, which comprise the great majority of marine invertebrates and fish. Some of these organisms, such as crabs, oysters and sea urchins develop through a larval phase drifting in the water column, while the juvenile and adults live associated with the sea bottom. Larvae contribute to connectivity between populations (Cowen et al., 2006), range expansion (Giménez et al., 2020a; Kelley et al., 2013; Yamada et al., 2021), and can drive recovery of local populations from mass mortalities (Giménez et al., 2020b). Moreover, larval stages are often more sensitive to temperature increases and exhibit a narrow subset of the species thermal niche compared to their juvenile and adult counterparts (Pandori & Sorte, 2019). Therefore, depending on the heatwave season, larvae can be impacted by smaller acute temperature increases compared to adults, which may affect the recruitment success, dispersion, and survival (McConaugha, 1992).

While the impact of warming on marine invertebrates is well-documented, a proper understanding of marine heatwaves effect on decapod crustacean larval performance is currently missing (Monteiro et al., 2023a; Monteiro et al., 2023b). Field investigations examining the impacts of past heatwaves on larval assemblages are limited to a few studies (McKinstry & Campbell, 2018; Morgan et al., 2019). Moreover, while marine heatwaves simulations and mesocosm experiments were carried out (Meunier et al., *in press*), few studies have focused on understanding the effects on larval stages (Giménez et al., 2021; Marochi et al., 2022; Nour et al., 2022). Furthermore, these studies often concentrate on marine heatwaves intensity, overlooking the cumulative effects of various components such as duration and timing. Additionally, the common practice of measuring heatwave impacts against a constant baseline temperature does not adequately separate the effect of the fluctuation inherent to the heatwaves from the effect of experiencing an increased average (but constant) temperature. Importantly, a growing body of literature shows that biological responses to fluctuating environments differ from those occurring under constant conditions (Gerhard et al., 2023; Kingsolver et al., 2015; Niehaus et al., 2012). Unlike exposure to a constant temperature, fluctuating environments can drive phenotypic plastic responses (Scheiner, 2016). Organisms must experience heatwaves according to traits such as the thermal tolerance range and critical biological time scales (Giménez, 2023; Jackson et al., 2021). Indeed, biological time scales, like the duration of larval development, are crucial as they shape responses characterised by temporal dynamics such as phenotypic plasticity (Dupont et al., 2024). Additionally, because of the sensitivity of metabolic rates to temperature, heatwaves have the potential to increase developmental rates, hence modifying the way they are experienced by organisms (Gimenez 2023). Therefore, there is a need to differentiate the impacts of the heatwave components, and to determine the conditions where the effect of heatwaves differs from those expected by experiencing an increased but constant temperature.

Here, we quantified the role of three primary components of marine heatwaves (i.e., intensity, timing, duration) on larval performance (survival, developmental time, and body mass at metamorphosis) through laboratory experiments, exposing larvae of the shore crab *Carcinus maenas* to warm events of different intensity, duration, and timing. To achieve this objective, we conducted two experiments. The first experiment manipulated the timing and intensity of the warm events while keeping the duration constant (i.e., 10 days, corresponding to the duration of the heatwaves frequently detected in the North Sea (Giménez et al., 2024). In the second experiment, larvae were exposed to warm events of different intensity starting at different times during their development and ending after metamorphosis, without a recovery period post warm event to simulate conditions where larvae are exposed to late summer heatwaves, common in the study area (Giménez et al., 2024). In the North Sea, *C. maenas* larvae are currently living close to their thermal optimum during summer (15-18 °C). As a result, they have a safety margin of only a few °C before negative effects occur. Therefore, we hypothesise that increasing the intensity of the event should reduce larval performance as temperatures approach critical thermal limits. We also believe that the effects of timing would point towards stage-dependent thermal tolerance with potential increased sensitivity at the time of metamorphosis (Anger, 2001; Dunn et al., 2016; Ismael et al., 1998). Additionally, we disentangled the effect of warm events from the effect of warming by determining the combinations of the components producing a true warm event effect (i.e., where responses differ from those occurring if larvae are exposed to the average temperature experienced during the experiments). Here, larvae were exposed to constant temperatures, and we then compared expectations obtained from such experiments with observations from experiments exposing larvae to warm events.

MATERIALS & METHODS

The European shore crab *Carcinus maenas* was used as a model system. *C. maenas* is an omnivorous crab, playing an important role in benthic ecosystems, with a native distribution over much of the European coast (Klassen & Locke, 2007; Young & Elliott, 2020). *C. maenas*, is also a global invader (Klassen & Locke, 2007), well established, for instance, on the coasts of North America (Yamada et al., 2021). Larvae develop through four zoeal stages, followed by a metamorphosis to megalopa that recolonises (= settles on) the juvenile-adult habitat (Dawirs, 1985; Spitzner et al., 2018).

When considering experimental approaches to study heatwave effects on marine organisms, different methodologies emerge (Boyd et al., 2018; Giménez, 2023; Giménez et al., 2021). First, one can simulate realistic heatwaves incorporating natural temperature variations. This approach enables a detailed examination of how specific heatwave conditions impact larval development but lacks mechanistic understanding and predictive capacity for different heatwave scenarios not directly studied in the experiment (Gerhard et al., 2023). Second, adopting a mechanistic approach involves using idealised heatwave conditions that are typically different from those experienced in the field (e.g., faster temperature increase rate). While this method involves limited realism (Boyd et al., 2018), it enhances the understanding and predictive ability regarding the impacts of future heatwaves and lays the groundwork for subsequent studies considering realistic heatwaves. In this study, we opted for the second approach although for semantic reasons, we refrained from using the term “heatwave” to describe the idealised heatwave simulated here. Indeed, the term heatwaves is already well-defined in the literature for field observations (Hobday et al., 2016) and we do not wish to imply that our idealised heatwaves are equivalent to actual heatwaves. We will use the term "warm pulse" and “warm press” to refer to the first and second experiment respectively, and “warm event” when referring to both experiments. In ecology, the term "pulse" is commonly used to describe a disturbance that is typically intense but short-lived, with conditions returning to their former level afterward (Bender et al., 1984). This concept has been applied to extreme events such as flooding, drought, and heatwaves (Harris et al., 2018; Lynch & Magoulick, 2016). In contrast, the term press defines a disturbance that once started continues to occur (Bender et al., 1984).

Animal collection and husbandry

Larvae were obtained from *C. maenas* berried females, collected in June 2023 during their reproductive period on the island of Helgoland (German Bight, North Sea: 54°10′53″N, 7°53′10″E) and transported to the laboratory at the Marine Station on Helgoland (AWI, 2023). Each berried female was maintained individually in a 5 L aquarium filled with aerated UV-treated filtered seawater (2 µm, salinity 32.5). Aquaria were kept in a temperature-controlled room at 18 °C ± 0.5 °C with a 12:12 light:dark cycle. Females were fed twice a week, and water was changed daily to ensure high water quality during hatching. Freshly hatched larvae were separated from the females and distributed randomly in groups of 10 individuals per beaker (60 ml). Each beaker was then randomly assigned to a treatment. Larvae were reared in natural UV-treated filtered (2 µm) seawater and fed daily with freshly hatched *Artemia* sp. Nauplii *ad libitum.* To ensure high water quality, water was changed daily before the food was renewed (see Torres et al. 2021 for larval rearing procedures).

Experimental design

Experiments were conducted in temperature-controlled rooms, with three replicate beakers per treatment combination. The experiment was repeated four times, using larvae from a different female for each repetition, in order to account for potential parental effects.

To differentiate the specific effect of warm events from those attributed to different temperatures, four groups of larvae (control groups) were reared at constant temperatures (15, 18, 21, and 24 °C) from hatching until metamorphosis to the megalopa. This was done using three replicate rearing beakers × four control temperatures × four females (total = 48 beakers; Fig. 5.1a).

Warm pulse: A full factorial design was carried out manipulating the intensity and timing (i.e., time of the start of the exposure) of a 10-day warm pulse (Fig. 5.1b). Here, we were interested in determining the effects of heatwaves of time scales shorter than the duration of the larval phase. The effects of those heatwaves are less studied in the literature, but they are often more frequent than prolonged heatwaves of several weeks to months of duration (Oliver et al., 2018). Larvae were reared from hatching at a constant seawater temperature (15 °C), representing the average water column temperature in June (Amorim et al., 2023) when the larvae start to hatch. This baseline temperature differed from the temperature at which females were maintained (i.e., 18 °C) because, in June, the temperature in the intertidal where the embryos develop is higher than the temperature of the seawater on the open coast. This distinction highlights the difference between the natural hatching conditions and the environmental baseline temperature used in our analysis.

To simulate warm pulses, larvae were exposed to elevated temperatures of 18, 21, and 24 °C. According to the marine heatwaves' definition by Hobday et al. (2016), the threshold (Q90) for classifying an event as a marine heatwave in the North Sea during summer corresponds to a temperature increase of approximately +1 °C above the climatology

(Deschamps *pers. obs.*). Therefore, the temperature range studied here can be considered as marine heatwaves. The exposure to elevated temperatures started on days 0, 5, 10, and 15 after hatching (i.e., timing) and lasted for 10 days. Before and after the exposure to higher intensities, larvae were kept at the baseline temperature of 15 °C, and continued their development until they reached the megalopa stage. Overall, this design used three replicate rearing beakers × three intensity levels × four timings × four females (total = 144 beakers; Fig. 5.1b)

Warm press: This design simulated a situation where individuals would encounter heatwaves at different times of the larval phase and then experience this temperature until metamorphosis. Such scenario would occur if larvae were hatching at different times with respect to the initiation of a summer heatwave. Larvae were again exposed to the same intensities and timing as in the previous experiments. However, the elevated temperatures lasted until larvae metamorphosed to the megalopa (Fig. 5.1c). Hence, in this experiment, the timing of the warm press covaried with their duration, i.e., earlier timing resulted in longer warm presses. This design consisted of three replicate rearing beakers × three intensity levels × four timings × four females (total = 144 beakers; Fig. 5.1c). From this experiment the 48 beakers from t_0 are the same as the control constant temperatures. Larvae of each different female were treated in separate experiments, so that at any given time we handled 36 (warm pulses) + 36 (warm presses + control) + 3 (15 °C constant) beakers.

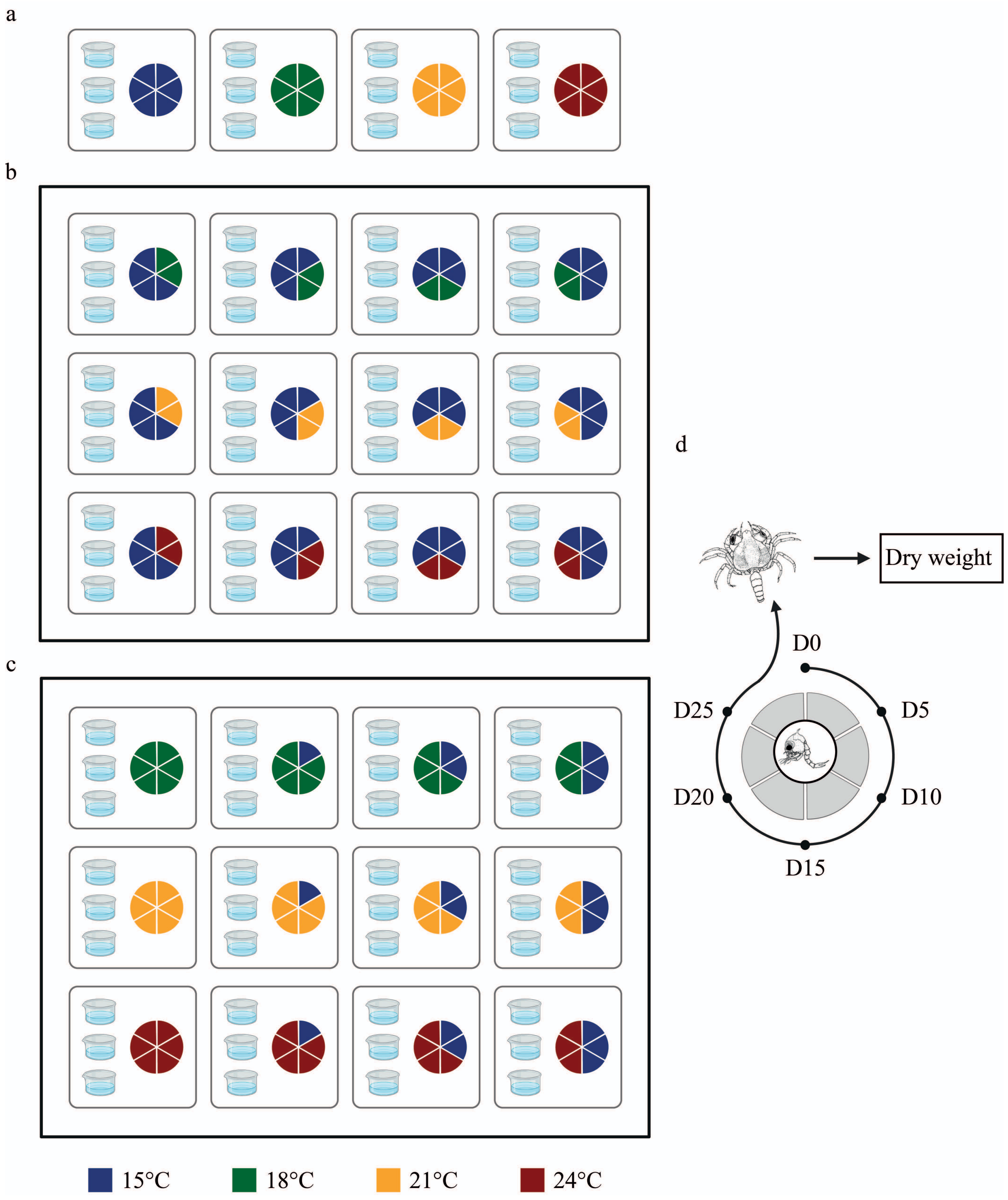

Figure 5.1. Experimental design for warm event simulations. Larvae were reared in groups of 10 individuals each in three replicate beakers representing each combination of the above mention factorial design. Pie charts symbolise the complete zoeal life cycle of *C. maenas,* with each sector corresponding to five days of development. **a.** Four controls were carried out wherein larvae were maintained at constant temperatures (15, 18, 21 & 24 °C) throughout their larval cycle until metamorphosis. **b.** Warm pulses experiment. Larvae were kept at the baseline temperature (15 °C) and exposed for 10 days to higher temperatures (18, 21 & 24 °C) starting on days 0, 5, 10 and 15. **c.** Warm presses experiment. Larvae were reared at the baseline temperature (15 °C) and then kept at higher temperatures (18, 21 & 24 °C) starting on days 0, 5, 10 and 15 until they reached megalopa. Note that days 0 for the warm press experiment are the same treatment as the control. **d.** Larval cycle of *C. maenas*. Zoea were reared until they

reached megalopa. At metamorphosis (within 24 h of moulting to megalopa), individual megalopa were sampled for further analysis of dry mass.

Larval performance was quantified as survival, development duration, instantaneous growth rate of megalopa, and body mass of the megalopa. During the daily water change, survival was recorded through visual inspection, and development duration was determined by counting moults and visual assessment of larval size. To determine the dry mass, recently moulted megalopa (within 24 h of metamorphosis) were transferred from the beaker onto a filter and gently rinsed with distilled water. Excess of water was removed using lint-free wipes (Kimtech Science™ Precision Wipes), and individual megalopa were placed into pre-weighted tin cartridges before being stored at − 20 °C. Samples were then freeze-dried for 24 h (Christ Alpha 1 − 4 freeze dryer) and dry mass was determined using a microbalance (Sartorius Cubis® MCA2.7S, ± 1 µg accuracy). We also determined the body mass of freshly hatched larvae (same procedure as for megalopa), in five replicates per female of origin, consisting of 50 larvae per replicate.

Data Analysis

All statistical analyses were conducted under R environment (R Core Team, 2020) with a threshold of significance set at 5 %.

Survival was calculated as the proportion of larvae surviving from hatching to each stage. Proportions were then transformed into the logistic scale. Because the logistic scale is defined for real numbers only, proportions were transformed before the analysis using the formula:

$$\mathrm{P} = \frac{\mathrm{p(N-1)+0.5}}{\mathrm{N}}$$

Where **p** is the proportion of survivors and **N** is the initial number of larvae assigned to each replicate (i.e., 10). Development duration to zoea II, III, IV, and megalopa was calculated as the time elapsed (in days) from hatching to the selected stage. The instantaneous growth rate was calculated using the formula:

$$\frac{\log\left({}^{\mathrm{DW_M}}/_{\mathrm{DW_{ZI}}}\right)}{\mathrm{D}}$$

Where **DW_M** is the megalopa dry mass, **DW_{ZI}** is the freshly hatched zoea I dry mass, and **D** is the time elapsed from hatching to metamorphosis to megalopa.

To evaluate the warm event effects on survival, development duration, and growth (i.e., dry mass, instantaneous growth rate), linear mixed effect models (LMMs) were performed separately. All model assumptions were verified by checking Residuals and Overdispersion using the *DHARMa* package (Hartig & Lohse, 2022). To assess model fit, model selection procedure was used based on the corrected Akaike Information Criterion (AICc) (Zuur et al., 2009). Specifically, the best-fitting model was determined by identifying the one with the lowest AICc value, with an exception made when the ΔAICc (i.e., difference between a candidate model and the model with the lowest AICc) was less ≤ 3. In such case, we compared both models using likelihood ratio tests (LRT). If models differed significantly, the lowest AICc model was selected. Otherwise, the model with the lowest number of parameters was chosen. If the diagnostic tests indicated that the residuals or dispersion violated model assumptions, the closest model in terms of AICc was chosen. In the first step, model selection based on Restricted Maximum Likelihood (REML) was initially performed to select the best random structure of the model. Because experiments were repeated four times with four different females, the female of origin (♀) was consistently included as a random factor, regardless of whether the AICc for a model without random terms was lower than any other model. In the second step, the model with the best random structure was refitted with Maximum Likelihood (ML), and subsequent model selection was carried out to determine the fixed factors using ML. For all response variables, the full mixed model included the fixed factor temperature intensity in interaction with the timing of the warm event.

An important objective was to determine if the responses to the warm events (characterised by their components) would differ from the response attributed to the average temperature experienced during each experiment (Fig. 5.2). We compared expectations from the average responses with observations as follows: First, we calculated the average temperature over the warm event experiments. Second, we used this value to predict the performance (survival, development duration, growth traits) using the statistical functions fitted to the effect of constant temperature (control treatment experiment) on each performance indicator (Fig. 5.2), always keeping ♀ in the random structure. Here, we computed the expectations of the LMMs using the function “predict”. For growth rates, we could not find a simple function fitting the response over the full temperature range; instead, we fitted separate polynomials in the log-transformed growth rates in the range 15 – 21 °C and a linear model for 21 – 24 °C. Each model was then used separately depending on the average temperature used to make expectations: the second model was specifically applied to predict instantaneous growth rates for scenarios involving 24 °C warm presses, starting either on day 0 (with a mean temperature of 24 °C) or day 5 (with mean temperatures ranging from 21.2 °C to 21.7 °C). Third, to assess the difference between the expected larval performance under average temperature experienced and those observed during warm event, a second LMM was performed. Here, a fixed factor, expected/observed (**EO**, categorical with 2 levels), was included in the model in interaction with temperature intensity and timing (female of origin was used as a random factor). In some cases, variance heterogeneity violated the assumption of homoscedasticity. Therefore, a variance heterogeneity term was added to the variance structure using the varIdent constructor function (R Package nlme); here, we modelled variance heterogeneity between the expected *vs.* observed groups. For the warm press experiment, it is important to emphasise that the observed and expected responses will coincide at t_0 (= time of hatching) as a warm press starting at t_0 corresponds to treatments where temperature was kept constant over the whole larval phase. Consequently, the absence of a significant difference between t_0 observation and prediction validates the accuracy of the model in predicting performance.

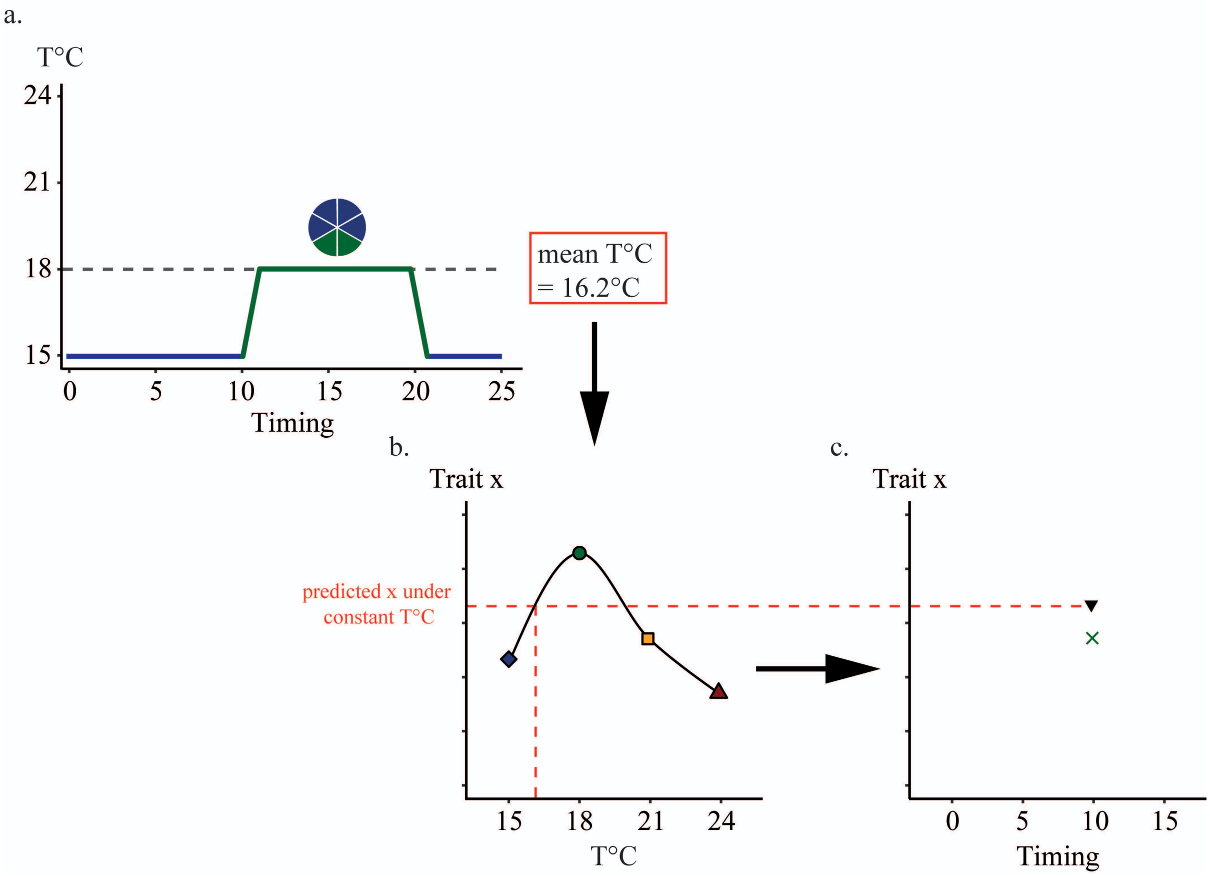

Figure 5.2. Workflow for predicting larval performance values (survival, development duration, and growth traits) under the average temperature experienced during warm event experiments. **a.** The average temperature experienced by the larvae if the temperature was

constant throughout the experiment was calculated for each replicate across the different warm event conditions. **b.** Expected trait values were obtained by fitting models with the control temperatures (15 °C ◆, 18 °C ●, 21 °C ■ and 24 °C ▲) as fixed effects and the individual females (♀) as a random effect. **c.** The expected trait values (▼) under the average temperature were compared with the observed values during warm events (×) by fitting LMMs. The fixed factor, expected/observed was included in the model, in interaction with temperature and timing. The ♀ was used as a random factor.

To illustrate the comparison between warm event conditions and the early summer baseline temperature (i.e., 15 °C), the differences between the performance observed after exposure to the baseline temperature and the one observed after exposure to the warm event conditions were calculated. This comparison was visualised in a heatmap, representing the space of fluctuations in timing and intensity. Larval performance was quantified as survival rates to megalopa and fitness with fitness calculated as the product of survival and body mass at metamorphosis. A difference < 0 indicated a positive effect of the warm event on larval performance, while a difference > 0 indicated a negative effect. No difference represented a neutral effect of the warm event on larval performance.

RESULTS

An important point in the analysis was to determine if any effects of the treatments characterising warm events were observed before experiencing the increased temperature. We checked for these effects by looking at performance at the second, third, and fourth zoeal stages and did not find any evidence of treatment effects occurring before the larvae actually experienced the warm event (see Supplementary Material Section I: Table S5.1, Fig. S5.1−S5.2). Instead, responses were observed either during the warm event or after the larvae returned to the baseline temperature.

Warm pulses experiment

The best models for survival and development duration (from hatching to megalopa) included the additive effect of intensity and timing (Fig. 5.3a, Table S5.2). Increased intensity (i.e., 24 °C: $p < 0.001$) resulted in reduced survival compared to low (i.e., 18 °C) and intermediate (i.e., 21 °C) intensities. Additionally, survival was significantly lower when the warm pulse started on day 15 compared to earlier timings. Survival under increased average (but constant) temperatures did not always match those observed under warm pulses (Table S3). Specifically, survival rates at 18 °C pulses were lower than those expected for the corresponding average temperature, when the warm pulse started 10 and 15 days after hatching. At the 21 and 24 °C pulse, survival rates were consistently lower than those expected under the average temperature, regardless of when the warm pulse occurred. The lowest survival rates were recorded during t_{15} warm pulse, with a significant drop to 34 % at 18 °C, 21 % at 21 °C, and 11 % at 24 °C, in contrast to the survival rates of approximately 75, 86, and 80 %, respectively, expected for the average temperature conditions.

Increased intensity resulted in shorter development duration. Larvae had longer development at a lower intensity (i.e., 18 °C) as compared to those at intermediate and high intensities ($p < 0.001$ in both cases) (Fig. 5.3b). Additionally, development duration was significantly longer when the warm pulse started at day 15 (compared to the earlier timings, i.e., t_0; $p < 0.001$). Again, the expectations for the average temperature experienced did not match the observed responses during the warm pulse experiment (Table S5.4). The differences between expectations and observations were more pronounced at the highest intensity, were observations consistently exceeded the expectations, regardless of the timing (Fig. 5.3b). For intermediate and lower intensities, longer development duration was observed during t_{15} warm pulses as compared to the average temperature conditions. The largest difference between observed and expected development durations occurred during an intense pulse (i.e., 24 °C) starting at t_{15}, where development duration was delayed by up to 3.5 days compared to the average temperature conditions.

Dry mass and instantaneous growth rates responded to both intensity and timing of the warm pulse (Figs. 5.3c, S5.3, Table S5.2). The intense pulse led to reduced dry mass ($p < 0.001$ when compared to 18 and 21 °C) but the reduction was less pronounced when the warm pulse started on day 10 compared to those starting earlier (t_0 *vs.* t_{10}; $p < 0.05$ and t_5 *vs.* t_{10}; $p < 0.001$). The instantaneous growth rate increased with intensity, but the increment was smaller for later warm pulses (Fig. S5.3). Expectations from the average temperature experienced during the warm pulse differed from observations (Table S5.5). Deviations from expectations for dry mass and instantaneous growth rates were stronger for the intense pulse, with reduction observed across all timing compared to the expectations (Fig. S5.3).

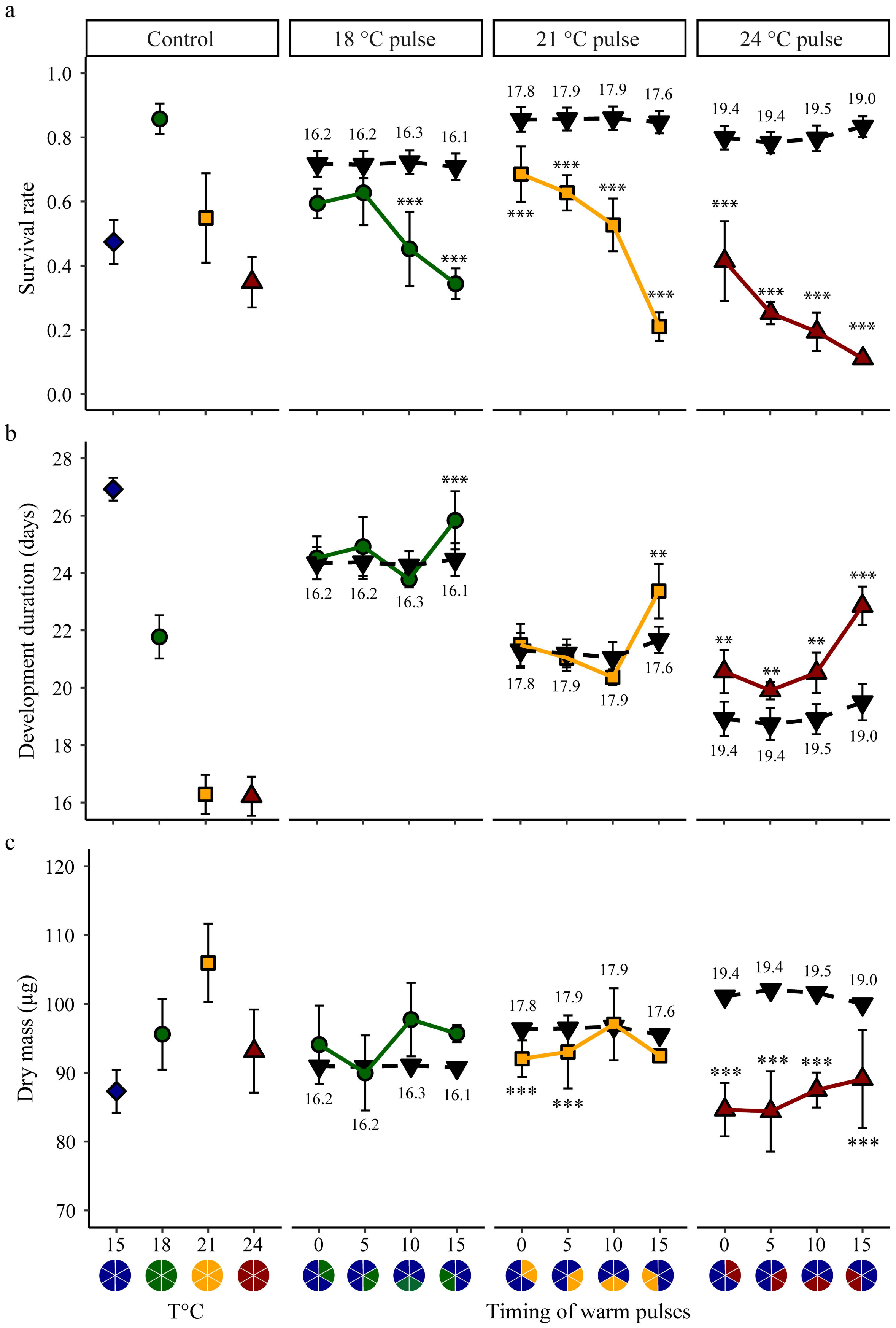

Figure 5.3. Survival rate, development duration, and dry mass after exposure to warm pulses. Comparison between observed (18 °C: ● ; 21 °C: ■ ; 24 °C: ▲ warm pulses) and expected (▼)

values under average temperature experienced throughout the experiment. **a.** Survival rate to megalopa, **b.** development duration from hatching to megalopa and **c.** Megalopa dry mass reared at control constant (left panel) or under warm pulse (right panels). Temperatures: 15 °C ◆, 18 °C ●, 21 °C ■ and 24 °C ▲. Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the average constant temperature experienced (°C) during the warm pulses. Asterisks indicate significant differences between expected and observed values for each treatment. $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Pie charts indicate control and warm pulse treatments.

Comparison between baseline 15 °C and warm pulse treatment revealed a “region of existence” delimited by a boundary (black isoline) above which the organisms’ performance is compromised. Survival was impacted by all warm pulse intensities with the outcome, either positive or negative, depending on the timing of the warm pulse (Fig. 5.4a). Intense pulses consistently resulted in lower survival compared to the constant 15 °C, regardless of the timing; low and intermediate pulses only decreased survival when they occurred after day 10, while earlier warm pulse increased survival. The threshold beyond which any warm pulse resulted in a decline in larval fitness was broader (Fig. 5.4b), with nearly all warm pulses leading to reduced fitness.

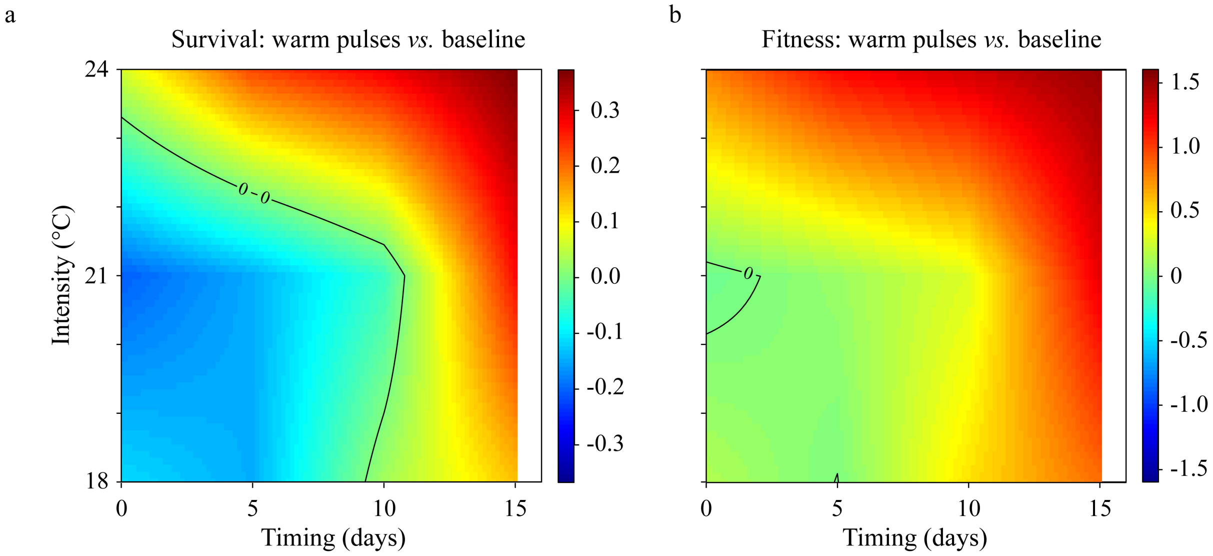

Figure 5.4. Difference in larval performance between the baseline constant temperature and warm pulse conditions. Differences in **a.** larval survival and **b.** fitness. Fitness is calculated as the total megalopa production (mg). Colour gradient represents the difference between response at the baseline temperature: 15 °C, and after exposure to warm pulses. Differences < 0 indicate positive effects of the warm pulses (i.e., the region below the “0” isoline). Differences > 0 indicate negative effects of warm pulses (i.e., the region extending beyond the "0" isoline). Differences ≈ 0 indicate no effects. Note the difference in the gradient scale limits.

Warm press experiment

Survival rate to megalopa decreased both with intensity (*p* < 0.001 for all comparisons) and timing (Fig. 5.5a). Consistently, the biggest drops in survival rates were observed during late warm presses. For example, during a late 24 °C press, only 9 % of larvae reached megalopa, compared to 35 % survival during early warm presses of the same intensity. The observed survival rates were much lower than those expected from the average temperature (Fig. 5.5a, Table S3).

Development duration to megalopa was significantly longer at the 18 °C press (*p* < 0.001 compared with intermediate and higher intensities) and when it started later in the larval cycle (*p* < 0.001 for all comparisons) (Fig. 5.5b). Expectations from average temperatures did not always match the observed development duration with deviations observed for the intermediate and intense presses starting at day 5 and 10 respectively (Fig. 5.5b, Table S5.4).

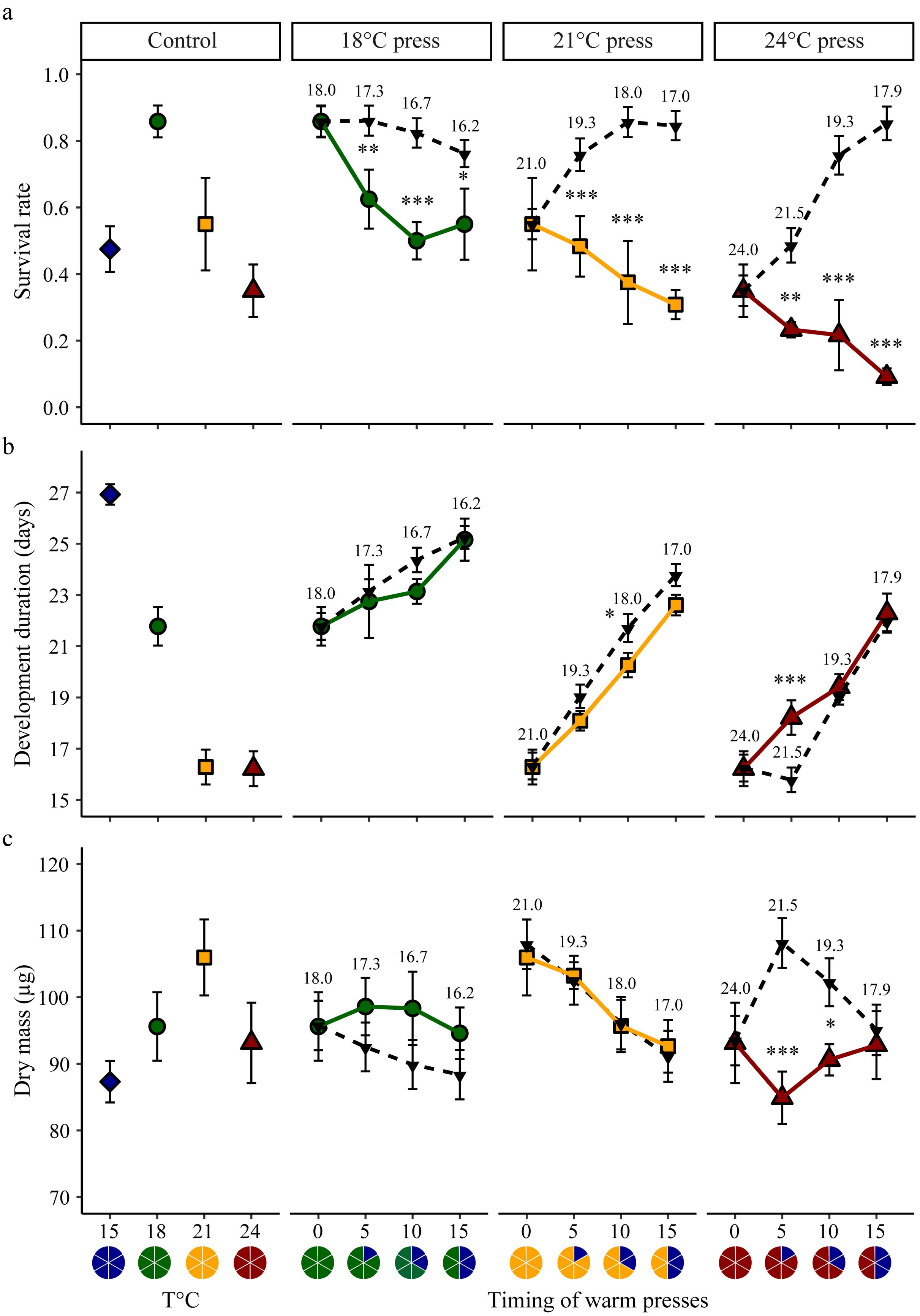

Figure 5.5. Survival rate, development duration, and dry mass after exposure to warm presses. Comparison between observed (18 °C: ● ; 21 °C: ■ ; and 24 °C: ▲ warm press) and expected

(▼) values under average temperature experienced throughout the experiment. **a.** Survival rate to megalopa, **b.** development duration from hatching to megalopa and **c.** Megalopa dry mass reared at control constant (left panel) or under warm press (right panels). Temperatures: 15 °C ◆ , 18 °C ●, 21 °C ■ and 24 °C ▲). Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the average constant temperature experienced (°C) during the warm presses. Asterisks indicate significant differences between expected and observed values for each treatment. $p < 0.05$*, $p < 0.01$**, $p < 0.001$***. Note that each timing 0 is equivalent to the controls (i.e., larvae reared at constant temperatures: 18, 21, and 24 °C from hatching until metamorphosis; left panel). Pie charts indicate control and warm press treatments.

The best models included the additive and interactive effect between intensity and timing for dry mass and instantaneous growth rates respectively (Table S5.6). At intermediate pulses, dry mass decreased with delayed timing (Fig. 5.5c). However, no clear patterns were observed at other intensities. The instantaneous growth rates declined with both the intensity and timing with a sharper decrease found at intermediate and high intensities compared to the low intensity (Fig. S5.4). Deviations from expectations under average temperature were also observed, however, significant deviations were not always consistent. For dry mass, they were restricted to warm presses of the highest intensity (Fig. 5.5c), while for growth rates they were inconsistent across the different intensities (Fig. S5.4).

As observed for the warm pulses, comparison between baseline 15 °C and warm press treatment showed that survival was again affected by all intensities with the effect varying depending on the timing. (Fig. 5.6a). Intense presses consistently led to lower survival compared to the constant 15 °C, regardless of when they occurred. The region of existence was limited to the bottom corner of the space of fluctuations in timing and intensity; low intensity presses increased survival rates in comparison to those observed at constant 15 °C. Intermediate presses resulted in lower survival for all presses occurring after 5 days and higher survival for all presses occurring at t_5 and earlier. The threshold beyond which any warm presses resulted in a decline in larval fitness was broader (Fig. 5.6b) with nearly all warm presses leading to reduced fitness, except for early ones below 21 °C.

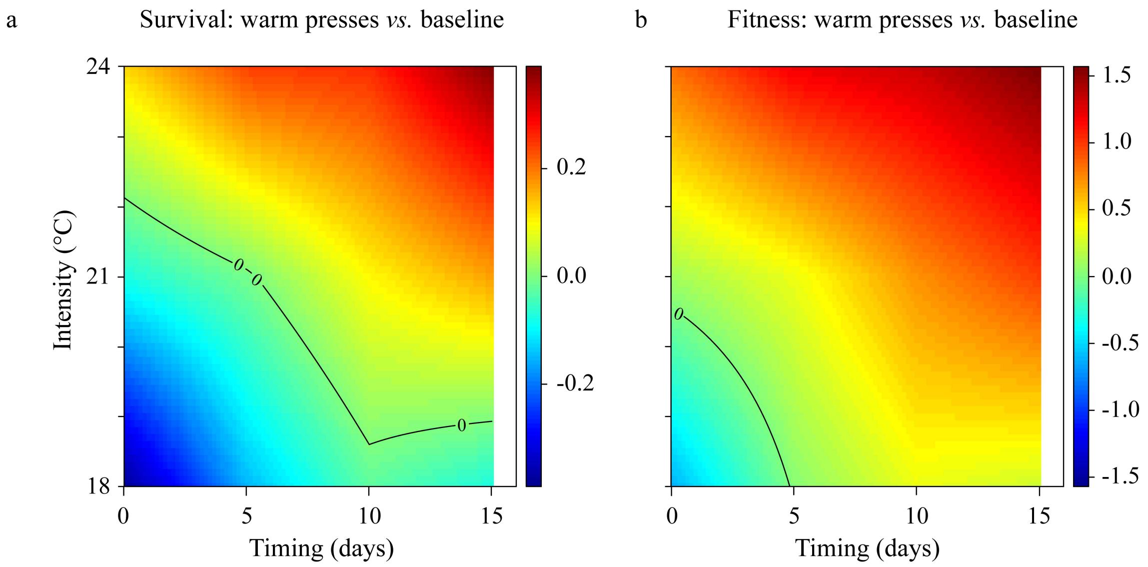

Figure 5.6. Difference in larval performance between the baseline constant temperature and warm presses condition. Differences in **a.** larval survival and **b.** fitness. Fitness is calculated as the total megalopa production (mg). Colour gradient represents the difference between response at the baseline temperature: 15 °C, and after exposure to warm presses. Differences < 0 indicate positive effects of the warm presses (i.e., the region below the “0” isoline). Differences > 0 indicate negative effects of the warm presses (i.e., the region extending beyond the "0" isoline). Differences ≈ 0 indicate no effects. Note the difference in the gradient scale limits.

DISCUSSION

We investigated the response of *C. maenas* larvae to warm events (i.e., idealised heatwaves) of different intensity, timing, and duration. Our study yielded two main findings. First, larval performance responded to the combined effects of the heatwaves’ components, in a manner that cannot easily be disentangled. Second, our study highlighted that in several combinations of timing and intensity, biological responses under heatwaves could not be predicted by using the average temperature experienced throughout the heatwave (i.e., constant conditions).

Combined effect of heatwave components

In this study, we identified a "region of existence" defined by a boundary, beyond which the organisms' performance becomes compromised compared to their performance at the baseline temperature of 15 °C. This region also identified the set of warm events that may be considered as “extreme” for the organism (Giménez 2023). As expected, the boundary responds to the fact that higher intensities lead to stronger reductions in survival and overall fitness. Additionally, the negative effects of intensity on survival and fitness were exacerbated when the warm events occurred later in the larval phase. Indeed, this interactive effect also reaches a point where the response occurs at low intensities. The effect of timing found in this study points towards the stage-dependent costs of fluctuations. These findings highlight the importance of timing in assessing organism's response to environment fluctuations, offering new insights that could reshape our understanding on the effect of marine heatwaves on organisms with complex life cycle.

The role of timing is further highlighted by the results of the second experiment in which late presses were shorter than early ones and led to a stronger negative effect on performance. This contradicts studies, predicting that the critical thermal maximum should decrease with the duration of the exposure to increased temperature (Rezende et al., 2014). However, this contradiction points to the last zoeal stage and metamorphosis to megalopa as a critical bottleneck. This result is consistent with the transition timing hypothesis (Levitis, 2011), where physiological tolerance is reduced in stages previous to major transitions. Indeed, transitions between ontogenetic stages are particularly sensitive to environmental factors such as temperature (Uriarte et al., 2019). Enhanced mortality typically occurs near the start and end of the larval phase in crustaceans (Anger, 1991; Dunn et al., 2016; Sulkin & McKeen, 1989) and early embryos appear to be more tolerant to temperature increases than later stages in sea urchins (Gall et al., 2021) and starfishes (Balogh & Byrne, 2020). Furthermore, studies on terrestrial organisms showed that early-stage insects can recover from exposure to high temperature stress if subsequent stages are not stressed. Similarly, temperature increase during later stages often leads to irreversible damage (Iltis et al., 2021; Ma et al., 2018; Zhang et al., 2015). Therefore, our results highlight a need to explore the consequences of a match/mismatch between the timing of a heatwave and that of metamorphosis in species with complex life cycles.

The effect of the heatwave components on the space of existence is relevant to understand heatwaves effects in nature. For any species, the boundary of the space of existence can be used to define the group of events experienced as "extreme" (Giménez, 2023), defined as "an episode where climate or climate-driven conditions trigger a negative threshold-like biological response" (Bailey & van de Pol, 2016). When such extreme events differ in timing and intensity, they are likely to differ from the event defined in the literature as heatwaves. For example, marine heatwaves are usually defined through climatological thresholds, as events "lasting for five days or more, with temperatures exceeding the threshold of 90th percentile of the historical baseline" (Hobday et al., 2016). The 90th percentile temperature is not constant but fluctuates with the seasons. Indeed, from spring to summer, when larvae of *C. maenas* develop, the 90th percentile increases (Giménez et al., 2024). Hence, late heatwaves (i.e., summer) will be associated with higher thermal thresholds than early ones (i.e., spring). Our findings revealed that, as development progresses, the boundary of the space of existence was reduced to lower intensities. Given the high threshold, it is likely that temperature fluctuations in summer below the threshold (therefore not classified as heatwaves) will still be enough to depress survival. In contrast, earlier in the season, during periods when the threshold is lower, temperature fluctuations may be classified as heatwaves, though they will not always negatively affect survival. Therefore, depending on the timing, some heatwaves may not always trigger biological responses (Bailey & van de Pol, 2016), while other warm events not classified as heatwaves could still have significant impacts. This emphasises the need to assess heatwaves on a seasonal basis when evaluating biological responses

Constant *vs.* pulse and press conditions

We identified a region in the space of fluctuations where biological responses cannot be predicted by the average temperature experienced over the developmental period (Fig. 5.7). This discrepancy is significant for two reasons: first, it points towards the potential failure of a mechanism or the triggering of a compensatory response, not observed under constant temperatures. Second, it helps to identify scenarios where responses to heatwave can be predicted from simple experiments, keeping organisms under constant conditions. Here, we found that regardless of the timing, under intermediate and intense pulse, constant temperature failed to predict the responses, while this failure was restricted to late timing during low intensity pulses. When the warm press occurred between 5 days after hatching onwards, prediction failures occurred whatever the intensity. The differences between the two experiments suggest a role for recovery time post-heatwave if such heatwaves occurred between days 5 and 10.

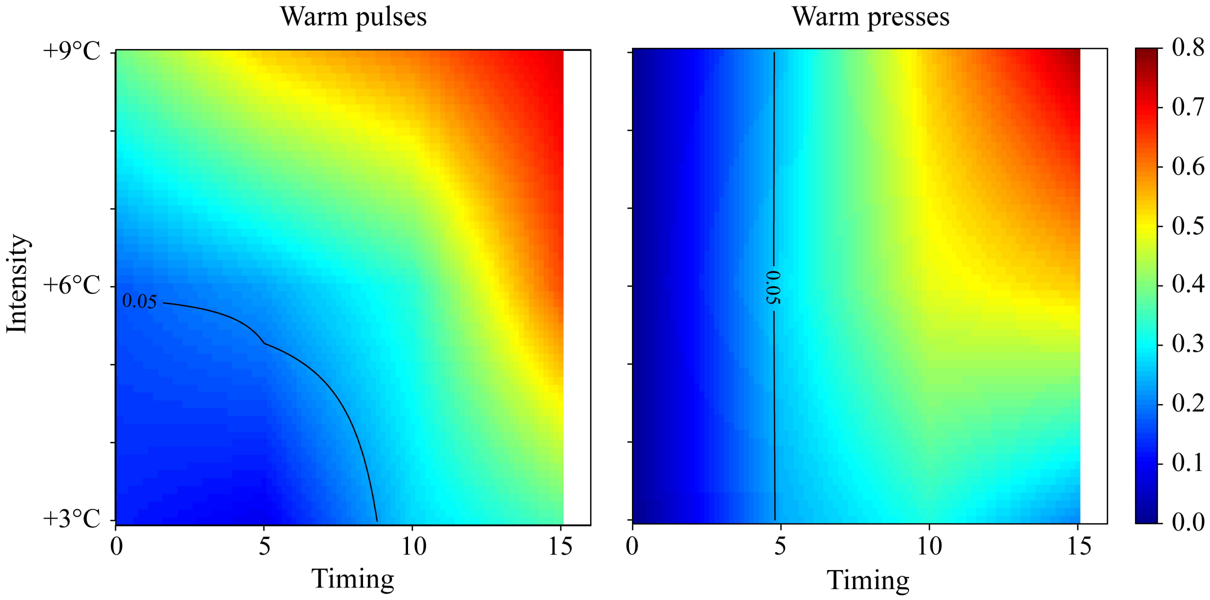

Figure 5.7. Difference between the observed survival during warm pulses and presses and the expectation for the average temperature experienced throughout the experiment (colour gradient). Intensity (left axis) is shown as °C (+3 for 18 °C, +6 for 21 °C, and +9 for 24 °C). The black line represents the threshold of statistical significance ($p = 0.05$).

Another important finding was that the strongest deviations from expectations made from the average temperature occurred in survival, while developmental time and megalopa body mass in response to warm events did not differ as much from expectations. It is expected that survivors will be those with robust physiological compensatory mechanisms to handle warm events. However, it is less evident that such mechanisms result in responses that do not differ from expectations under constant temperatures. Theory suggests that thermal fluctuations should lead to costs, such as prolonged development or reduced growth (Pettersen et al., 2024). However, in our study, these costs appear high enough to impact survival.

Temperature fluctuations in a given environment can influence biological systems through mechanisms distinct from those at play in constant environments (Gerhard et al., 2023). This discrepancy can be explained by Jensen's inequality, originating in nonlinear relationships between temperature and biological responses (Koussoroplis et al., 2017; Ruel & Ayres, 1999). For instance, studies have shown that constant temperatures do not accurately predict the performance of an ectotherm organism subject to fluctuating temperatures (Kingsolver et al., 2015; Niehaus et al., 2012). Hence, some mechanisms cannot be explained when the non-linearity is considered. Indeed, during a heatwave, the temperature might surpass some thermal threshold, triggering irreversible physiological damage or leading to physiological perturbations that require long recovery times. Such phenomena would not occur if individuals are exposed to low average temperatures over a long time. Conversely, matches between responses to constant temperature *vs.* warm event would occur if temperature operates cumulatively on developmental processes.

Effect of realistic heatwaves

An important question from this study concerns how realistic heatwaves drive larval performance. While our results can be used for prediction, they can also guide for future research, keeping in mind that daily temperature changes under natural conditions occur much slower than those used in our experiments. For instance, our findings suggest that the temperature of spring heatwaves in the German Bight (i.e., maximum temperature ranging from 6.1 °C to 16.3 °C: Giménez et al., 2024) does not reach the level required to negatively affect performance, even considering the abrupt temperature change experienced in the laboratory. Additionally, the effects of spring heatwaves could be accurately estimated using expectations from experiments with constant temperatures. However, the effect of summer heatwaves on larval survival may not be well-predicted if they occur when larvae are at advanced stages of development.

While we did not manipulate heatwave components such as the rate of temperature increase, our study can serve as an initial exploration of the space of heatwave components. Indeed, with a temperature increase rate set to a constant and high value, we found that early warm events only affected larval performance during high intensities. Based on the assumption that realistic heatwaves have lower rates of temperature increase, providing larvae with sufficient time to acclimate, we can hypothesise that early heatwaves are unlikely to impact survival. This result suggests the importance of focusing on heatwaves occurring later in the larval cycle. It will be interesting in future experiments to investigate the effect of varying temperature increase rates, combined with intensity, in order to simulate more complex and realistic heatwave scenarios.

CONCLUSION

In this study, we demonstrate that the timing, intensity, and duration of heatwaves can influence biological performance, resulting in varied larval responses depending on the scale of the heatwave components. We have also identified a "region of existence" where warm pulses are not considered extreme events for the organisms. This region's boundaries may vary, narrowing or expanding based on the organisms' traits. An expansion of this region would likely benefit species that are adapted to warmer conditions, potentially facilitating their spread and encouraging ecological invasions. By considering the dynamics of heatwaves rather than constant conditions, we can determine more precisely how organisms could respond under realistic scenarios. This understanding is crucial for informing conservation strategies for species that have complex life cycles and are highly sensitive to temperature changes.

Acknowledgments

We would like to thank Leo Tekotte for his assistance in larval rearing. His contribution was supported by the Deutsche Forschungsgemeinschaft through the Research Training Group 2010: RESPONSE. This study is part of MMD doctoral dissertations. MMD was supported by the AWI INSPIRES program, Germany. MB acknowledges the support received from the Federal German Ministry of Education and Research through the CoastalFutures project. Experiments were performed at the Marine Station Helgoland.

SUPPLEMENTARY MATERIAL

Section I: Before effects

An important point in the analysis was to determine if any effects of the treatments characterising warm pulses and presses were observed before experiencing the warm events. We checked for these effects by looking at performance at the second, third and fourth zoeal stages. The interaction between intensity and timing was retained in the model for development to zoea II, III and IV during warm pulses and presses (Table S1).

Table S5.1. Model selection based on AICc for development duration at zoea II (ZI), zoea III (ZIII) and zoea IV (ZIV) in response to warm pulses and presses timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The best models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

Model selection	**Warm pulses**						**Warm presses**					
	Linear scale			**Logarithmic scale**			**Linear scale**			**Logarithmic scale**		
	ZII	**ZIII**	**ZIV**	**ZII**	**ZIII**	**ZIV**	**ZII**	**ZIII**	**ZIV**	**ZII**	**ZIII**	**ZIV**
Random factors (REML)												
t × T°C | ♀	605	289	391	-274	-339	-319	232	329	316	-254	-311	-389
T°C | ♀	230	288	377	-249	-341	-327	233	330	308	-250	-300	-384
t | ♀	**181**	296	376	**-302**	-336	**-340**	**214**	**308**	**297**	**-278**	**-321**	**-413**
1 | ♀	220	**286**	**373**	-260	**-345**	-335	222	326	299	-236	-309	-394
Fixed factors (ML)												
t × T°C	**153**	**267**	**362**	**-375**	**-423**	**-418**	**188**	**310**	**278**	**-348**	**-386**	**-497**
t + T°C	180	312	406	-326	-350	-343	214	357	372	-309	-302	-372
T°C	189	606	623	-317	-65	-335	223	585	382	-302	-296	-364
T	211	383	520	-293	-277	-227	228	385	495	-292	-268	-257

No significant variations in development were observed for zoea II and III at t_{10} and t_{15} across all intensities (Fig. S5.1−S5.2). Moreover, development duration at a constant temperature of 15 °C was similar to those observed after t_{10} and t_{15} warm events (Fig. S5.1−S5.2). This lack of difference can be attributed to a "before" effect as the larvae were moulting to zoea III one day prior to the onset of the warm event, hence remaining under the baseline temperature conditions. The t_{10} observation is attributed to a "start" effect as the larvae experienced the warm pulses for two days only before reaching zoea III. Similar patterns emerged for zoea IV where no significant differences in development were detected at t_{15} between 21 and 24 °C warm events and development duration were similar than under 15 °C constant condition. Given that larvae experienced the warm events for only 2.5 days, the development under 21 and 24 °C warm events at t_{15} can be attributed to a “start” effect.

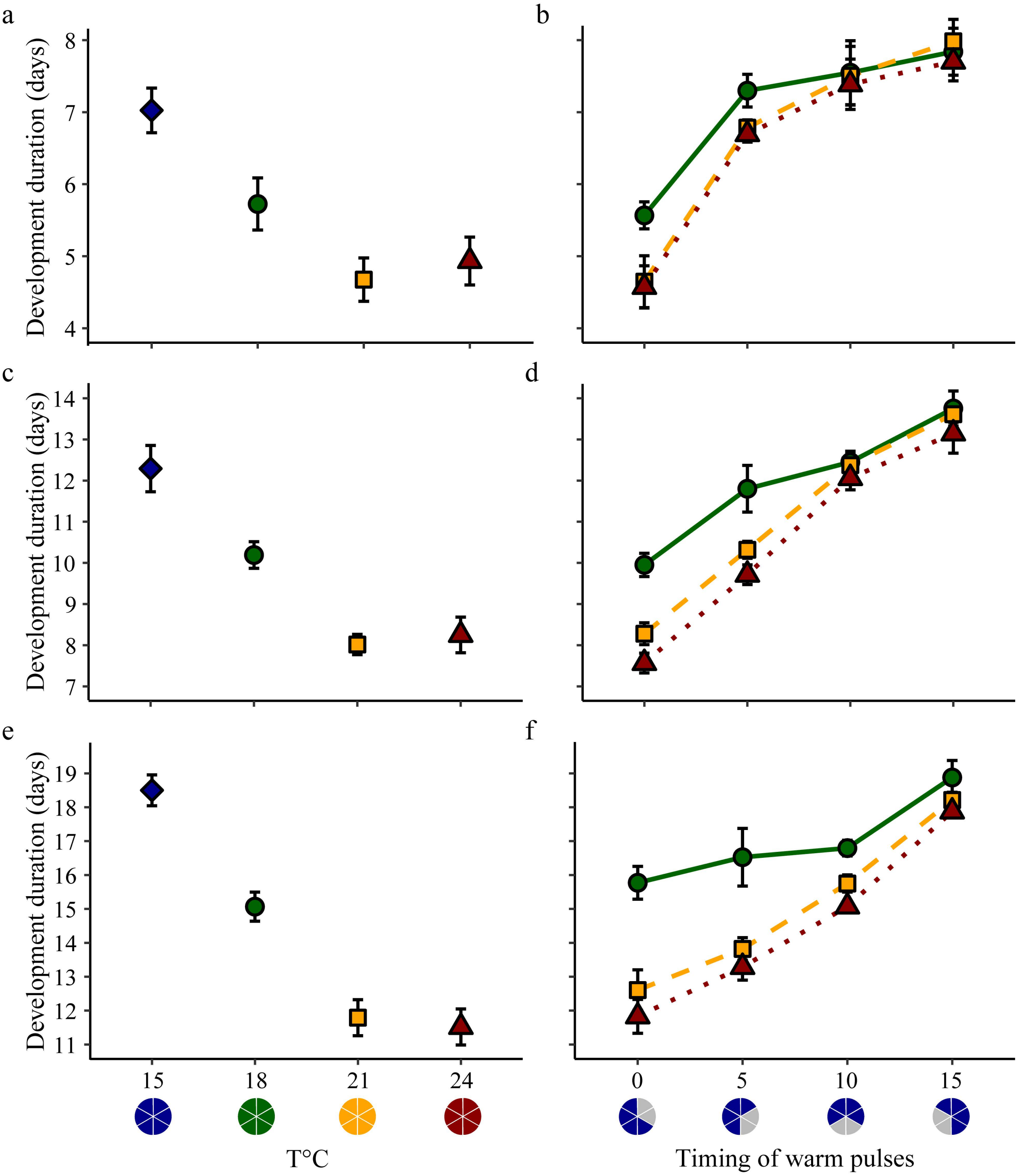

Figure S5.1. Duration of larval development from hatching until **a.** zoea II, **b.** zoea III and **c.** zoea IV. in response to constant temperature (control; left panels) and in response to short warm pulses at different timing and temperature (right panels). Values shown are the mean ± standard error for each treatment among the four females of origin. Temperatures: 15 °C: ◆ 18 °C: ● 21 °C: ■ 24 °C: ▲. The grey sections of the pie represent the timing of each warm pulses.

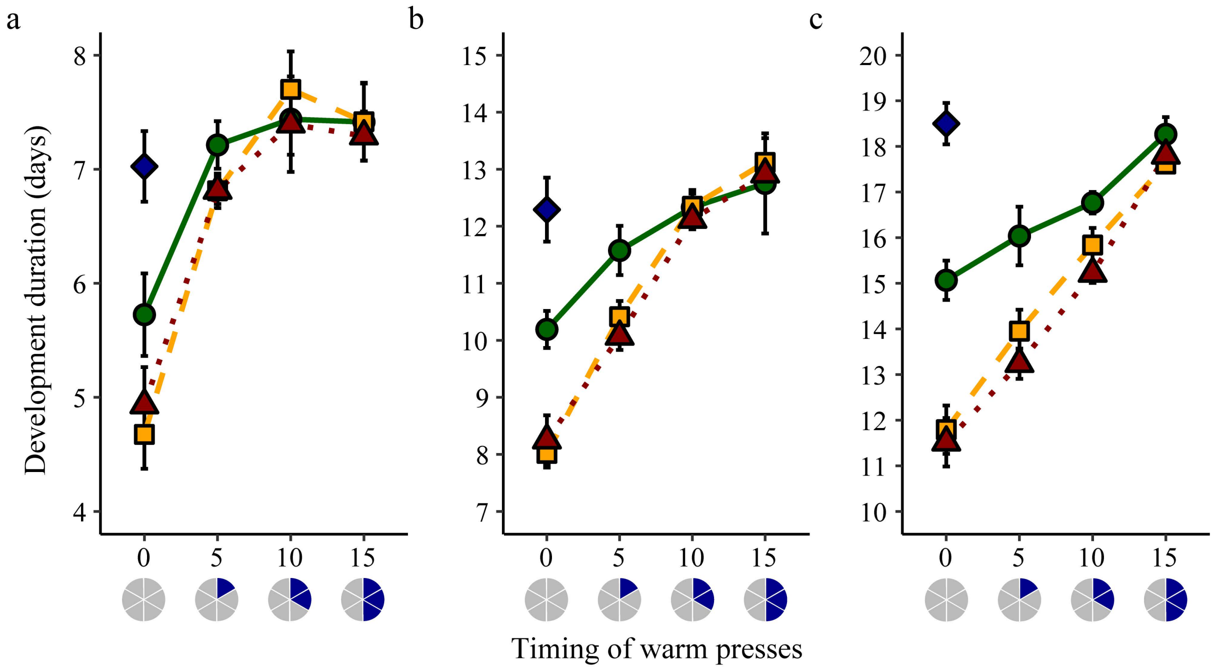

Figure S5.2. Development duration from hatching until **a.** zoea II, **b.** zoea III and **c.** zoea IV in response to long warm presses at different timing and temperature. Values shown are the mean ± standard error for each treatment among the four females of origin. Temperature: 15 °C: ◆ 18 °C: ● 21 °C: ▫ 24 °C: ▲. The grey sections of the pie represent the timing of each warm pulses.

Section II: Post heatwaves effects

Table S5.2. Model selection based on AICc for development duration until megalopa, survival from hatching to megalopa, megalopa dry mass and instantaneous growth rate from hatching to megalopa in response to warm pulses timing (t) and intensity (T °C). Results are shown for linear and logistic for survival, linear and logarithmic scales for development, and linear for dry mass and instantaneous growth rate. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

	Survival rate		**Development duration (days)**		**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model selection	**Linear scale**	**Logistic scale**	**Linear scale**	**Logarithmic scale**	**Linear**	**Linear**
Random factors (REML)						
t × T°C | ♀	34	447	558	-209	5024	-3230
T°C | ♀	15	430	545	-221	4887	-3369
t | ♀	25	440	555	-213	4883	-3361
1 | ♀	**6**	**420**	**536**	**-232**	**4881**	**-3370**
Fixed factors (ML)						
t × T°C	-40	4924	543	-301	4924	**-3495**
t + T°C	**-42**	**4918**	**535**	**-307**	**4918**	-3495
T°C	6	4926	566	-275	4926	-3466
T	1	4942	626	-209	4942	-3464

Table S5.3. Model selection based on AICc for proportion of survival. Comparison between expected and observed (EO) survival to megalopa in response to warm pulses and presses timing (t) and intensity (T°C). Results are shown for linear and logistic scales. Female of origin (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The best models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

		Warm pulse		**Warm press**	
	Model selection	**Linear scale**	**Logistic scale**	**Linear scale**	**Logistic scale**
T°C prediction	***Random factors (REML)***				
	T°C | ♀	36	179	36	179
	1 | ♀	**34**	**176**	**34**	**176**
	Random factors (REML)				
	t × T°C | ♀	-526	311	662	662
	T°C | ♀	-536	298	651	651
	t | ♀	-528	306	722	722
	1 | ♀	**-541**	**294**	**641**	**641**
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	-679	234	**-259**	**609**
	3 two-way				
	EO × t + EO × T°C + T°C × t	**-683**	**226**	-244	629
	2 two-way				
	EO × T°C + EO × t	-665	245	-212	660
	EO × T°C + T°C × t	-631	272	-144	730
	EO × t + T°C × t	-647	282	-227	641
	Two-way				
	EO + T°C × t	-607	313	-135	736
	EO × T°C + t	-614	290	-128	744
	EO × t + T°C	-630	299	-199	669
	Additive				
	EO + T°C + t	-589	330	-121	749
	EO + T°C	-592	325	-126	743
	EO + t	-376	568	-10	861
	T°C + t	-426	478	5	880
	T°C	-427	475	89	874
	t	-216	722	-15	958
	EO	-381	653	-26	855

Table S5.4. Model selection based on AICc for development duration. Comparison between expected and observed development to megalopa (EO) in response to warm pulses and press timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales. Female of origin (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The best models are indicated in bold. Female of origin (♀) was always included in the model as a random factor.

		Warm pulse		**Warm press**	
	Model selection	**Linear scale**	**Logarithmic scales**	**Linear scale**	**Logarithmic scales**
T°C prediction	***Random factors (REML)***				
	T°C | ♀	192	-65	192	-65
	1 | ♀	**187**	**-66**	**187**	**-66**
	Random factors (REML)				
	t × T°C | ♀	695	-801	644	-838
	T°C | ♀	686	-810	641	-841
	t | ♀	688	-808	645	-837
	1 | ♀	**681**	**-815**	**639**	**-842**
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	659	-986	**612**	**-1017**
	3 two-way				
	EO × t + EO × T°C + T°C × t	**647**	**-997**	616	-1003
	2 two-way				
	EO × T°C + EO × t	650	-992	865	-719
	EO × T°C + T°C × t	667	-979	619	-999
	EO × t + T°C × t	662	-978	640	-970
	Two-way				
	EO + T°C × t	679	-963	642	-967
	EO × T°C + t	670	-975	866	-718
	EO × t + T°C	666	-974	884	-696
	Additive				
	EO + T°C + t	682	-960	885	-696
	EO + T°C	722	-920	1237	-355
	EO + t	1232	-420	1254	-344
	T°C + t	698	-929	884	-696
	T°C	736	-893	1235	-356
	t	1237	-410	1252	-346
	EO	1241	-410	1389	-206

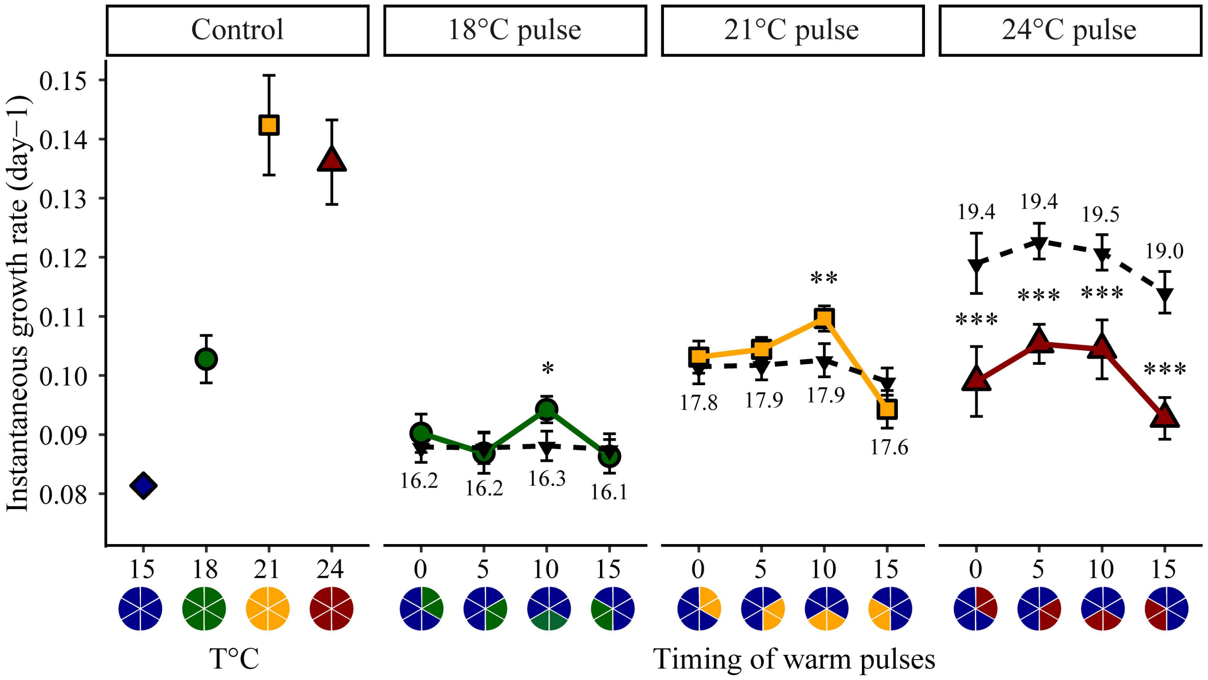

Figure S5.3. Instantaneous growth rate during warm pulses. Comparison between observed (18 °C: ● ; 21 °C: ■ ; 24 °C: ▲) and expected (▼) growth rates for larvae reared at constant (control: left panel) or une warm pulses (right panels). Temperature: 18 °C ●, 21 °C ■ and 24 °C ▲. Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the mean constant temperature experienced (°C) during the warm pulses. Asterisks indicate significant differences between expected and observed values for each treatment. $p < 0.05$*. $p < 0.01$**, $p < 0.001$***. Pie charts indicate control and warm pulse treatments.

Table S5.5. Model selection based on AICc for growth traits comparison between expected and observed (EO) in response to warm pulses and presses timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales. Female (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The best models are indicated in bold. Female of origin (♀) was always included in the model as a random factor.

		Warm pulse		**Warm press**	
	Model selection	**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**	**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model for T°C prediction	***Random factors (REML)***				
	T°C | ♀	2 step-approach	**-327**	2 step-approach	2 step-approach
	1 | ♀		-297		
	Random factors (REML)				
	t × T°C | ♀	6826	-8262	**6245**	**-9683**
	T°C | ♀	6815	**-8262**	6271	-8726
	t | ♀	6833	-8232	6264	-8677
	1 | ♀	**6827**	-8235	6268	-8421
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	6849	-8534	**6266**	-9935
	3 two-way				
	EO × t + EO × T°C + T°C × t	**6843**	**-8539**	6308	**-9843**
	2 two-way				
	EO × T°C + EO × t	6859	-8537	6446	-9789
	EO × T°C + T°C × t	6848	-8526	6307	-9838
	EO × t + T°C × t	6944	-8368	6364	-9763
	Two-way				
	EO + T°C × t	6950	-8356	6366	-9760
	EO × T°C + t	6864	-8524	6446	-9784
	EO × t + T°C	6960	-8365	6503	-9709
	Additive				
	EO + T°C + t	6970	-8353	6504	-9706
	EO + T°C	6996	-8353	6577	-9684
	EO + t	8525	-8317	6559	-9685
	T°C + t	6976	-8345	6504	-9701
	T°C	7007	-8345	6577	-9679
	t	8536	-8309	6560	-9680
	EO	8531	-8318	6634	-9662

Table S5.6. Model selection based on AICc for survival from hatching to megalopa, development duration until megalopa, megalopa dry mass and instantaneous growth rate in response to warm presses timing (t) and intensity (T°C). Results are shown for linear and logistic for survival, linear and logarithmic scales for development, and linear for dry mass and instantaneous dry mass growth rate. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The best models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

	Survival rate		**Development duration (days)**		**Dry mass (μg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model selection	**Linear scale**	**Logarithmic scale**	**Linear scale**	**Logarithmic scale**	**Linear**	**Linear**
Random factors (REML)						
t × T°C | ♀	23		523		5024	-3577
T°C | ♀	9	428	499	-252	4887	-3565
t | ♀	24	438	514	-246	4883	**-3578**
1 | ♀	**5**	**419**	**494**	**-262**	**4881**	-3569
Fixed factors (ML)						
t × T°C	-41	411	**498**	**-333**	4924	**-3703**
t + T°C	**-49**	**404**	504	-310	**4918**	-3561
T°C	-18	434	629	-174	4926	-3555
T	31	481	635	-174	4942	-3208

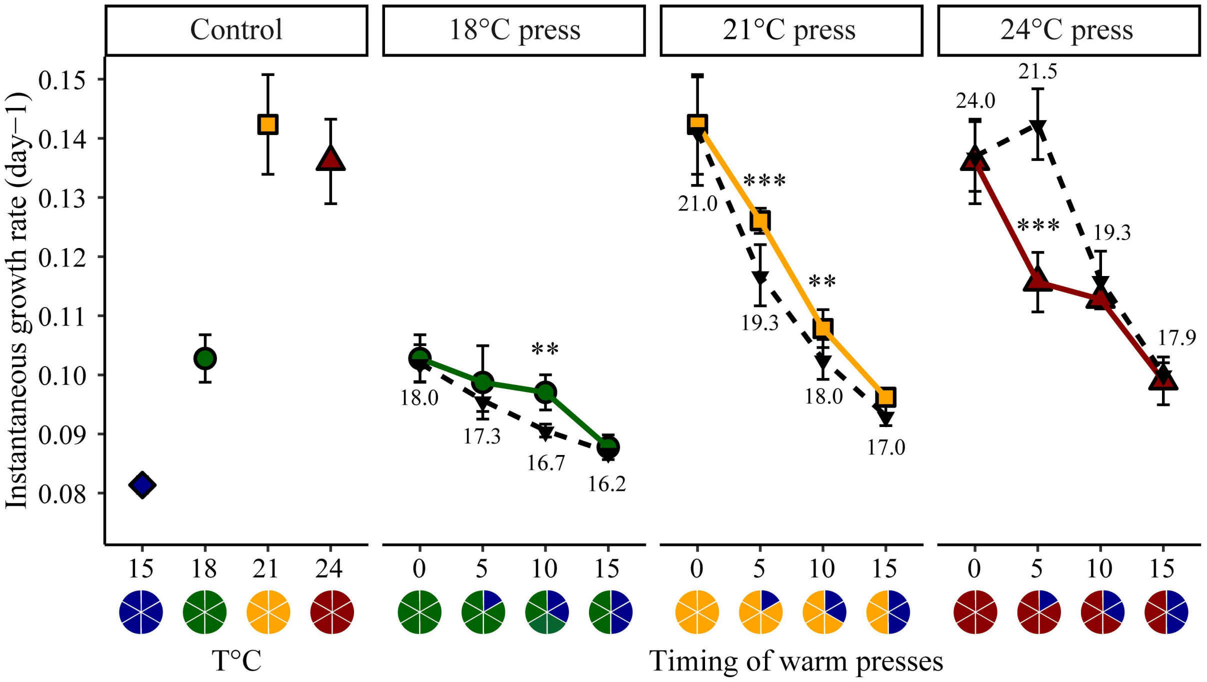

Figure S5.4. Instantaneous growth rate during warm presses. Comparison between observed and expected (▼) growth rate from hatching to megalopa under 18 °C (●), 21 °C (■) and 24 °C (▲) constant temperature. Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the mean constant temperature experienced (°C) during the warm presses. Note that each timing 0 corresponds to the control treatments (see left panels). Pie charts indicate control and warm press treatments. Non-significant effect at t0 validates the accuracy of the model in predicting growth rate.

CHAPTER

6

Heatwaves to the rescue: Responses of larvae of the invasive crab *Hemigrapsus sanguineus* to marine heatwaves

Heatwaves to the rescue: Responses of larvae of the invasive crab *Hemigrapsus sanguineus* to marine heatwaves

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Abstract

Biological invasions, driven by climate change and human activities, pose significant threats to biodiversity and ecosystems worldwide. While much research has focused on the impact of rising mean temperatures on species invasions, the role of extreme weather events such as marine heatwaves, in facilitating biological invasions is less understood. This study investigated the response of larvae of the invasive Asian shore crab *Hemigrapsus sanguineus* to laboratory-simulated marine heatwaves. We quantified the effects of warm events of varying intensity (current: 18 °C and 21 °C, and future in the German Bight: 24 °C), duration, and timing on larval performance (survival, development duration, dry mass and growth rates). Intensity, duration, and timing constitute primary components of marine heatwaves and larval performance was driven by their interactive effects. Performance could not be always predicted by the average temperature experienced during development, which suggest that average temperature conditions during a heatwave may be poor predictors of performance in the field. Warm events had a positive effect on larval performance, especially when they occurred during zoea IV stage. By contrast, exposure to colder temperatures, especially occurring during zoea III, resulted in larvae following an alternative developmental pathway, characterised by an extra stage (zoea VI) before reaching the megalopa. Hence, ontogenetic patterns in thermal tolerance and developmental plasticity are candidate mechanisms underpinning responses to heatwaves. Positive responses of *H. sanguineus* to laboratory warm events contrasted with negative responses occurring in the native competitor (shore crab *Carcinus maenas*) under similar experimental conditions. Overall, matches between heatwaves and key developmental stages may enhance larval performance promoting the spread and establishment of *H. sanguineus* in non-native habitats despite its native competitors.

INTRODUCTION

Biological invasions, driven by climate change and human activity, are major ecological threats to biodiversity and ecosystems worldwide (Gallardo et al., 2016; Occhipinti-Ambrogi & Savini, 2003; Robinson et al., 2020). Climate change can facilitate invasions by modifying the nature of vectors and pathways and by altering abiotic and biotic conditions in an environment (Robinson et al., 2020). Ultimately, the introduction of new species can lead to shifts in species dominance, changes in ecosystem functioning, and effects on ecosystem services (Gallardo & Aldridge, 2013; Pejchar & Mooney, 2009; Strayer & Hillebrand, 2012).

Global change is responsible for an increase in the frequency of extreme weather events such as drought, storms, and heatwaves (IPCC, 2022). These extreme climatic events can influence and even promote invasions (Harris et al., 2018; Robinson et al., 2020). Therefore, it is essential to understand the mechanisms driving the response of invasive species to extreme events, as their biological responses to fluctuating environments may differ from those observed under constant conditions (Gerhard et al., 2023; Kingsolver et al., 2015; Niehaus et al., 2012; Stocker et al., 2024). For example, as demonstrated in **Chapter 5** of this thesis, the timing of heatwaves can have negative effects on performance of larvae of the marine shore crab *Carcinus maenas*, and the effects are not well predicted by the average temperature experienced during development.

Along with other extreme weather events, heatwaves are currently causing social and ecological concerns due to increases in their frequency, duration, and magnitude, in the recent decades (Frölicher et al., 2018; Oliver et al., 2018). Marine heatwaves are defined as periods of five days or more during which sea temperatures exceed a predefined threshold (Hobday et al., 2016). They can potentially facilitate biological invasions through several mechanisms. First, they can favour the establishment of species exhibiting high thermal tolerance (Bates et al., 2013), allowing them to survive and thrive (Robinson et al., 2020; Smith et al., 2023; Sorte et al., 2010). This is particularly true for invaders in a lag phase or those already established but unable to outcompete native species under typical environmental conditions (Atkinson et al., 2020). Models predict that years characterised by marine heatwaves should contribute to sustain populations at the distribution limit by opening phenological windows of opportunity (Giménez et al., 2020). Marine heatwaves can also enhance the performance of non-natives while impairing that of native species when non-native species are better at tolerating increased temperature (Espinosa-Novo et al., 2023; Griffith et al., 2021). Indeed, temperatures characterising heatwaves events are likely to exceed the physiological tolerance limits of native species. In environment were interspecific competitive interaction exist, marine heatwaves could therefore reduce the native species competitive abilities (Diez et al., 2012; Gilson et al., 2021; Smith et al., 2023). For instance, experimental studies have demonstrated that under simulated heatwave conditions, invasive seaweed outperformed native species, and invasive clams were less affected than their native competitor (Crespo et al., 2021). Additionally, the performance of invasive oysters remained unaffected under heatwave scenarios (Gilson et al., 2021) and invasive mussels also showed resilience to a +4°C heatwave (Xu et al., 2023). Field studies have further supported these findings, with the emergence of invasive species following extreme heatwave events (Arafeh-Dalmau et al., 2019; Thomsen et al., 2019).

The potential for marine heatwaves to facilitate biological invasions is dependent on several factors. First, the invading organisms must be able to tolerate lower temperatures once conditions return to normal. This is particularly relevant for eurythermal species, which can thrive across a broad thermal range (Smith et al., 2023), as well as for organisms with physiological adaptations that allow them to endure unfavourable environmental conditions, such as hibernation (Spyksma et al., 2024), diapause, or resting stages (Baumgartner & Tarrant, 2017). Second, if the invading organism undergoes multiple life stages, with changes in thermal tolerance during development. This would be the case for organisms where juveniles and adults are less sensitive to cold temperature than earlier stages. Third, if the invading organisms are capable of shifting their thermal habitat, they may also be able to withstand colder temperatures after a heatwave. This could occur, for instance, in amphibians that transition from aquatic to terrestrial habitats, or crabs that move from pelagic to intertidal zones.

A critical question concerns the effect of marine heatwaves on propagules of non-native species which can promote invasion through “propagule pressure” (Simberloff, 2009). For many marine organisms, particularly those with adult benthic stages, pelagic larvae constitute their main source of dispersion, although they are more sensitive to temperature increase than their juvenile and adult counterparts (Pandori & Sorte, 2019). While larvae of native species are known to sustain metapopulation persistence and recovery, those of non-native species are likely to promote poleward range expansion if a new habitat became available through climate change (Giménez et. al. 2020).

Here, we studied the response of larvae from the shore crab *Hemigrapsus sanguineus* to heatwaves characterised by varying intensities, timings, and durations. *H. sanguineus* is a global invader, native to the east coast of Asia that has successfully established populations along the coasts of North America (McDermott, 1991) and North Europe (Dauvin, 2009; Jungblut et al., 2017). In North America the arrival of *H. sanguineus* led to important changes in the benthic community (Gerard et al., 1999) and this species is currently outcompeting another global invader, the European shore crab *Carcinus maenas* (Epifanio, 2013). On the European coast, larvae of *H. sanguineus* appears to benefits form high temperatures where those of the native *C. maenas* struggle to grow (Espinosa-Novo et al., 2023; Giménez et al., 2021). In our experiments, we manipulated three primary components of marine heatwaves (Hobday et al., 2016), i.e., intensity, timing, and duration. In the first experiment, larvae were exposed to warm events, varying in timing and intensity with a duration of 10 days, while in the second experiment, larvae were initially exposed to the baseline temperature and then to warm events of different intensity, starting at different times but all extending until metamorphosis. We also distinguished the effects of heatwave components from general warming effects by comparing performance observed in the experiments with that expected from the average temperature experienced during the same period of development. The latter was computed from experimental treatments where larvae were exposed to constant temperature from hatching to metamorphosis to megalopa. We hypothesise that longer periods of higher temperature, representing longer heatwave events in the field, should increase performance of *H. sanguineus* larvae especially towards the advanced stages as they are known to struggle at low temperatures (Espinosa-Novo, 2023). Moreover, more intense heatwaves could have the potential to “rescue” the organism from the consequences of low temperature experienced earlier in the larval cycle by creating suitable thermal conditions.

MATERIALS & METHODS

The experimental design used in this study follows the one presented in **Chapter 5** (see Fig. 5.1) with the exception that the timing of the second experiment was adjusted to cover the full length of *H. sanguineus* larval phase, that is longer than *Carcinus maenas* larval phase under the same temperature conditions. Because heatwaves are complex phenomena, characterised by many components and by day-to-day changes in temperature, we have chosen not to use the term "heatwave" to describe the idealised warm events simulated in the laboratory. In the experimental literature, the "press and pulse" framework is often used to describe a disturbance in an ecological system (Bender et al., 1984; Harris et al., 2018), and has been applied for the case of flood, drought, and heatwaves (Harris et al., 2018; Lynch & Magoulick, 2016). Here we follow that nomeclature and define a “warm pulse” as those simulated in the first experiment, i.e., a warm event, that is intense but short-term, with temperature conditions returning to the original lower value. In contrast, the term “warm press” will be used in the context of the second experiment, i.e., an event where the warm period continues to occur until the end of the experiment. The term “warm event” was used when referring to both experiments.

Animal collection and husbandry

Four *H. sanguineus* berried females were collected during their reproductive period on the island of Helgoland (German Bight, North Sea: 54°10′53″N, 7°53′10″E) and transported to the laboratory at the Biologische Anstalt Helgoland (AWI, 2023). Each female was housed separately in a 5 L aquarium containing UV-treated, filtered and aerated natural seawater (0.2 µm mesh size, 32 ‰). Aquaria were kept in a 18 °C temperature-controlled room (± 0.5 °C) and subjected to a 12-hour light/dark cycle. The females were fed twice a week, and the water was changed daily to ensure high quality of the water at hatching.

After hatching, larvae were reared in groups of 10 in 60 mL beakers filled with UV-treated filtered and aerated natural seawater (0.2 µm, 32 ‰) and fed daily with freshly hatched *Artemia sp.* nauplii. Daily water changes were conducted before feeding (see Torres et al. 2021 for the complete procedure). Larvae from each of the four females where reared separately (i.e., four separate experiments) in order to account for potential effects associated to the female of origin. All experiments were carried out in temperature-controlled rooms at the selected temperatures, with three replicates beakers per treatment combination.

Experimental design

To differentiate the specific effect of warm events from those attributed to temperature increase, a group of larvae (control) were reared at constant temperatures of 15, 18, 21 and 24 °C for the whole larval phase.

In the first experiment, we studied the effect of warm pulses representing heatwaves of 10 days (shorter than the larval cycle of *H. sanguineus*), mirroring the frequently occurring heatwaves in the German Bight (Giménez et *al*., 2024). Freshly hatched larvae were randomly assigned to a full factorial design with twelve treatment combinations. These treatments consisted of four levels of onset timing (on days 0, 5, 10 and 15 counting from the day-0 of hatching) and three intensities (18, 21 and 24 °C) (see example Fig. 6.1a and Fig. 5.1b of **Chapter 5** for the complete experimental design). Before and after exposure to warm pulses, larvae were kept at 15 °C, reflecting the average early summer water temperature around Helgoland (Fig. 6.1b). This is also the lowest temperature at which *H. sanguineus* larvae have been observed in the field and successfully develop to the megalopa stage (Giménez et al., 2020). This 15 °C baseline differed from the 18 °C conditions in which the adult females were kept, as temperatures in the intertidal zone, where embryos develop, are higher than those of the water column temperature where larvae develop. Overall, this design was based on three replicates beakers, three intensities, four timings and four females (total = 144 beakers).

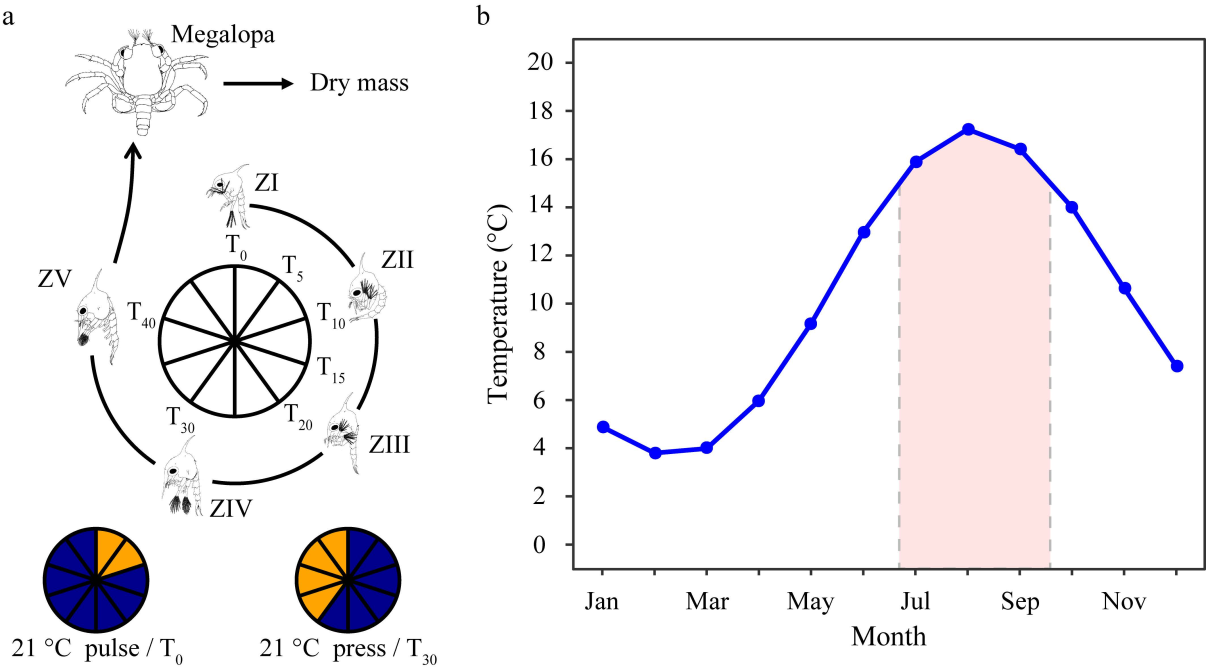

Figure 6.1. Experimental design and *H. sanguineus* larval thermal window **a.** The pie charts represent the complete zoeal cycle of *H. sanguineus*, with each sector corresponding to five days of development. The coloured pie charts illustrate an example of a 21°C warm pulse (left) and warm press (right) event. Larvae were maintained at a baseline temperature of 15°C and exposed to a 21°C warm event, either for 10 days (warm pulses) or until they reached the megalopa stage (warm presses). ZI: Zoea I, ZII: Zoea II, ZIII: Zoea III, ZIV: Zoea IV, ZV: Zoea V. Tx indicates the timing of exposure to the warm event. **b.** The 15°C baseline was chosen based on the seasonal temperature cycle (°C) data at Helgoland (adapted from Fig. 7 of Amorim et al., (2023) and the larval thermal window (red shadow) for *H. sanguineus* according to Giménez et al., (2020).

The second objective was to study the effect of warm presses of progressively longer durations, simulating a situation where longer heatwaves would be encountered by individuals at different times of the larval phase and then experienced until metamorphosis. Larvae were exposed to warm presses of the same intensities as in the previous experiments but with onset on days 0, 10, 20, 30 and 40, and lasted until metamorphosis to megalopa (see Fig. 6.1a for example). Consequently, earlier starts resulted in longer periods of exposure to increased temperature. Warm presses starting on hatching day spanned the entire larval cycle, therefore serving also as control constant temperature. For this experiment, there were three replicates, three intensity levels, five timings, and four females (total = 180 replicate beakers).

We assessed larval performance by measuring survival, development duration, growth, and body mass of the megalopa. Survival rates were monitored through visual inspection of replicate beakers during the daily water change; survival to each stage (zoea II-V and megalopa) were calculated as proportions. Proportions were then transformed into logistic scale. Because logistic scale is defined for positive real number only, proportions were transformed before analysis using the formula defined in **Chapter 5**. Development duration to each stage was evaluated by counting the number of larvae that moulted each day and calculating the average development duration per replicate beaker.

Dry mass was determined with a Sartorius Cubis® MCA2.7S microbalance (± 1µg); megalopa were gently placed on a filter and rinsed with distilled water. After drying off the excess water, each individual was placed in a pre-weighed tin cartridge, frozen at − 20 °C and then freeze-dried for 24 hours (Christ Alpha 1-4 freeze dryer) before weight determination. Dry mass of freshly hatched larvae was also determined based on five replicates of 50 individuals each per female of origin. Dry mass of both freshly hatched larvae and megalopa were used to calculate the instantaneous growth rate using the formula:

$$\frac{\log\left({}^{\mathrm{DW_M}}/_{\mathrm{DW_{ZI}}}\right)}{\mathrm{D}}$$

Where $\mathbf{DW_M}$ is the megalopa dry mass, $\mathbf{DW_{ZI}}$ is the freshly hatched zoea I dry mass, and **D** is the time elapsed from hatching to metamorphosis to megalopa.

When exposed to the 15 °C baseline (experienced in the early-summer) some larvae followed an alternative developmental pathway consisting of six (instead of five) zoeal stages (see Results). In a separate analysis, we quantified the proportion of larvae reaching the megalopa through that long pathway, as the ratio of larvae developing through the long pathway and the total number of larvae that survived to the megalopa stage (either through the long or short pathway). The proportions were then transformed into logarithmic and logistic scales using rescaled values.

Data Analysis

All statistical analyses were conducted under R environment (R Core Team, 2020) with a threshold of significance set at 5 %.

For both experiments, linear mixed effect models (LMMs) were performed separately and model assumptions were confirmed by examining residuals and overdispersion with the DHARMa package (Hartig and Lohse 2022). Model fit was evaluated using a selection process based on the corrected Akaike Information Criterion (AICc) (Zuur et al., 2009). The optimal model was chosen as the one with the lowest AICc value, although, if ΔAICc between any candidate model and the model with the lowest AICc was ≤ 3, both models were compared using likelihood ratio tests (LRT). If the models significantly differed, the one with the lower AICc was selected; if not, the model with fewer parameters was favoured. If the best model failed to validate assumptions, the next best model was selected. To account for data dependency, a model selection based on Restricted Maximum Likelihood (REML) was initially performed to determine appropriate random factors. Given that experiments were conducted across four different females, '♀' was consistently included as a random factor in all models. In the next phase, the model with the best random structure was refitted using Maximum Likelihood (ML), and model selection continued to identify the fixed factors. The full mixed model for all response variables included the fixed factor of temperature intensity interacting with the timing of the warm event.

We also assessed whether the effects of the treatments appeared before the warm event occurred. This was investigated by testing if larval performance in early zoeal stages was correlated to treatment effects before the warm event was experienced (see Supplementary Material: Table S6.1, Fig. S6.1-S6.2).

We quantified if responses to warm events, as defined by their timing and intensity, would differ from those expected under average experimental temperatures. For this purpose, we first calculated the average temperature experienced throughout each replicate. For instance, if an individual larva developed over five days experiencing the sequence of daily temperatures “15-15-20-20-15” (all in °C), the average temperature experienced for this specific replicate would be 17 °C. Second, using this average, we predicted larval performance traits based on LMMs fitted to the control constant temperatures. Last, we compared these expectations with the observed performance during heatwaves using a second LMM. In some cases, variance heterogeneity violated the assumption of homoscedasticity. To address this, a variance heterogeneity term was incorporated into the model's variance structure using the varIdent constructor function, allowing us to account for differences in variance between the expected and observed groups. When assessing larval performance under constant temperature compared to performance during warm events, two scenarios are possible. First, if the performance expected under constant temperature matches those observed under the warm event, any observed changes in larval performance can be directly attributed to the temperature increases. Conversely, if there is a significant difference between the observed and expected outcomes, any changes are linked to the warm event itself (defined by its components). For the warm press experiment, it is important to emphasise that the observed similarity at t_0 for performance traits is anticipated since t_0 represents the baseline constant temperatures of 18, 21, and 24 °C, used to predict values. Consequently, the absence of significant difference between t_0 observation and prediction validates the accuracy of the model in predicting performance.

To illustrate the comparison between warm event conditions and the early summer baseline temperature (i.e., 15 °C), the differences between the performance observed after exposure to the baseline temperature and the one observed after exposure to the warm event were calculated. This comparison was visualised in a heatmap, representing the space of fluctuations in timing and intensity. Larval performance was quantified as survival rates to megalopa and fitness, with fitness calculated as the product of survival and body mass of megalopa. A difference < 0 indicated a positive effect of the warm event on larval performance, while a difference > 0 indicated a negative effect. To differentiate strong positive or negative effects from weak/neutral ones, we defined differences in survival between -0.1 and 0.1, and in fitness between -0.5 and 0.5, as indicative of weak or neutral effects. Values outside these ranges indicated strong effects.

Development through an alternative pathway

At low temperature several larvae developed through two alternative pathways varying in the number of zoeal stages (long: six stages; short: five stages; see results). To better understand responses through the different pathways, we first computed (for both experiments) the proportion of megalopa originated from the long pathway in response to the warm event components. This information helped us to determine if the origin of the megalopa was driven by the event components. Because we found that very few larvae followed the long pathway in the pulse experiment, we focused on the press experiment for subsequent analysis. Hence, for the warm press experiment, we calculated the proportions of ZV either moulting to megalopa, moulting to zoea VI or dying; these quantities helped us to determine if a developmental switch to the long pathway occurred as a stress response to the warm press components at the time when larvae were at the zoea V stage. A switch to the long pathway, characterised by longer developmental time and lower rate of morphogenesis, is interpreted as a stress response where metabolic maintenance and growth are prioritised over morphogenesis (Criales & Anger, 1986; Giménez & Torres, 2002). We also computed the proportion of ZVI moulting to megalopa, to determine the contribution of this pathway to the success in completing the larval phase. Statistical analyses (LMMs) were performed only for the warm press treatments because the warm pulse treatments produced very few megalopa originated from the long pathway (9 out of the 382 individuals).

Once larvae were assigned to the different pathways, a comparison was made between the dry mass of megalopa developing through the different pathways. Due to some combinations of intensity and timing not resulting in any larvae following the long pathway, and because the number of larvae following the latter varied greatly between females, the analysis was conducted in two steps. First, a LMM was applied to dry mass, with the fixed factor 'pathway' (categorical with two levels: long and short) and '♀' as a random factor. Then a second model was tested, including the pathway as a fixed factor interacting with intensity and timing. Only treatments where larvae from both pathways were observed in all three intensities were considered. In both cases, variance heterogeneity violated the assumption of homoscedasticity. LM were therefore transformed into Generalized Least Squares models (GLS) and a variance heterogeneity term was added to the variance structure (i.e., long *vs.* short pathway).

RESULTS

Warm pulse experiment

Survival to megalopa depended on the interactive effect of intensity and timing (Fig. 6.2a; see best model in Table S6.2) while development duration responded additively (Fig. 6.2b, Table S6.2). Survival increased during high intensity and late pulses compared to earlier ones ($p < 0.01$ for time = t_0 *vs.* t_{10} and t_{15}; $p < 0.001$ for t_5 *vs.* t_{10} and t_{15}). Development duration decreased with increasing intensity ($p < 0.001$ for all comparisons) and was lower after a pulse starting at t_{15} as compared to those starting at t_0 ($p < 0.001$) and t_5 ($p < 0.01$). For dry mass, only intensity was retained in the model (Table S6.2) and higher dry mass was observed during intense pulses compared to milder ones ($p < 0.001$ for both intensities) (Fig. 6.2c). In contrast, growth responded to the interacting effect of intensity and timing (Fig. S6.3, Table S6.2). While higher growth rates were observed during intense pulses, late timing (t_{15}) resulted in decreasing growth rates as compared to earlier timing (t_{15} vs. t_0, t_5 and t_{10}: $p < 0.001$ for all three comparisons).

Expectations made for the effects of average temperature experienced throughout the warm pulse on survival, development duration, and growth rates did not always coincide with observations (Fig. 6.2). For survival, intermediate intensity resulted in lower survival after pulses starting at t_0, t_5 and t_{10} ($p < 0.001$ for all three comparisons) compared to the expectations under constant temperature (Fig. 6.2a, Table S6.3). Intense pulses occuring earlier in the larval cycle resulted in lower survival than expected under constant temperature. For development duration (Fig. 6.2b, Table S6.4), differences between expected and observed durations were more pronounced at mild and high intensities, with shorter development than expected under constant average temperature during t_{15} pulse ($p < 0.05$ for 21 °C and $p < 0.001$ for 24 °C). For growth rates, observations diverged from expectations after intermediate pulses starting on t_{15} ($p < 0.001$) as well as after intense pulses starting on t_{10} and t_{15} ($p < 0.001$ for both comparison) with lower growth rate than expected (Fig. S6.3). However, for dry mass, expectations made for the average temperature experienced throughout the warm pulse experiment coincided with observations at all intensities and timings (Fig. 6.2c, Table S6.5) with one exception (low intensity pulses starting on t_0: $p < 0.05$) .

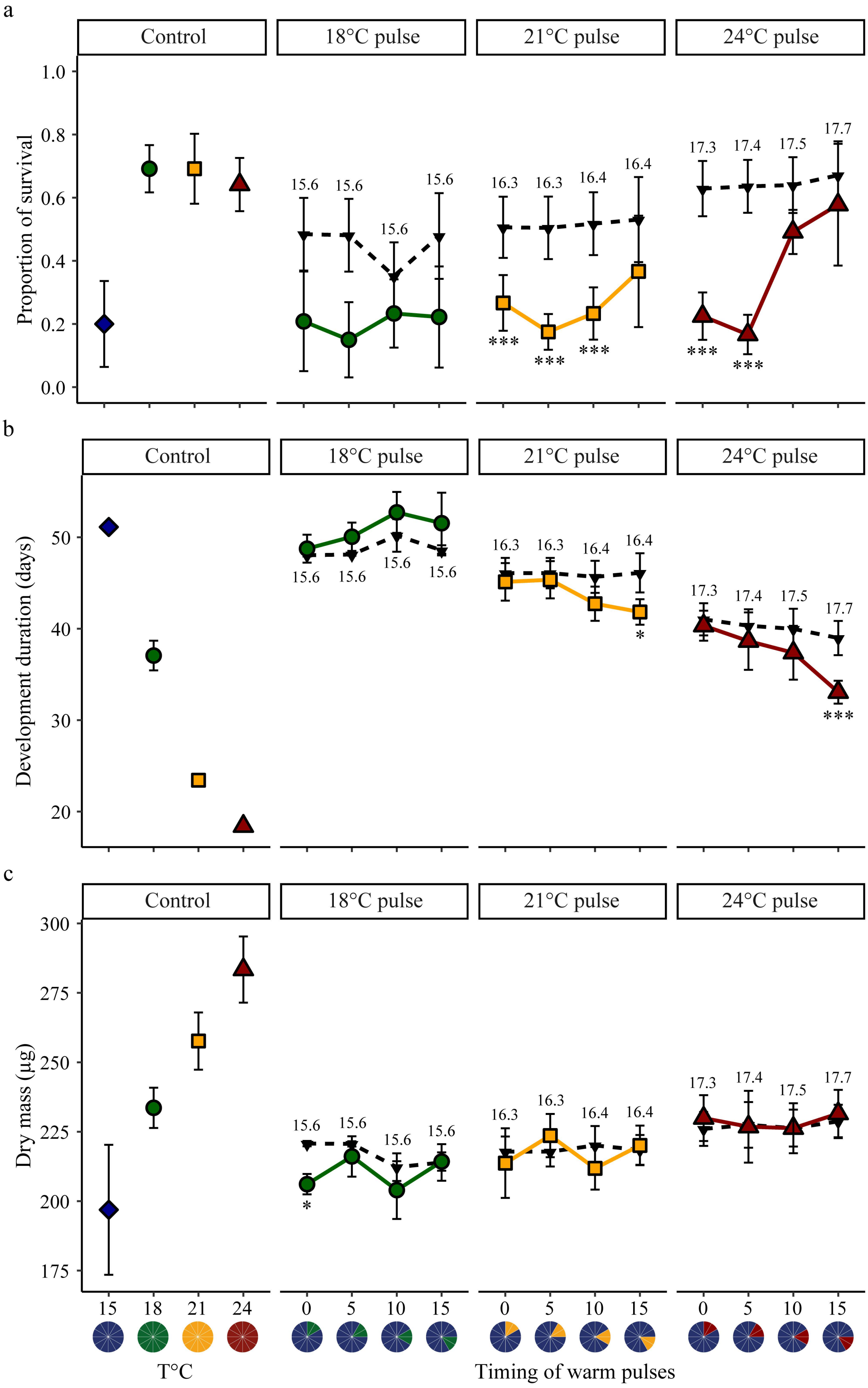

Figure 6.2. Survival rate, development duration, and dry mass after exposure to warm pulses. Comparison between observed (18 °C pulses: ● ; 21 °C pulses: ■ ; 24 °C pulses: ▲) and

expected (▼) values under average temperature experienced throughout the experiment. **a.** Survival rate to megalopa, **b.** development duration from hatching to megalopa and **c.** Megalopa dry mass reared at control constant (left panel) or under warm pulses (right panels). Temperatures: 15 °C ◆, 18 °C ●, 21 °C ■ and 24 °C ▲. Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the average constant temperature experienced (°C) during the warm pulses. Asterisks indicate significant differences between expected and observed values for each treatment. $p < 0.05$*. $p < 0.01$**, $p < 0.001$***. Pie charts indicate control and warm pulse treatments.

Figure 6.3 summarises differences between warm pulses and baseline temperature (15 °C) in survival and fitness. Both heatmaps help to identify a region of high intensities (> 18 °C) and late timing where a warm pulse strongly favoured survival and fitness. No combinations of intensity and timing resulted in a strong negative effect for survival (Fig. 6.3a). Nearly all warm pulses led to higher fitness, except low intensity pulse (18°C) occurring 15 days after hatching (Fig. 6.3b).

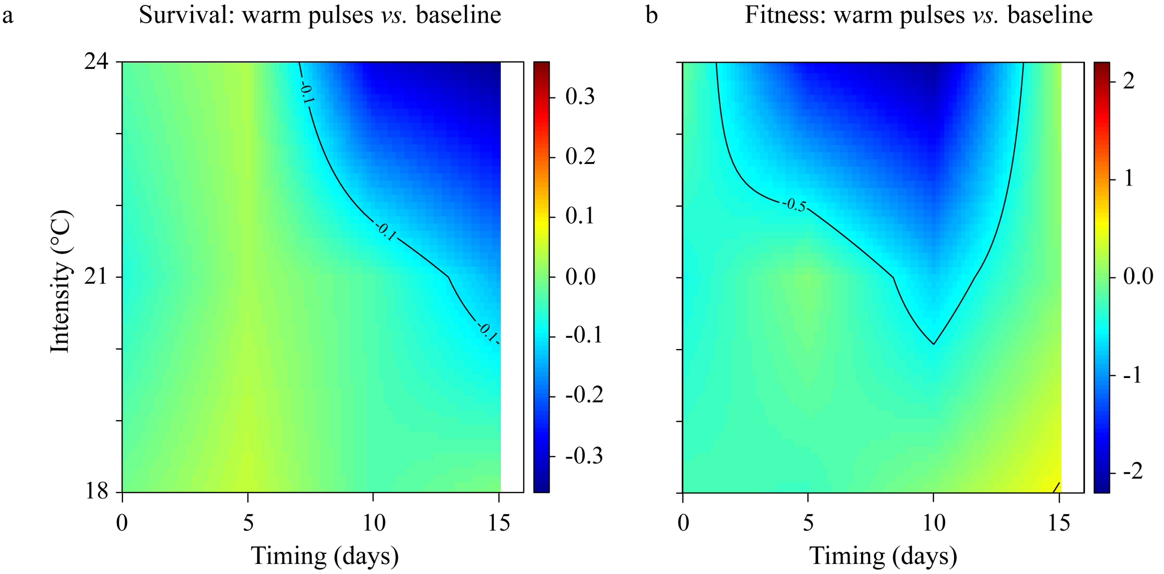

Figure 6.3. Difference in larval survival and fitness between total production at a baseline temperature of 15 °C and the total production during warm pulses. **a.** Survival and **b.** fitness. Fitness is calculated as the total megalopa production (mg). Colour gradient represents the difference: Differences < -0.1 for survival and < -0.5 for fitness indicate a strong positive effect of the warm pulses (i.e., within the region limited by the isoline). Differences ranging between -0.1 and +0.1 for the survival and between -0.5 and +0.5 for the fitness indicate a weak/neutral effect of the warm pulses; differences in that range are not significant. Note: the heatmaps have a narrower colour range than the scale, in order to better visualise the effects which ranged from weak or neutral (green) to positive (blue), and were never strongly negative (red).

Warm press experiment

Survival responded only to the onset timing while development duration, dry mass, and growth rates responded to the interacting effect of timing and intensity (Fig. 6.4; Table S6.6). Survival decreased as the timing of the warm press was delayed, indicating a progressive negative effect of low temperature (from 70 % at t_0 to 30 % at t_{40}, regardless of the intensity). Development duration increased with decreasing intensity and increasing timing, with the shortest observed during intense press starting on t_0 (≈ 18 days ± 0.43) as compared with that observed at t_{40} (≈ 48 days ± 1.05; $p < 0.001$) (Fig. 6.4b). The same pattern was observed during low and intermediate intensities. Dry mass (Fig. 6.4c) was higher after the most intense presses as compared to low and intermediate ones, when presses started at t_0 (24 °C *vs.* 18 °C; $p < 0.001$), t_{10} ($p < 0.001$ for both comparisons), t_{20} ($p < 0.001$ for both comparisons) and t_{30} (24 °C *vs.* 18 °C: $p < 0.001$, 24 °C *vs.* 21 °C; $p < 0.05$). Growth rates increased with increasing intensity while they decreased with later timing (Fig. S6.4).

Expectations made for the effects of the average temperature experienced throughout the warm presses on survival, development duration, and growth coincided with observations in most cases (Fig. 6.4). The exceptions were the t_{40} presses where survival was significantly lower than expected at intermediate and high intensities while development duration was longer than expected for all intensities. For growth, the expectations made for the average temperature did not always coincide with observations, but the differences were negligeable. In contrast, there was a strong mismatch between expected and observed dry mass, with much higher observed dry mass, especially for intense and delayed presses.

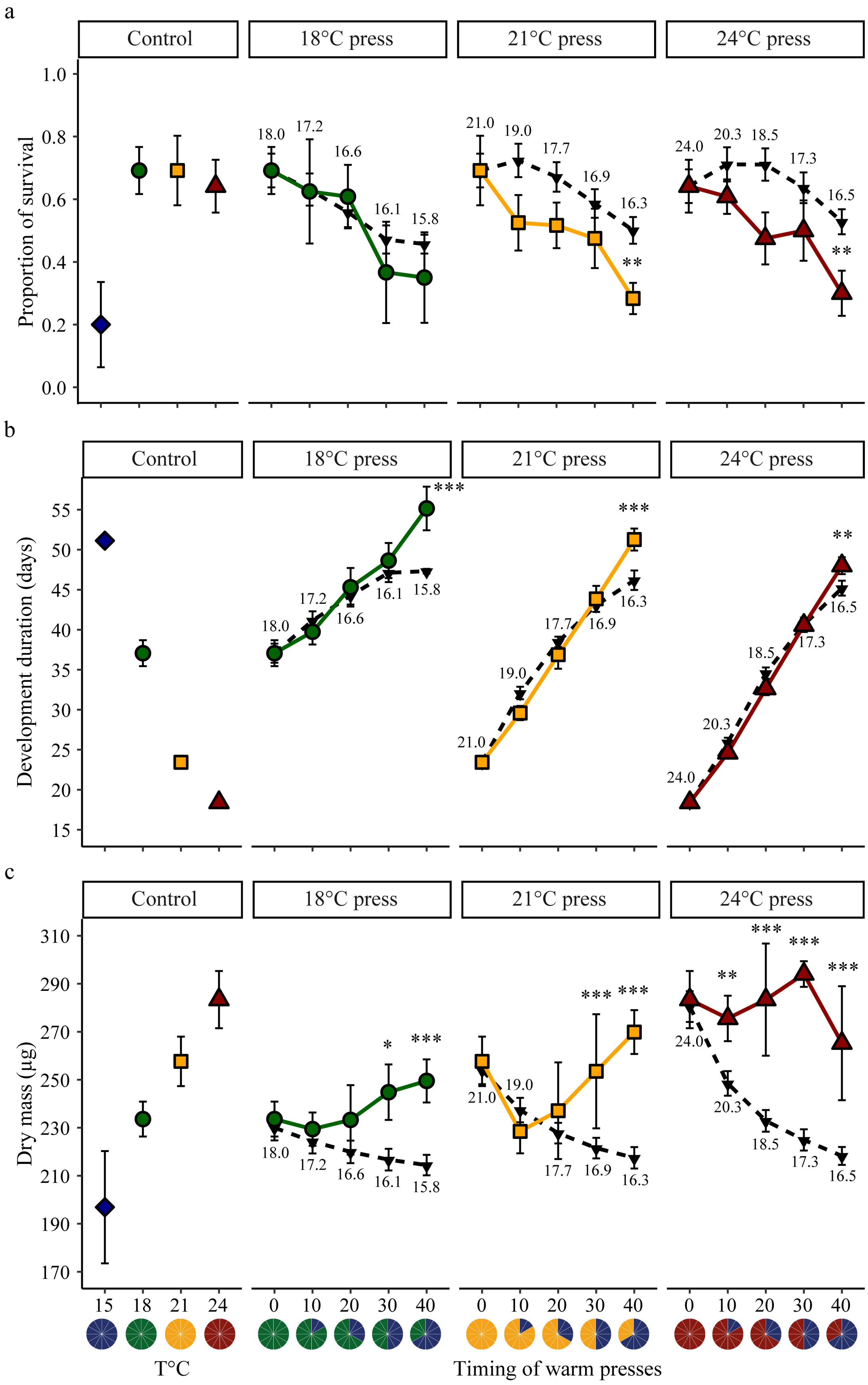

Figure 6.4. Survival rate, development duration, and dry mass after exposure to warm presses. Comparison between observed (18 °C presses: ● ; 21 °C presses: ■ ; 24 °C presses: ▲) and

expected (▼) values under average temperature experienced throughout the warm presses. **a.** Survival rate to megalopa, **b.** development duration from hatching to megalopa and **c.** Megalopa dry mass reared at constant temperature (control, left panel) or under warm presses (right panels). Temperatures: 15 °C ◆ , 18 °C ●, 21 °C ■ and 24 °C ▲. Each point represents the mean value ± standard error for each treatment per female (n = 4). Values above or below the black dotted line represent the average constant temperature experienced (°C) during the warm presses. Asterisks indicate significant differences between expected and observed values for each treatment. $p < 0.05$*. $p < 0.01$**, $p < 0.001$***. Note that each timing 0 is equivalent to the controls (i.e., larvae reared at constant temperatures: 18, 21, and 24 °C; left panel). Pie charts indicate control and warm press treatments.

Figure 6.5 summarises differences between warm presses and baseline temperature (15 °C) in survival and fitness. Early timing favours larvae irrespectively of the intensity. In contrast to the warm pulses, comparison between baseline 15 °C and warm press treatments showed that larval survival (Fig. 6.5a) and fitness (Fig. 6.5b) were higher than under baseline conditions for all combination of timing and intensity.

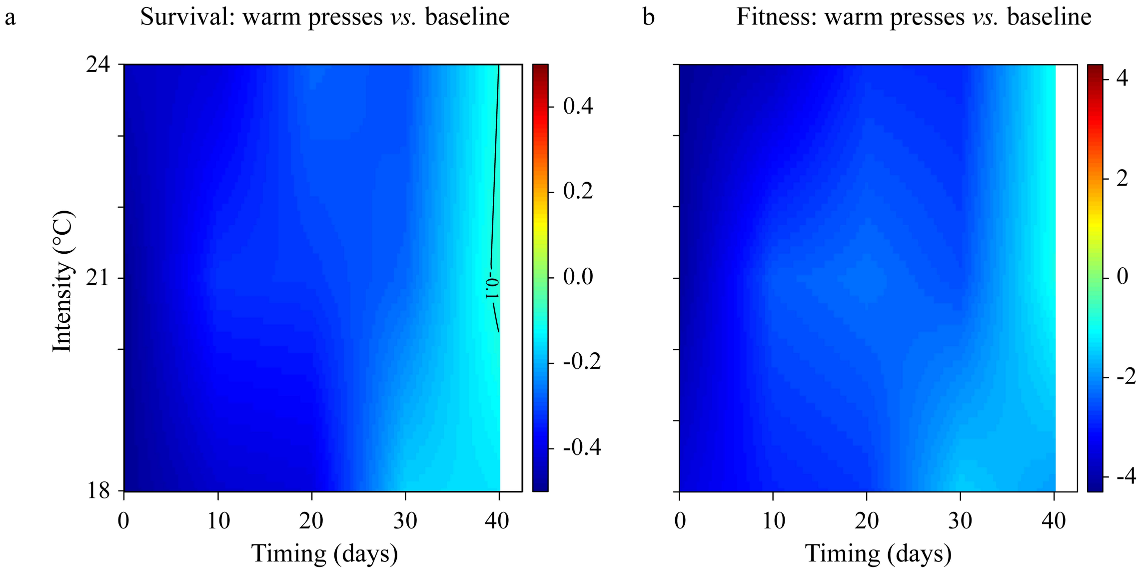

Figure 6.5. Difference in larval survival and fitness between the baseline temperature of 15 °C and warm presses for each combination of timing and intensity. **a.** Survival and **b.** fitness. Fitness is calculated as the total megalopa production (mg). Colour gradient represents the difference: Differences < -0.1 for survival and < -0.5 for fitness indicate a strong positive effect of the warm pulses (i.e., within the region limited by the isoline). Differences ranging between -0.1 and +0.1 for the survival and between -0.5 and +0.5 for the fitness indicate a weak/neutral effect of the warm pulses; differences in that range are not significant. Note: the heatmaps have a narrower colour range than the scale, in order to better visualise the effects which ranged from weak or neutral (green) to positive (blue), and were never strongly negative.

Development through an alternative pathway

Some larvae reached the megalopa stage by developing through an alternative pathway characterised by an additional stage (i.e., zoea VI). The proportion of larvae following the long pathway varied with the timing, intensity, and type of warm event. In the warm pulses experiment (Fig. 6.6a), most larvae followed the short pathway especially if the warm pulse occurred early in development (t_0 and t_5) or if it was of intermediate and high intensity. Few larvae followed the long pathway at other treatment combinations.

In the warm press experiment, the proportion of larvae following the long pathway responded to the timing of the warm press (Fig. 6.6b; Table S6.7: best model did not retain intensity) but varied considerably among larvae from different females (Fig. 6.6b: note standard errors). The response to timing was sigmoidal, with an abrupt increase from t_{10} onwards ($p < 0.01$ for comparison of t_0 *vs.* t_{30} and t_{40}; $p < 0.05$ for comparison of t_{10} *vs.* t_{30} and t_{40}).

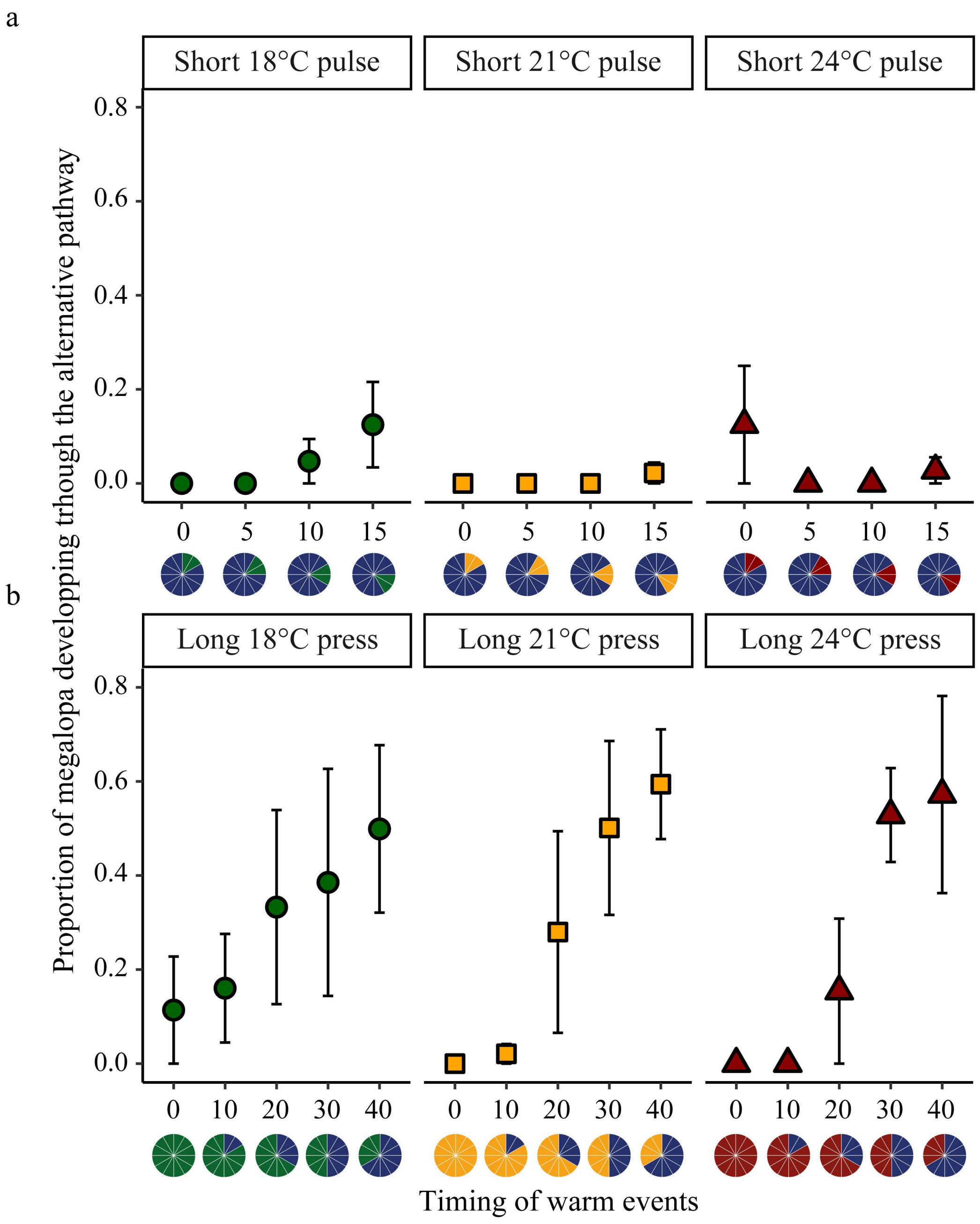

Figure 6.6. Proportion of larvae taking the alternative pathway (i.e., extra zoeal stage: ZVI) to reach the megalopa stage during warm **a.** pulse and **b.** press experiments of different timing and intensity (18 °C: ●, 21 °C: ■ and 24 °C: ▲). Values shown are the mean ± standard error for each replicate within each female (n = 4). Pie charts indicate control and warm event treatments. Note that the slices for warm pulses represent 5 days while the slices for warm presses correspond to 10 days. Statistical analysis was conducted for warm presses only due to insufficient data for the warm pulse experiment.

In the warm press experiment, we computed the proportion of ZV moulting to ZVI (i.e., following the long pathway), to quantify stress responses. This proportion increased with timing and decreased with intensity (Fig. 6.7), while the opposite pattern was found for the proportion of larvae moulting directly to megalopa (i.e., following the short pathway). Hence, more larvae followed the long pathway if temperature was lower or if the onset of the warm press occurred later; those conditions also increased larval mortality. Zoea V followed the long pathway at all timings at 18 °C, but only when the warm press occurred from T_{10} onwards for the 21 °C presses, and from T_{20} onwards for 24 °C. The proportion of ZVI that successfully developed to megalopa (Fig. 6.7) provides a quantification of the contribution of the long pathway towards the success in completing the larval phase. This contribution increased consistently with timing at 18 °C presses, but not for 21 °C and 24 °C presses, where after T_{30}, the proportion decreased again.

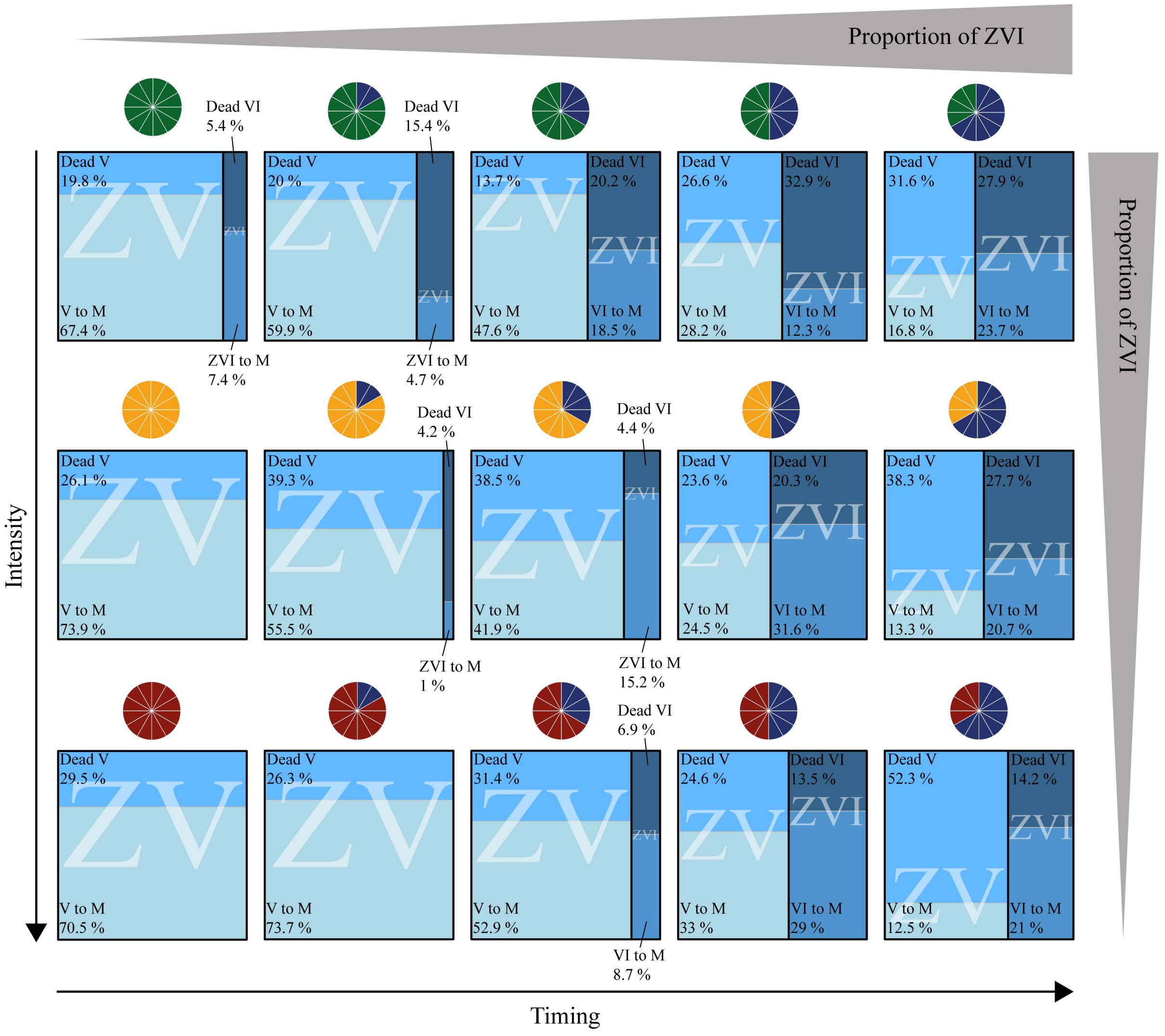

Figure 6.7. Development outcomes of larvae reaching ZV. Proportions of ZV reaching megalopa (■), dying before reaching megalopa and/or ZVI (■), ZVI reaching megalopa (■) and dying before reaching megalopa (■). Pie charts indicate warm press treatments. Note: the proportion of ZVI reaching the megalopa is different from those observed in Fig. 6.6 as they are calculated according to the number of ZV whether than the total number of megalopa.

Dry mass of megalopa (Fig. 6.8) was significantly higher for larvae originating from the long pathway (298.93 ± 2.67 µg) compared to those originating from the short pathway (230.67 ± 4.68 µg, $p < 0.001$). Additionally, for the combinations of timing and intensity that led to at least one larva following the alternative pathway (i.e., T_{20}, T_{30}, T_{40} across all three intensities), the best model included the three-way interaction between timing, intensity, and pathway (Table S6.8). In all cases, dry mass was consistently higher for megalopa from the long pathway, regardless of timing and intensity ($p < 0.001$ for all combinations) (Fig. 6.8).

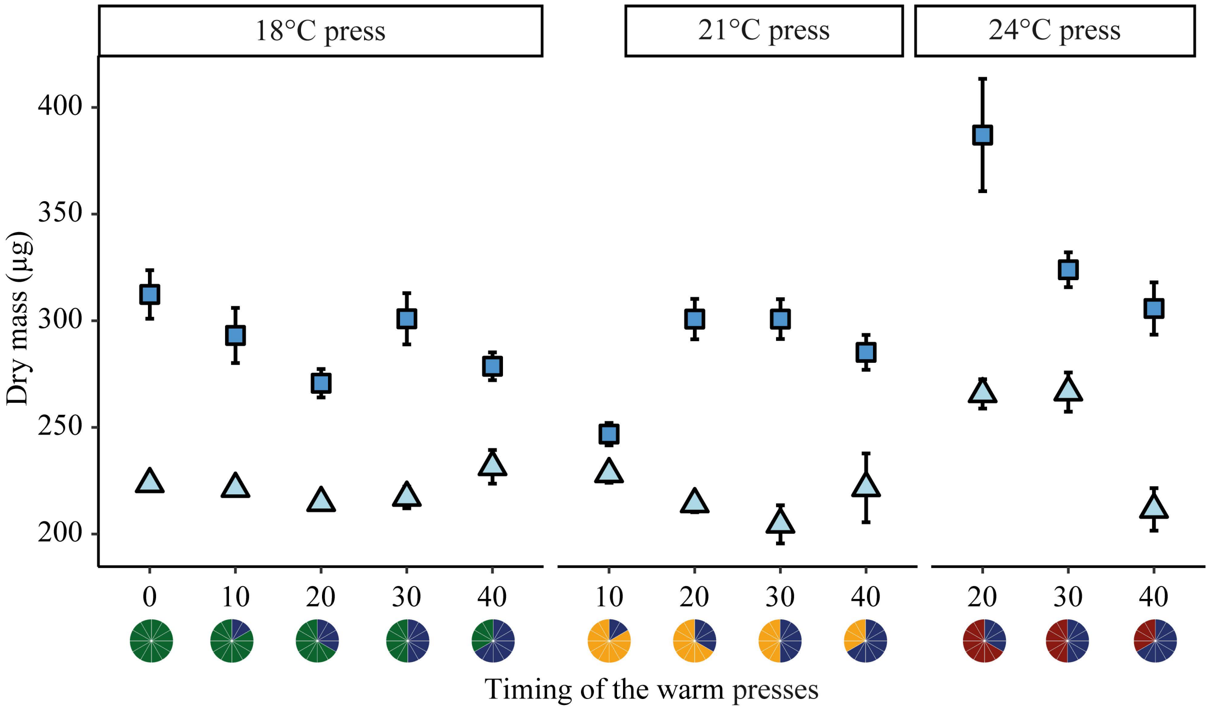

Figure 6.8. Dry mass of megalopa after exposure to warm presses. Comparison between megalopa originating from the short pathway (△) and the long pathway (■). Each point represents the overall mean value ± standard error for each treatment. Pie charts indicate warm press treatments. Note: T_0 21 °C and 24 °C presses, as well as T_{10} 24 °C presses, are not shown due to the absence of megalopa developing through the long pathway.

DISCUSSION

We found that responses of larvae of *H. sanguineus* to warm events cannot always be decomposed into the isolated effects of each component, nor can they be predicted based on the average temperature experienced during development. Additionally, responses to warm events varied among performance traits, sometimes showing counterintuitive patterns where stressful conditions (as quantified by survival) resulted in increased size at metamorphosis which usually reflect more suitable environmental conditions. Comparisons of survival and fitness between larvae exposed to warm pulses and those reared at a 15 °C baseline, indicate improved performance during warm pulses. This positive effect was even more pronounced in the press experiment, where late exposure to a long cold period (20 days after hatching) increased survival considerably compared to the baseline. These findings reveal two distinct mechanisms driving *H. sanguineus* larval response: an ontogenetic pattern in thermal tolerance and developmental plasticity, wherein larvae develop through an alternative pathway and reached higher dry mass at metamorphosis. Understanding these mechanisms is crucial for several reasons. First, they provide insight into the potential responses of *H. sanguineus* in natural settings, illustrating why expectations based on constant condition experiments may not accurately model responses to heatwaves. Second, they highlight the differences in response compared to larvae of the shore crab *C. maenas* (see **Chapter 5**). This is particularly relevant since juveniles and adults of *C. maenas* and *H. sanguineus* coexist and compete along both the European and North American coasts (Jensen et al., 2002; Jungblut et al., 2017). In what follows, we discuss our results in the context of mechanisms and implications for effects of heatwaves.

Ontogenetic patterns in thermal tolerance can explain the failure of average temperatures in predicting the observed performance. Ontogenetic patterns in larvae of *H. sanguineus* have already been identified with regard to osmoregulation (Torres et al., 2021) and those patterns are known for other species with complex life cycles (Uriarte et al., 2019). Indeed, we found that constant temperature could predict the survival observed only during warm events ranging from 21 °C to 24 °C, if they occurred before the 15th day (warm pulses) or after the 30th day (warm presses). The ontogenetic pattern can be observed in the effect of timing on larval performance. In the pulse experiment, intense pulses increased survival, reduced development duration, and increased dry mass only if they occurred later in the larval phase. Conversely, performance dropped to low levels when warm pulses were experienced early in development, regardless of intensity. This indicates that unsuitable thermal conditions encountered later in the larval phase negatively impacted performance.

To understand mechanisms such as stage-dependent thermal tolerance, it is crucial to explore how heatwaves can influence biological time (Giménez, 2023). Indeed, when time is considered on a biological scale (Fig. 6.9, top panels), we observe that *H. sanguineus* low survival occurred when zoea IV stage consistently encountered unsuitable thermal conditions (15 °C). Conversely, when stage IV developed during warm pulses (i.e., t_{10} and t_{15}), survival was higher. If these warm events occurred even later (starting at t_{40}), after stage IV, or if they did not occur at all (constant 15 °C), survival was low (Fig. 6.9, bottom panels). The matching between the warm events and the development through stage IV resulted in a significant contraction of development in stages II-III. This highlights stage IV as a critical stage for ontogenetic development of *H. sanguineus*. In the field, a late heatwave could similarly produce a "rescue effect", reducing larval mortality, and increasing recruitment by shortening overall developmental time and mitigating additional mortality risk present in the pelagic habitat. This aligns with previous studies on *H. sanguineus* suggesting that advanced stages are more sensitive to low temperatures; In the German Bight, the larval thermal range lies between 15 °C (Espinosa-Novo et al., 2023; Giménez et al., 2020), and 27 °C (Deschamps, *pers. obs.*). Such sensitivity to lower temperatures has been proposed as a factor contributing to the poleward limit of *H. sanguineus* distribution in the coast of the USA (Stephenson et al., 2009) and Europe (Giménez et al., 2020).

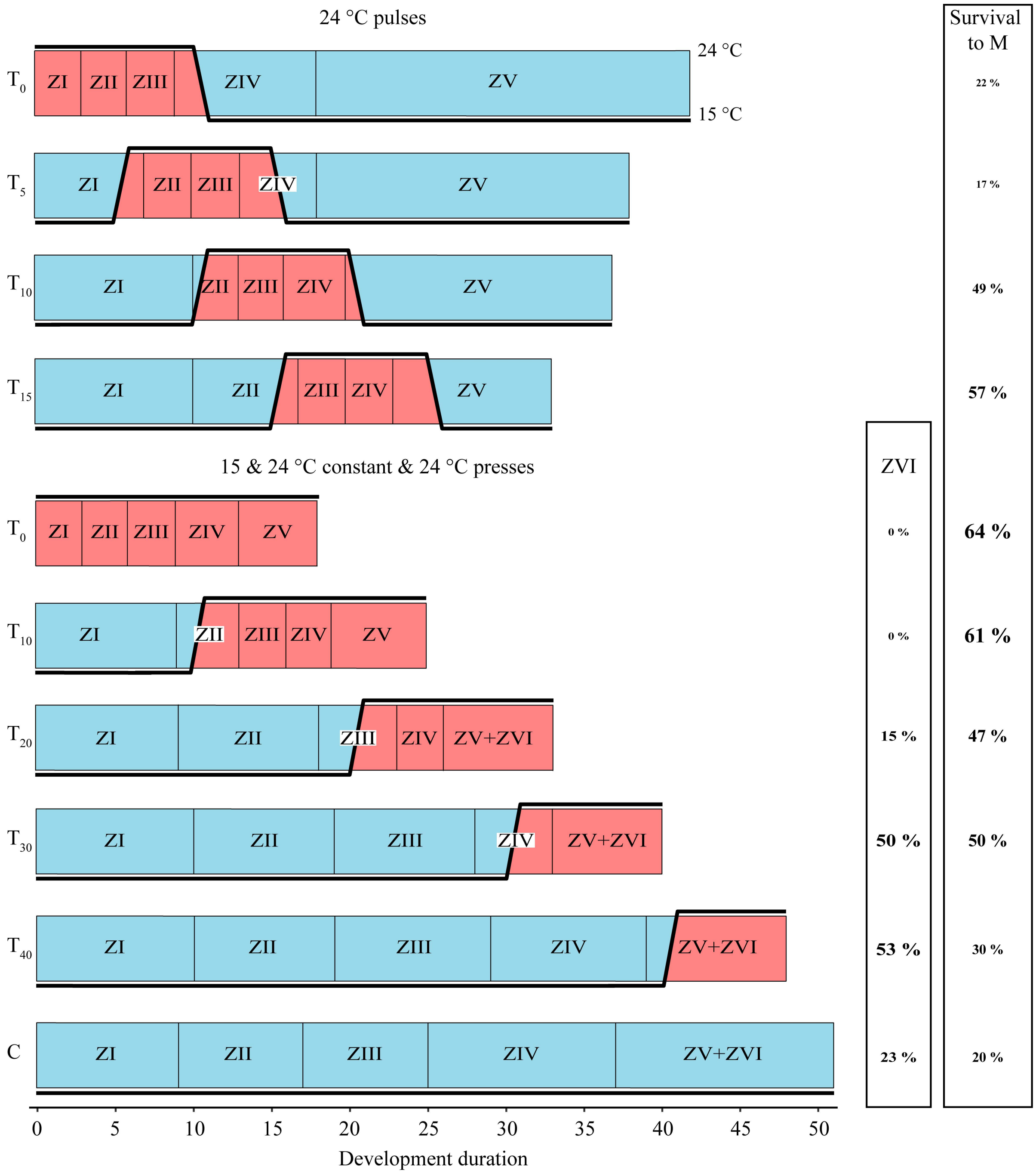

Figure 6.9. Development duration (days) for each stage during 24 °C (red) pulses (top panels), 24°C presses, 24°C and 15°C (blue) constant (bottom panels). Rectangles indicate the development duration. Black lines delimitate the warm event (change from 15 to 24 °C). ZI: zoea I, ZII: zoea II, ZIII: zoea III, ZIV: zoea IV, ZV: zoea V, ZVI: zoea VI. The percentages on the right side indicate the proportion of zoea progressing through the long pathway as well as the survival to the megalopa stage. A decrease in size of the numbers reflects a corresponding decline in percentage.

The second mechanism concerns developmental plasticity, which explains why two indicators of fitness (survival and body mass) were negatively correlated during warm presses, i.e., survival decreased but body mass increased with warm presses experienced later in the larval life. Results from warm presses exceeding 21 °C point towards a threshold between day 10 and day 20 beyond which a mechanism is triggered and larvae develop through the long pathway. Such larvae experienced an extended feeding period, allowing them to accumulate more body mass before metamorphosis; hence, developing through the long pathway, contributed to the overall larval success under low temperatures. At the same time, not all ZVI moulted to megalopa; instead, under intermediate and intense presses conditions, the proportion of surviving megalopa from the long pathway increased only until T_{30}, after which it declined. This suggests that the late onset of the warm presses was insufficient to rescue ZVI larvae from the unsuitable conditions experienced during most of the previous stages.

Switching to alternative developmental pathways occurs in response to stressful conditions in shrimps and crabs (Criales & Anger, 1986; Geißel et al., 2024; Giménez & Torres, 2002; Pestana & Ostrensky, 1995), but also in nematodes, insects, and amphibians (Pfennig, 2021). Hence, this form of developmental plasticity as a mechanism underlying the effects of heatwaves, may not be restricted to *H. sanguineus*. In our experiment, the long pathway was triggered for warm presses when the zoea III developed at 15 °C. This suggests that the mechanism responsible for such switch occurs either at this stage or subsequent stages, as carry over effects. Unfortunately, we were not able to separate larvae at stage III to test this hypothesis. However, our results are consistent with a previous study where larvae of an estuarine crab developing through a longer pathway (triggered in stage III), had higher biomass than those from the shorter pathway (Giménez & Torres, 2002) which directly impacted juvenile body size.

It is important to highlight that had we chosen a different baseline, such as 18°C, which corresponds to mid-summer temperatures in the German Bight (Fig. 6.1), the results would have been notably different. At 18 °C, conditions are optimal for *H. sanguineus*, along with 21 °C, meaning the positive effects of the warm event would have been less pronounced compared to a 15 °C baseline. Additionally, larvae would not have developed through the alternative pathway, as this pathway is typically triggered by unfavourable conditions. However, it is acknowledged that early summer development for *H. sanguineus* can be advantageous. Although developing at 15 °C results in lower survival rates and reduced body mass at the megalopa stage, the megalopa can settle during the peak of summer when temperatures are highest, allowing juveniles to grow faster compared to those developing in mid to late summer (Espinosa-Novo, 2023). Therefore, the occurrence of a marine heatwave at the beginning of summer creates suitable conditions for both larvae and juveniles, as growth will be faster for both stages. Interestingly, a 15 °C baseline represents more than just early summer temperatures in the German Bight; it may also indicate cooler summers where 18°C is never or barely reached, as observed in years like 2012 and 2015 (Giménez, *pers. obs.*). This makes the choice of a 15 °C baseline for *H. sanguineus* more suitable than the 18 °C baseline, as it accounts for both typical early summer conditions and cool summers.

Understanding those mechanisms can help us to better infer the relevance of marine heatwaves in promoting recruitment in *H. sanguineus* as well as the interactions with the competitor *C. maenas*. Because of the combination of stage-specific tolerance and developmental plasticity, late heatwaves could serve as a "rescue factor" for *H. sanguineus* larvae, thereby sustaining recruitment and supporting population growth. For example, a temperature of 15 °C is usually reached by June in the German Bight (Amorim et al., 2023). However, intense marine heatwaves, occurring before June may extend the period enabling successful larval development if larvae were released when temperatures reached 15 °C, at the early-summer (Giménez et al., 2020). Besides, those heatwaves are likely to contract the larval phase further expanding the phenological window, allowing successful larval release and development before temperature drops below 15 °C (Giménez et al., 2020). For example, phenological models predicted an expansion of the phenological window during the long European summer heatwaves of 2018 around the coast of Bergen, Norway (Giménez et al., 2020). Similar effects have been observed in other invasive species (Beck et al., 2024; Ruesink et al., 2005; Spyksma et al., 2024; Wesselmann et al., 2024). Therefore, in regions where cooler water temperatures previously limited invasions by preventing spawning, marine heatwave may now trigger spawning and facilitate the establishment of non-native species as it has been demonstrated for the non-native Pacific oyster, *Magallana gigas* (Beck et al., 2024).

Another aspect is how the same heatwave would impact both *H. sanguineus* and *C. maenas* and balance the rate of recruitment of both species. While late warm pulses caused increased fitness of *H. sanguineus*, the opposite happened for *C. maenas* (Fig. 6.10). Consequently, the two species do not share the same region of the space of fluctuations in intensity and timing where fitness is not compromised (Giménez, 2023). Similar differences in patterns of tolerance may operate on other organisms such as mussels (Xu et al., 2023), clams (Crespo et al., 2021) and oysters (Gilson et al., 2021) with heatwaves favouring invasive over native species. Moreover, *H. sanguineus* can expand its region of existence through developmental plasticity, a trait not observed in *C. maenas*. They do not share the same set of warm events that may be characterised as “extreme”. Marine heatwaves are likely to intensify the existing competition between the two species by increasing the number of individuals incorporated to the existing populations. In principle, species can coexist if the competitive dominant species struggles to colonise habitats (e.g., competition colonisation trade-offs; Miller et al., 2024). However, heatwaves should increase the capacity of *H. sanguineus* to re-colonise habitats. Notably, there are overlaps in diet and habitat use between *H. sanguineus* and *C. maenas* (Jensen et al., 2002), and in some regions, rising densities of *H. sanguineus* have been hypothesised to contribute to the marked decline in *C. maenas* populations (Baillie & Grabowski, 2019; Lohrer & Whitlatch, 2002). Given that marine heatwaves can enhance the survival of *H. sanguineus* while reducing that of C. *maenas*, it is highly possible that these events will further tip the competitive balance in favour of *H. sanguineus*. Additionally, *C. maenas* juveniles experience higher predation rates and stronger aggressive conspecific interactions, including cannibalism pressures (Geburzi et al., 2018; Lohrer & Whitlatch, 2002; Moksnes et al., 1998) compared to *H. sanguineus*. As a result, marine heatwaves may further disadvantage *C. maenas*, accelerating the decline of native populations.

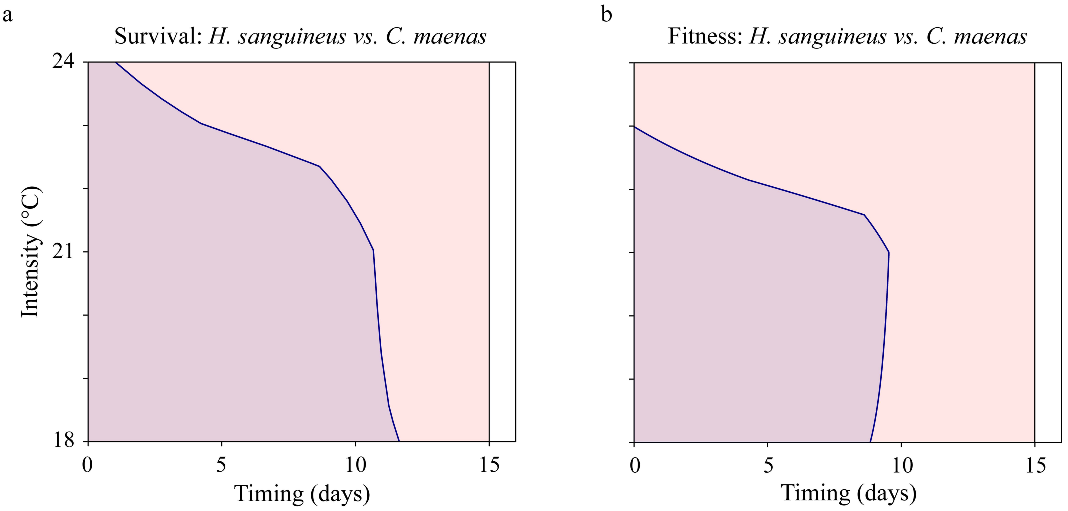

Figure 6.10. Difference between the warm pulse conditions and the 15 °C baseline. Comparison between *H. sanguineus* and its native competitor, *C. maenas* in terms of **a.** survival and **b.** fitness. The regions in red (for *H. sanguineus*) and blue (for *C. maenas*) represent areas where warm pulses had a positive or neutral effect on survival and fitness. Data for *C. maenas* were adapted from **Chapter 5**. Areas outside these regions indicate a strong negative impact of warm pulses on both survival and fitness.

The comparison of *H. sanguineus* and *C. maenas* also highlights differences in how co-existing species may experience a heatwave, when defined by a climatological criterion (e.g., temperatures exceeding a predefined threshold for more than five consecutive days (Hobday et al., 2016)). While in some species, heatwaves may not seriously affect an organismal performance, warm events, not considered as heatwaves, may have important consequences on developmental time and phenology. It is not possible to easily predict responses from experiments keeping organisms under constant conditions because of the mismatch between observations and expectations and the species-specific responses to temperature. In *H. sanguineus*, the threshold beyond which temperature alone cannot accurately predict the impact of a warm event is set at early timings and low temperatures, in contrast to *C. maenas*. Moreover, unlike *C. maenas*, the effect of temperature during the warm event, can be predicted by constant temperature for most of the heatwave scenarios of the German Bight. These findings underscore the importance of understanding the mechanisms by which heatwaves duration, intensity, and timing can shape biological responses of marine organisms, particularly those with complex life cycles.

CONCLUSION

In this study, we demonstrate how the timing, intensity, and duration of idealised heatwaves significantly affect biological processes, leading to diverse responses in the larval development of an invasive species. By analysing the dynamics of heatwaves instead of static conditions, we gain a more accurate understanding of how organisms may react in realistic environmental scenarios. This insight is crucial for developing strategies to manage and mitigate the impacts of invasive species in a context of climate change. As marine heatwaves are predicted to become more prolonged, frequent, and severe, species that are thermally resilient or highly invasive are likely to benefit, often at the expense of native species. Given these expected changes, native species in the German Bight are projected to encounter increased stress, potentially resulting in their competitive exclusion by species such as *H. sanguineus*, which are better adapted to deal and thrive under heatwaves.

Acknowledgments

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SUPPLEMENTARY MATERIAL

Before disturbance effects

A key aspect of the analysis involved assessing whether the effects of the treatments appeared before the disturbance occurred. This was investigated by examining the performance in earlier zoeal stages. The interaction between intensity and timing was retained in the model for all early stages irrespectively of the development duration (Table S6.1).

Table S6.1. Model selection based on AICc for development duration to zoea II (ZII), zoea III (ZIII), to zoea IV (ZIV) and to zoea V (ZV) in response to warm pulses and presses timing (t) and intensity (T °C). Results are shown for linear and logarithmic scales. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

Model selection	**Linear scale**				**Logarithmic scale**			
	ZII	**ZIII**	**ZIV**	**ZV**	**ZII**	**ZIII**	**ZIV**	**ZV**
Warm pulse								
Random factors (REML)								
t × T°C | ♀	647	685	830	917	-294	-397	-319	**-289**
T°C | ♀	256	261	**418**	**561**	-263	-393	**-327**	-258
t | ♀	**304**	**249**	449	597	**-316**	-404	-298	-242
1 | ♀	243	251	432	589	-276	**-405**	-318	-243
Fixed factors (ML)								
t × T°C	**178**	**224**	**411**	**570**	**-390**	**-489**	**-404**	11
t + T°C	283	414	627	638	-182	-221	-137	-57
T°C	294	426	714	633	-171	45	-43	**-95**
t	347	565	643	650	-126	-103	-122	-71
Warm press								
Random factors (REML)								
t × T°C | ♀	359	435	444	446	-350	-498	-584	-655
T°C | ♀	379	577	628	629	-336	-375	-475	-560
t | ♀	**338**	**400**	**419**	**448**	**-374**	**-525**	**-608**	**-676**
1 | ♀	370	566	619	625	-341	-380	-480	-564
Fixed factors (ML)								
t × T°C	**312**	**379**	**400**	**433**	**-466**	**-645**	**-723**	**-784**
t + T°C	385	560	715	792	-269	-272	-248	-268
T°C	393	570	727	804	-261	-264	-237	-256
t	398	632	829	977	-246	-208	-155	-127

During warm pulses, larvae developing to zoea II exhibited no significant differences in development duration at t_{10} and t_{15} warm pulses, regardless of intensity (Fig. S6.1a). Additionally, larvae took the same amount of time to developed at a constant temperature of 15 °C. This pattern may be explained by a "before" effect, as larvae reached zoea II before experiencing the warm pulse (i.e., around 9 days for fluctuations starting at t_{10} and t_{15}), thus remaining under the baseline condition. A similar trend was observed in zoea III, where t_{15} warm pulse led to no significant differences in development duration as well as similar development than observed under 15 °C constant conditions (Fig. S6.1b). Larvae were exposed to the warm pulse for only two days (developing to zoea III in less than 17 days during warm pulses starting at t_{15}), suggesting that larvae require a longer duration of exposure to warmer temperatures to exhibit developmental changes. In contrast, t_{10} warm pulses resulted in shorter development periods at 21 °C and 24 °C. Specifically, development to zoea III under 18 °C pulses starting at t_{10} took 15 days, indicating that approximately 5 days within the warm pulse are necessary to begin observing developmental variations in response to warm pulses. In later zoeal stages (Fig. S6.1c-d), larvae consistently reached specific developmental stages more than five days after the start of the warm pulse. This demonstrates that the effect of the treatment always manifested during or after the exposure.

This pattern was also evident during warm presses. Larvae reached stage II in about 9 days, matching development duration observed at constant 15 °C, with similar duration across intensities during t_{10}, t_{20}, t_{30}, and t_{40} heatwaves (Fig. S6.2a). The pattern remained consistent across all zoeal stages; as larvae progressed to later stages, the number of non-significant timing differences reduced: for zoea III (developing in 19 days), there are no significant differences at t_{20}, t_{30}, and t_{40} (Fig. S2b); for zoea IV (≈ 28 days), differences disappear at t_{30} and t_{40} (Fig. S6.2c); and by zoea V (≈ 39 days), only t_{40} shows no significant difference (Fig. S6.2d).

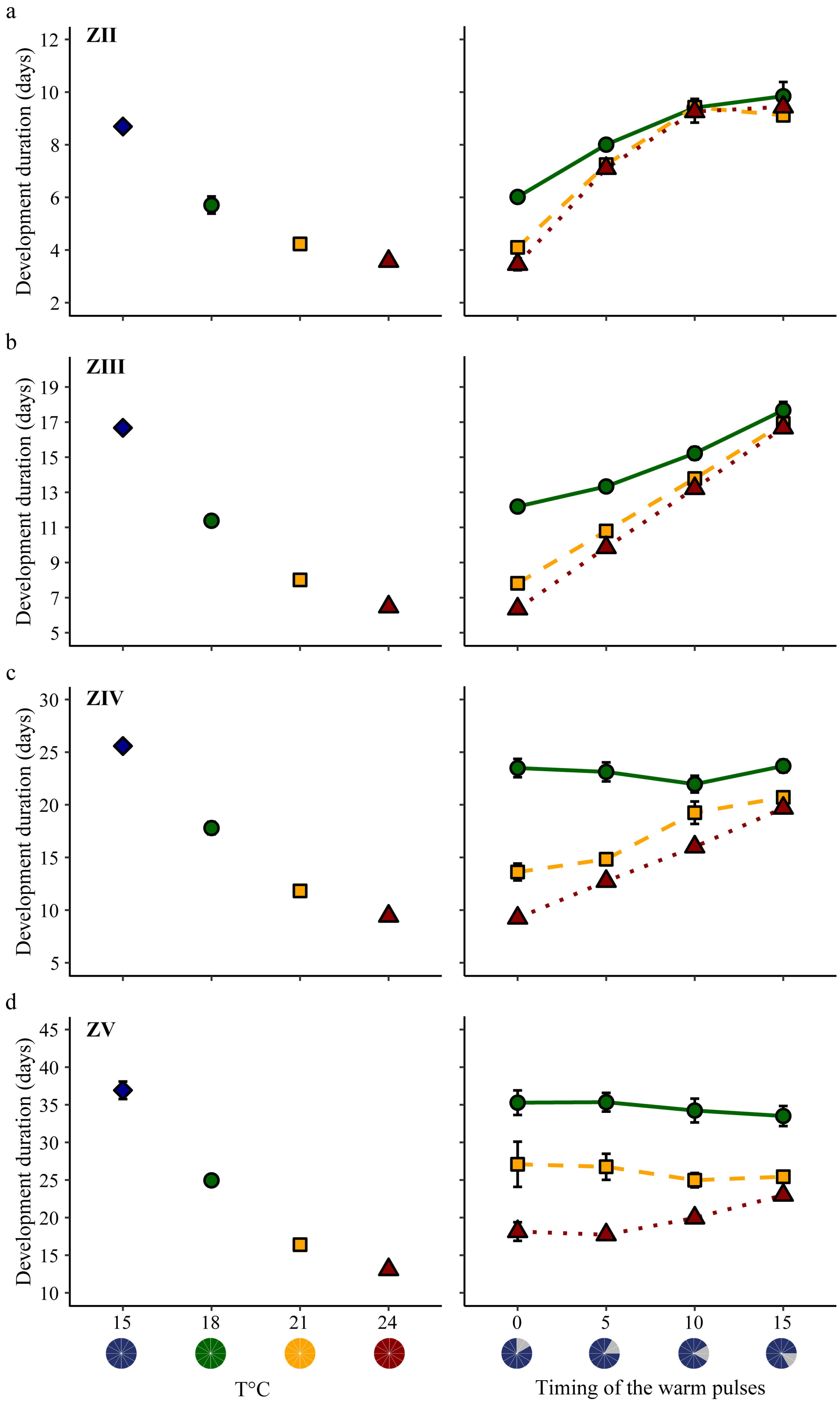

Figure S6.1. Development duration from hatching to **a.** zoea II **b.** zoea III **c.** zoea IV and **d.** zoea V in response to constant control temperature (left panels) and to warm pulses at different timing and temperature (right panel). Values shown are the mean ± standard error for each treatment among the four females of origin. Temperature: 15 °C (◆), 18 °C (●), 21 °C (■), 24 °C (▲).

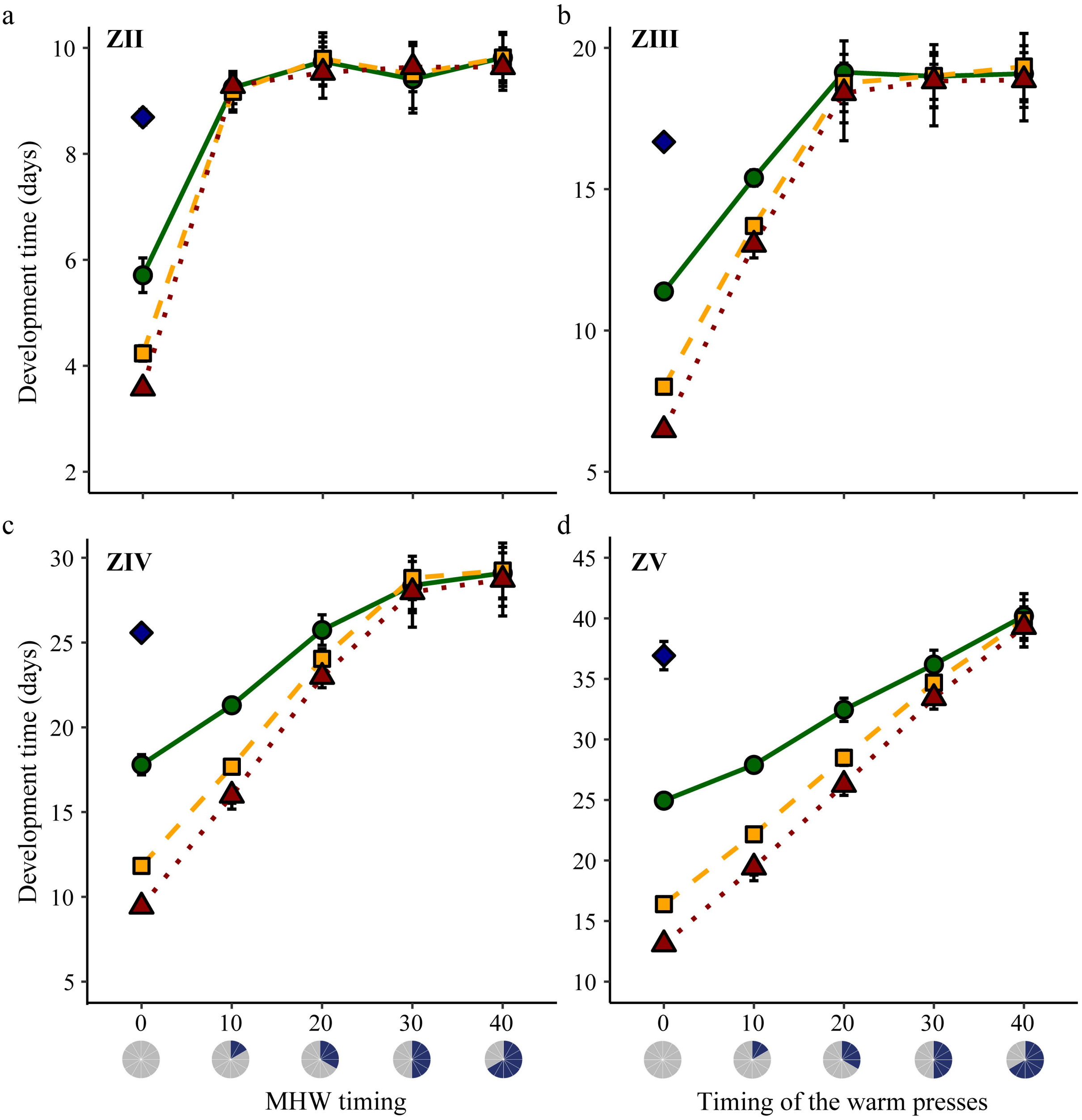

Figure S6.2. Development duration from hatching to **a.** zoea II **b.** to zoea III **c.** to zoea IV and **d.** zoea V in response to warm presses at different timing and temperature. Values shown are the mean ± standard error for each treatment among the four females of origin. Temperature: 15 °C (◆), 18 °C (●), 21 °C (■), 24 °C (▲).

Section II: Post disturbance effects

Table S6.2. Model selection based on AICc for survival from hatching to megalopa, development duration until megalopa, megalopa dry mass, and instantaneous growth rate from hatching to megalopa in response to warm pulse timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales for development, linear and logistic for survival, and linear for dry mass and instantaneous growth rate. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

	Survival rate		**Development duration (days)**		**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model selection	**Linear scale**	**Logistic scale**	**Linear scale**	**Logarithmic scale**	**Linear**	**Linear**
Random factors (REML)						
t × T°C | ♀	430	424	2100	-88	3341	-2186
T°C | ♀	-24	**405**	589	-94	3161	**-2192**
t | ♀	-3	432	597	-103	3161	-2177
1 | ♀	**-22**	410	**575**	**-115**	**3150**	-2183
Fixed factors (ML)						
t × T°C	**-73**	**398**	607	-174	3211	**-2320**
t + T°C	-64	402	**602**	**-178**	3205	-2295
T°C	-42	420	612	-165	**3202**	-2292
t	-66	400	713	-65	3257	-2271

Table S6.3. Model selection based on AICc for proportion of survival comparison between expected and observed (EO) in response to warm pulse and press timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales. Female (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold.

		Warm pulse		**Warm press**	
	Model selection	**Linear scale**	**Logistic scale**	**Linear scale**	**Logistic scale**
T°C prediction	***Random factors (REML)***				
	T°C | ♀	**20**	**165**	**20**	**165**
	1 | ♀	26	169	26	169
	Random factors (REML)				
	t × T°C | ♀	102	817	-674	1744
	T°C | ♀	**-158**	**798**	-581	**1062**
	t | ♀	70	977	**-677**	1246
	1 | ♀	-148	831	-586	1076
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	**-265**	756	-852	**250**
	3 two-way				
	EO × t + EO × T°C + T°C × t	-258	754	**-862**	343
	2 two-way				
	EO × T°C + EO × t	-251	768	-584	573
	EO × T°C + T°C × t	-244	**751**	-861	234
	EO × t + T°C × t	-252	**751**	-857	245
	Two-way				
	EO + T°C × t	-238	749	-856	**241**
	EO × T°C + t	-241	766	-582	569
	EO × t + T°C	-244	766	-579	579
	Additive				
	EO + T°C + t	-233	764	-578	576
	EO + T°C	-212	793	-551	601
	EO + t	-232	764	-469	739
	T°C + t	-102	762	-550	595
	T°C	-88	791	-522	621
	t	-101	762	-439	760
	EO	-210	792	-445	762

Table S6.4. Model selection based on AICc for development duration comparison between expected and observed (EO) in response to warm pulse and press timing (t) and intensity (T°C). Results are shown for linear and logarithmic scales. Female (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions.

	Model selection	Warm pulse		Warm press	
		Linear scale	**Logarithmic scales**	**Linear scale**	**Logarithmic scales**
T°C prediction	***Random factors (REML)***				
	T°C | ♀	**184**	-81	184	-81
	1 | ♀	189	**-82**	**189**	**-82**
	Random factors (REML)				
	t × T°C | ♀	941	-431	1244	-1008
	T°C | ♀	932	-438	**1231**	-1018
	t | ♀	936	-426	1263	-1022
	1 | ♀	**931**	**-431**	1255	**-1022**
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	965	-575	**1242**	-1237
	3 two-way				
	EO × t + EO × T°C + T°C × t	**958**	**-584**	1242	**-1246**
	2 two-way				
	EO × T°C + PO × t	959	-583	1645	-561
	EO × T°C + T°C × t	**956**	-584	1350	-1163
	EO × t + T°C × t	971	-571	1250	-1244
	Two-way				
	EO + T°C × t	966	-574	1350	-1164
	EO × T°C + t	957	-584	1699	-550
	EO × t + T°C	972	-572	1645	-564
	Additive				
	EO + T°C + t	968	-574	1698	-554
	EO + T°C	989	-555	2409	71
	EO + t	1317	-248	1720	-176
	T°C + t	971	-561	1698	-556
	T°C	992	-543	2407	68
	t	1316	-245	1720	-178
	EO	1310	-254	2435	147

Table S6.5. Model selection based on AICc for growth traits comparison between expected and observed (EO) in response to warm pulse and press timing (t) and intensity (T°C). Female (♀) was always included in the model as a random factor. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold.

		Warm pulse		**Warm press**	
	Model selection	**Dry mass**	**Instantaneous growth rate**	**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model for T°C prediction	***Random factors (REML)***				
	T°C | ♀	-230	**-1605**	-230	**-1605**
	1 | ♀	**-231**	-1596	**-231**	-1596
	Random factors (REML)				
	t × T°C | ♀	**4527**	**-5041**	**12807**	**-14054**
	T°C | ♀	4536	-5017	13237	-13440
	t | ♀	4587	-4927	12858	-13885
	1 | ♀	4590	-4918	13236	-13415
	Fixed factors (ML)				
	Three-way				
	EO × T°C × t	4594	-5315	**12909**	**-14397**
	3 two-way				
	EO × t + EO × T°C + T°C × t	**4588**	**-5317**	12922	-14389
	2 two-way				
	EO × T°C + PO × t	4588	-5317	13079	-14240
	EO × T°C + T°C × t	4584	-5312	13029	-14276
	EO × t + T°C × t	4597	-5272	12966	-14358
	Two-way				
	EO + T°C × t	4595	-5261	13066	-14245
	EO × T°C + t	4585	-5312	13186	-14126
	EO × t + T°C	4598	-5151	13123	-14209
	Additive				
	EO + T°C + t	4596	-5261	13224	-14096
	EO + T°C	4593	-5264	13288	-14032
	EO + t	4627	-5241	13268	-14056
	T°C + t	4597	-5145	13344	-13985
	T°C	4594	-5149	13409	-13921
	t	4628	-5125	13388	-13945
	EO	4623	-5245	13336	-13989

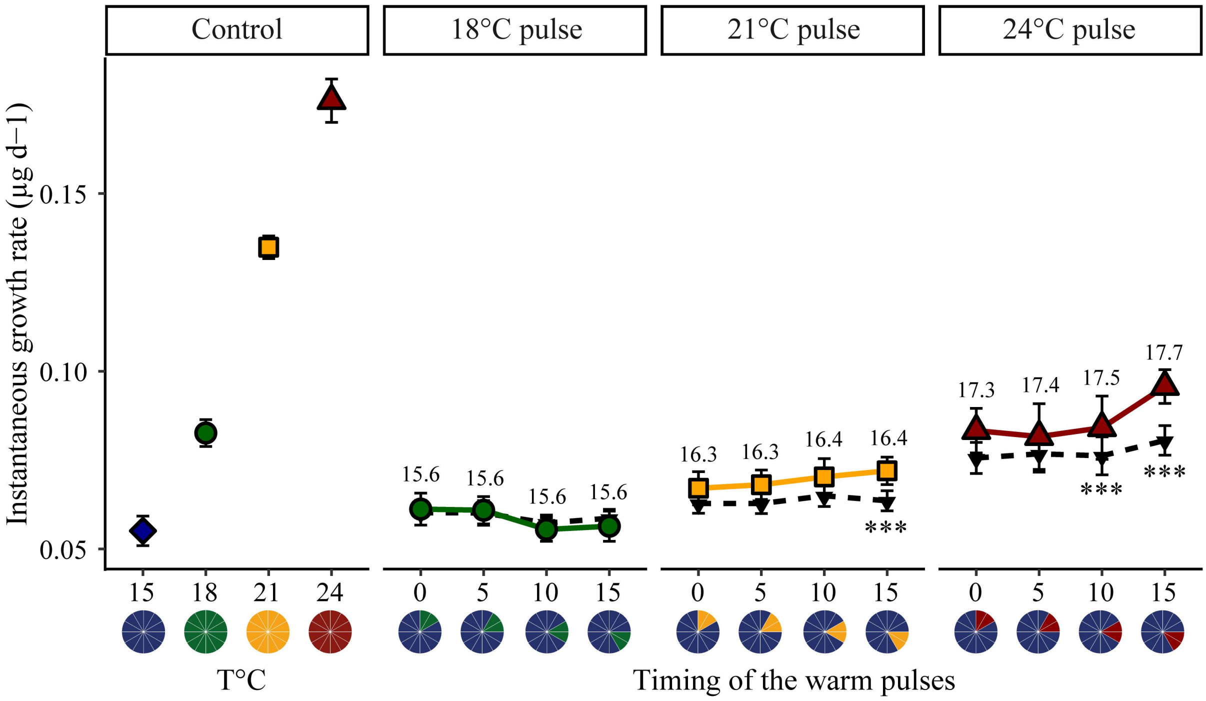

Figure S6.3. Comparison between observed growth rates during warm pulses (18 °C (●), 21 °C (■) and 24 °C (▲)) and expected growth rates if temperature was constant throughout the whole experiment (▼). Values shown are the mean ± standard error for each replicate within each female (n = 4). Values above the expected growth rate represents the average temperature (°C) experienced during the warm pulse. **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

Table S6.6. Model selection based on AICc for survival from hatching to megalopa, development duration until megalopa, megalopa dry mass, and instantaneous growth rate from hatching to megalopa in response to warm press timing (t) and intensity (T°C). Results are shown for linear and logistic scales for survival, linear and logarithmic scales for development, and linear scales for dry mass and instantaneous growth rate. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

	Survival rate		**Development duration (days)**		**Dry mass (µg × ind^{-1})**	**Instantaneous growth rate (day^{-1})**
Model selection	**Linear scale**	**Logarithmic scale**	**Linear scale**	**Logarithmic scale**	**Linear**	**Linear**
Random factors (REML)						
t × T°C | ♀	77	600	680	-437	9379	**-6262**
T°C | ♀	**47**	**569**	**681**	**-447**	**9434**	-6199
t | ♀	98	620	721	-437	9379	-6230
1 | ♀	62	584	714	-436	9437	-6181
Fixed factors (ML)						
t × T°C	-6	564	**691**	**-557**	**9520**	**-6423**
t + T°C	-17	554	801	-285	9523	-6296
T°C	31	599	248	67	9548	-623
t	**-22**	**549**	808	-277	9538	-6255

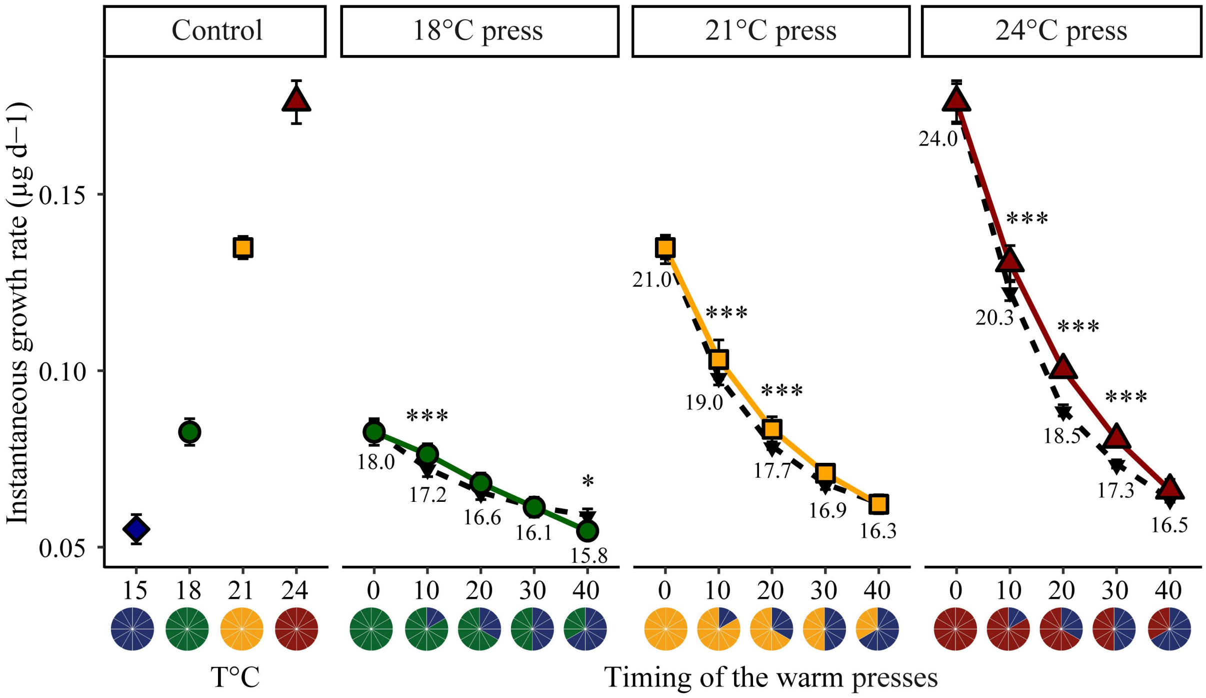

Figure S6.4. Comparison between observed growth rates during warm presses (18 °C (●), 21 °C (■) and 24 °C (▲)) and expected growth rates if temperature was constant throughout the whole experiment (▼). Values shown are the mean ± standard error for each replicate within each female (n = 4). Values above the expected growth rate represents the average temperature (°C) experienced during the press. **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

Table S6.7. Model selection based on AICc for the proportion of larvae going following an alternative pathway (zoea VI) in response to warm press timing (t) and intensity (T°C). Results are shown for linear, logarithmic, and logistic scales. Model selection was performed using Restricted Maximum Likelihood (REML) and Maximum Likelihood (ML), for random and fixed factors respectively. The bests models are indicated in bold. Red indicates violation of model assumptions. Female of origin (♀) was always included in the model as a random factor.

	Proportion of ZVI		
Model selection	**Linear scale**	**Logarithmic scale**	**Logistic scale**
t × T°C | ♀	**50**	**406**	**566**
T°C | ♀	62	426	577
t | ♀	51	438	**581**
1 | ♀	71	444	596
t × T°C	8	387	557
t + T°C	-8	x	550
T°C	-4	386	561
t	-11	**380**	**548**

Table S6.8. Model selection based on AICc for megalopa dry mass comparison between long and short pathways (P) in response to warm press timing (t) and intensity (T°C). Only the combination of timing and intensity resulting in at least one megalopa following the long pathway were included in the model (i.e., T_{20}, T_{30}, T_{40}). The bests models are indicated in bold.

Model selection	
Three-way	
P × T°C × t	**4572**
3 two-way	
P × t + P × T°C + T°C × t	4611
2 two-way	
P × T°C + P × t	4654
P × T°C + T°C × t	462
P × t + T°C × t	4626
Two-way	
P + T°C × t	4637
P × T°C + t	4665
P × t + T°C	4667
Additive	
P + T°C + t	4709
P + T°C	4709
P + t	4786
T°C + t	4930
T°C	4935
t	4976
P	4787

CHAPTER

7

GENERAL DISCUSSION
&
CONCLUSION

1. Results Overview

The overall goal of this thesis was to investigate the impact of marine heatwaves (MHWs) on zooplankton community dynamics and larval performance of decapod crustaceans within the North Sea ecosystem, using field observations and laboratory experiments. The thesis was structured into two distinct sections, each focusing on specific objectives and methodological approaches. In what follows, a general overview of the results will be presented separately for each section and then discussed collectively in the subsequent sections.

1.1. Quantification of MHW impacts on the North Sea mesozooplankton community

The focus of the first section was on the community level, with the objective of quantifying the season-specific impact of MHWs on zooplankton community dynamics in the North Sea. The key findings of this analysis can be summarised as follows: the response of mesozooplankton varied depending on the season in which the MHWs occurred. Most changes in abundance and community structure were observed in spring and autumn, while no MHW impacts were detected in summer and winter, highlighting the importance of examining MHW effects on a seasonal basis, particularly for communities shaped by seasonal variations. The taxa most affected were copepods, which generally responded positively to MHWs. Interestingly, copepods were unable to consistently adjust their phenology in response to MHWs occurring before their typical annual bloom, and therefore experienced an increased number of MHWs days and MHW intensity over time. This increase occurred mainly after the 1990s; therefore, before that time copepods rarely encountered MHWs. Post-1990, the environment became more prone to MHWs, which could have contributed to the observed increase in copepod abundances.

Although MHWs occurring before the bloom did not significantly alter the timing of the bloom for the majority of the taxa, they did affect the bloom durations of nearly all taxa. Several MHW components, including the maximum temperature increase rate, the proportion of MHW days within the bloom, and the MHW intensity, influenced these bloom durations. Prolonged blooms were associated with higher MHWs intensity, while shorter blooms were linked to an increase in the proportion of MHWs days and a higher temperature increase rate. These shifts in timing could have repercussions on higher trophic levels, such as fish larvae and decapod crustacean larvae (e.g., *C. maenas* and *H. sanguineus*), for which copepods are generally considered a high-quality nutritional resource (Anger, 2001; Drillet et al., 2006; Støttrup, 2003).

1.2. MHW effects on larval performance

The second section focused on the individual level, with the goal of understanding how key components of MHWs impact the larval performance and population dynamics of two competing decapod crustaceans in the North Sea: the native shore crab (*Carcinus maenas*) and the invasive Asian shore crab (*Hemigrapsus sanguineus*). Both species overlap in diet and habitat use (Jensen et al., 2002). For instance, *H. sanguineus* demonstrates a strong dominance over *C. maenas* in competition for rock shelters, with the occupancy of *C. maenas* juveniles decreasing by 75 % in areas where *H. sanguineus* is present (Epifanio, 2013). In terms of diet, both *H. sanguineus* and *C. maenas* juveniles show similar preferences, such as feeding on mussels, with *H. sanguineus* exhibiting a higher predation efficiency (Epifanio, 2013). The competitive advantage of *H. sanguineus* is further evident in regions like the Gulf of Maine and southern New England, where increasing densities of this invasive species has been hypothesised to contribute to the marked decline in *C. maenas* populations (Baillie & Grabowski, 2019; Lohrer & Whitlatch, 2002). Beyond competition, *C. maenas* juveniles also face higher predation rates by *H. sanguineus* and increased aggressive interactions with their conspecifics, including cannibalism (Geburzi et al., 2018; Lohrer & Whitlatch, 2002; Moksnes et al., 1998). These additional pressures may intensify the competition between the two species, further reducing *C. maenas* numbers.

The main findings revealed several significant insights. First, regardless of the species, the effects of warm events (experimental heatwaves), defined by their intensity, duration, and timing, could not always be predicted based on larval performance under constant but elevated temperatures. This highlights that the effects of MHWs on larval performance are markedly different from those of long-term warming. Second, MHW components acted in combination, and yielded different outcomes depending on the specific conditions of the MHWs components and the species, emphasising the importance of studying these components collectively rather than in isolation. For *C. maenas*, exposure to intense and/or late warm events led to a significant decrease in survival rates, developmental duration to the megalopa stage, and megalopa dry mass. Interestingly, when the event occurred later in the larval phase, the effects were even more pronounced, with even low-intensity MHWs leading to a decrease in larval performance. In contrast, *H. sanguineus* appeared to benefit from warm events, with positive effects on larval performance, particularly when the heatwave coincided with the zoea IV. Interestingly, prolonged exposure to colder temperatures preceding the MHWs, triggered an alternative developmental pathway, characterised by an additional stage before reaching the megalopa. Last, the contrasting responses of the two species (*H. sanguineus* thriving under heatwaves while *C. maenas* suffered) suggest that intense and/or late MHWs may promote the biological invasion of the invasive *H. sanguineus* at the expense of the native *C. maenas*.

2. Timing is everything: individual and community-level timing

One of the key findings of this thesis is the critical role that MHW timing plays in shaping organism and community responses. The thesis demonstrates that the timing can significantly affect organisms, not only in relation to seasonal temperature fluctuations but also in relation to organism phenology and its biological clock (Giménez, 2023). Therefore, the understanding of MHW impacts on biological systems will require a temporally explicit approach that examines not only the frequency, duration, and intensity of these events but also their timing, depending on the time scale of the system studied. This will provide deeper insights into how the occurrence of MHWs influences marine ecosystems based on when they occur.

2.1. Seasonal timing

The ecological effects of MHWs will depend on when the event occurs in species with seasonal cycles. Indeed, one of the key hypotheses linking the timing of extreme climatic events with population dynamics is that for organisms closely synchronised with environmental conditions, the impact of the event will depend largely on when it occurs (Cinto Mejía & Wetzel, 2023). Additionally, highly synchronised populations tend to follow cyclical patterns (i.e., seasonality), meaning the effect of the event will vary depending on whether it occurs during the growth, decline, or peak phase of the population cycle (Cinto Mejía & Wetzel, 2023). This is particularly true for zooplankton, whose response to rising temperatures depends not only on the magnitude of the change but also on its seasonal timing. Key life cycle events, such as the emergence of resting eggs, development, and moulting, are highly sensitive to temperature fluctuations and are tightly linked to other environmental factors such as light availability and food supply (Mackas et al., 2012).

Most studies investigating the impact of MHWs on communities and organisms have predominantly focused on summer extremes, as these events are often associated with temperatures exceeding species' thermal tolerance limits. **Chapters 3** and **4** of this thesis revealed that MHWs in both winter and summer showed no significant evidence of altering mesozooplankton community structure in the North Sea. Instead, the most notable changes occurred during spring and autumn MHWs, with shifts in community structure and increases in the abundance of various taxa, including copepods. These findings highlight spring and autumn as crucial time windows for MHW effect on zooplankton community.

These results emphasise that MHWs, while usually studied as a stressful event for the organisms, are not always destructive (Turner et al., 1998) as they affect organisms mostly through positive or neutral effects (Harvey et al., 2022). For instance, MHWs occurring in spring and summer appeared to be beneficial to most copepods of the North Sea. Beneficial effects may be explained by several reasons: (1) Because the temperatures during these MHWs are unlikely to exceed the upper thermal limit. Maximum temperatures during spring and autumn MHWs (14 °C and 19.4 °C, respectively, Deschamps *pers. obs.*) were below the thermal tolerance limit of taxa at Helgoland Roads (e.g., *T. longicornis*: ~ 22.5 °C: Halsband-Lenk et al., 2002; *Acartia tonsa* and *A. clausii*: ~ 26 °C: (González, 1974). (2) These seasons are characterised by major changes in the zooplankton production in the North Sea (Quante et al., 2016). The spring season brings higher concentrations of dissolved inorganic nutrients, increased temperatures, and more sunlight, all of which promote phytoplankton growth and result in a large phytoplankton bloom (Wiltshire et al., 2008). This surge in food availability triggers a subsequent rise in zooplankton production, leading to a zooplankton bloom that follows the phytoplankton bloom. In contrast, during autumn, light slowly decreases and lower temperatures cause a decline in phytoplankton levels, which in turn reduces zooplankton populations. As a result, MHWs may enhance growth rates in spring, while in autumn, they may slow down the decline phase.

By showing evidence of the importance of seasonal timing in shaping zooplankton responses to MHW events, **Chapter 3** also indirectly highlights the importance of the synchrony between MHWs and other environmental parameters necessary for zooplankton growth. While MHWs characterised by temperatures within the organism’s thermal range might create favourable thermal conditions for zooplankton development, factors such as limited food and light availability will still constrain their growth (van Beusekom & Diel-Christiansen, 2009). As a result, even with suitable temperatures, a winter MHW is unlikely to impact the mesozooplankton community as the photoperiod will always limit the development of the species (Beaugrand & Kirby, 2018) and its associated food resources (e.g., phytoplankton). These findings also underscore the need to differentiate between long-term warming and MHWs as distinct phenomena. Indeed, Wiltshire & Manly, (2004) and later (Sommer & Lewandowska, 2011) suggested that warming could enhance the survival of herbivorous copepods, leading to higher densities and potentially delaying the phytoplankton bloom. However, the findings from **Chapters 3** and **4**, which indicate that winter MHWs did not affect copepod phenology nor alter the mesozooplankton community structure and abundance, do not align with this hypothesis. This discrepancy likely arises because the effects of MHWs differ substantially from those of sustained warming. As shown in **Chapters 5** and **6**, increased but constant temperature yields different outcomes compared to MHW conditions. A discrete event of increasing temperature, followed by a return to typical cold winter temperatures, may not be sufficient to significantly enhance copepod densities. Additionally, it is crucial to note that the hypothesis of increased grazing pressure during winter warming is not universally accepted; some studies, such as Wiltshire et al. (2008), have found no significant change in copepod winter density over time nor any effect of temperature on these densities, which aligns with the findings of **Block I** of this thesis.

The link between heatwaves' timing and synchrony with other environmental parameters has already been shown in freshwater crustacean zooplankton communities where the response to heatwave events was dependent on the timing of the temperature increase (Huber et al., 2010). When heatwaves occurred shortly before or after the clear-water phase (i.e., the period of food limitation for crustacean zooplankton) the success of summer cyclopoid copepods and bosminids increased (Huber et al., 2010), highlighting that the timing of the heatwave created suitable environmental conditions and enhanced the growth of the organisms.

2.2. Ontogenetic timing

In addition to its seasonal timing, MHWs effects also depend on when the event occurs during the development of an organism. **Chapters 5** and **6** demonstrated that MHWs can influence the larval performance of decapod crustacean larvae, but the strength and direction of these effects will vary based on the timing of the event within the larval stages. For *C. maenas* and *H. sanguineus*, the timing at which intense MHWs impacted survival and fitness differed, yet showed some similarities. Survival of *C. maenas* larvae decreased with later timing, while the opposite pattern was observed for *H. sanguineus* (Fig. 7.1). These findings indicate a stage-specific sensitivity to MHWs that determines the timing of susceptibility during development. In both species, stage ZIV seems to be a critical period of vulnerability, as survival rates fluctuate depending on whether this stage overlaps with or falls outside the MHW (Fig. 7.1). For larvae of *C. maenas*, which have a thermal tolerance ranging from 10 to 25 °C (deRivera et al., 2007) and thrive at 15 °C, a MHW during stage IV results in reduced survival and fitness. In contrast, for larvae of *H. sanguineus*, 15 °C represents suboptimal conditions, and therefore the species will benefit from the MHWs, especially when the latter occurs during stage IV. These results support the idea that the timing of extreme weather events will predict the physiological changes resulting from the event (Cinto Mejía & Wetzel, 2023).

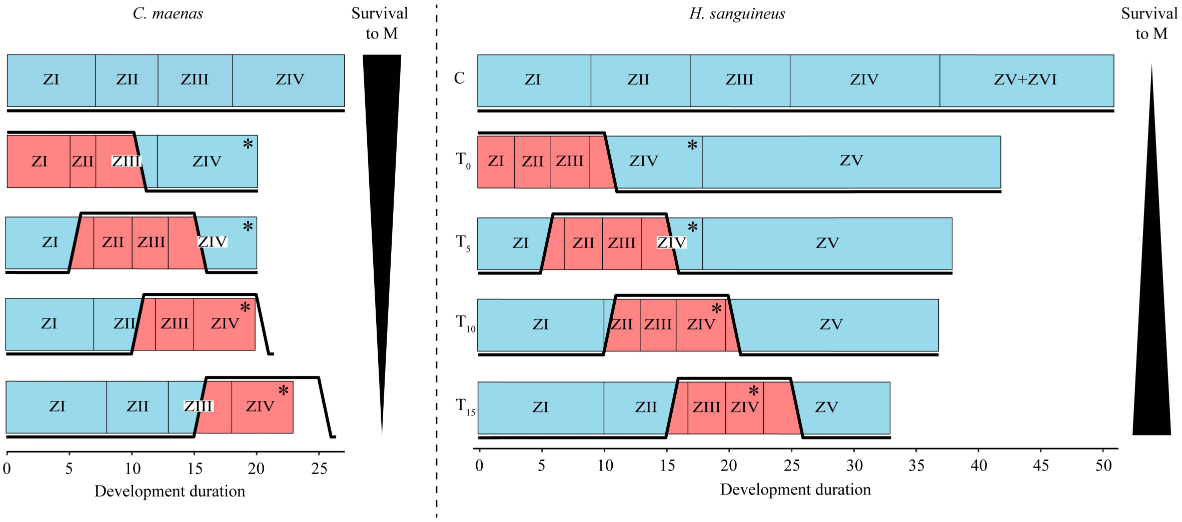

Figure 7.1. Mean development duration (days) for each stage of *C. maenas* (left) and *H. sanguineus* (right) during 24 °C pulses. The direction of the arrows indicates decrease/increase in survival to M (megalopa). Asterisks indicate the most sensitive stage. (See **Chapters 5** and **6** for details).

Stage-specific temperature sensitivity is widespread in many organisms from terrestrial and aquatic ecosystems (Kingsolver & Buckley, 2020; Miller et al., 2013; Verween et al., 2007). Early-stage insects can recover from exposure to high temperature stress if subsequent stages are not stressed. Similarly, a temperature increase during later stages often leads to irreversible damage (Iltis et al., 2021; Ma et al., 2018; Zhang, Rudolf, et al., 2015). In amphibians, heatwaves during late developmental stages can also lead to increased mortality, whereas earlier developmental stages are not similarly affected (Ujszegi et al., 2022).

While informations on the effect of ontogenetic timing of MHWs on marine organisms are sparse, it is well known that enhanced mortality occurs near the start and end of the larval phase in crustaceans (Anger, 1991; Dunn et al., 2016; Sulkin & McKeen, 1989). For other marine organisms with complex life-cycles, such as sea urchins and starfish, early embryos appear more tolerant to temperature increases than later stages (Balogh & Byrne, 2020; Gall et al., 2021). While the ecological consequences of MHWs depend on the timing of the event during an organism's ontogeny, it is also important to recognise that biological changes occur not only on a continuous scale (e.g., growth, development) but also on a discrete scale. MHWs occurring during key phenological events, such as breeding, moulting, or migration, can have important implications for the organisms (Cinto Mejía & Wetzel, 2023). For example, MHWs occurring during mating of insects can be detrimental to fitness while having little effect when occurring before or after the event (Pilakouta et al., 2023). Similarly, as organisms with complex life cycles often face critical bottlenecks during transitions between ontogenetic stages (Uriarte et al., 2019), MHWs occurring closer to a major transition such as the metamorphosis to megalopa will likely have a stronger effect than those occurring earlier.

3. Implications for species interactions & biological invasions

Results from this thesis revealed that the impact of MHWs can differ greatly depending on the specific conditions of the MHWs components and also between the taxa studied. Therefore, beyond affecting individual organisms, MHWs in the North Sea have the potential to disrupt ecological interactions between species.

3.1. Mismatch situation in response to MHW

Numerous studies have documented the impact of climate warming on the phenology of zooplankton (Borkman et al., 2018; Corona et al., 2024; Ji et al., 2010; Mackas et al., 2012), but very few have examined their phenological response to MHWs.

Chapter 4 revealed that most copepod taxa did not shift their phenological timing in response to MHW conditions prior to their bloom. However, phenological changes are influenced not only by shifts in bloom timing but also by changes in bloom duration (Giménez, 2011). Results from **Chapter 4** support this, revealing a contraction in bloom duration (whether total, onset, or decline) in response to increases in several MHW components. Similarly, **Chapters 5** and **6** demonstrated a reduction in larval development time under MHW conditions for *H. sanguineus,* and to a lesser extent, for *C. maenas* (Fig. 7.1). While theoretical models predicted a contraction in bloom duration linked to rising temperatures (Giménez, 2011), this is the first time such changes have been highlighted in response to MHWs.

Bloom contractions could have profound effects on higher trophic levels, potentially leading to trophic mismatches between the timing of copepods and crab larvae as food supply, and their predators. The match/mismatch hypothesis suggests that, under seasonal abundance patterns, prey abundance (e.g., copepods, crab larvae) regulates predator populations (e.g., fish larvae). As such, interannual variations in predator recruitment would depend on the degree of overlap between the annual peaks of prey and predator (Beaugrand et al., 2003; Cushing, 1990). When these peaks coincide ("match"), high predator recruitment is expected, whereas a reduced overlap ("mismatch") can result in increased mortality and lower recruitment (Beaugrand et al., 2003) (Fig. 7.2).

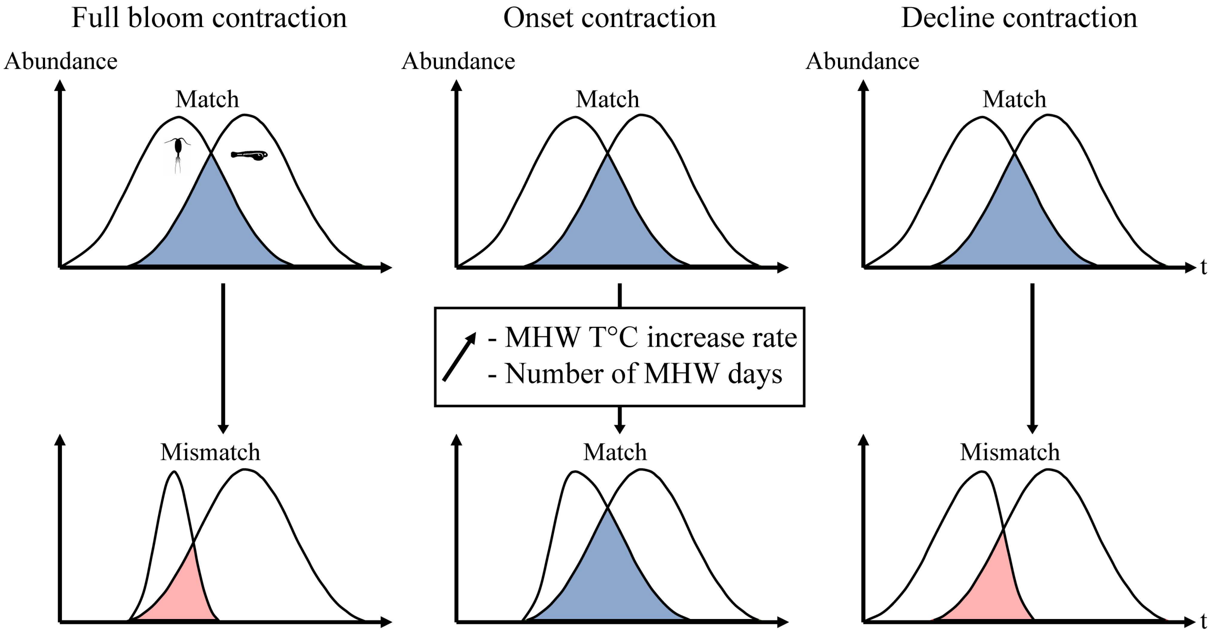

Figure 7.2. Copepod bloom contraction (total, onset, decline) and potential mismatch situation with higher trophic levels in response to increasing MHW components.

Bloom contraction in summer copepods such as *Acartia* spp., and *Pseudo/Paracalanus* spp., could induce a mismatch situation with fish larvae known to hatch during the same period. For instance, in the North Sea, the herring, *Clupea harengus*, typically spawns between August and October (Hufnagl et al., 2015). *Acartia* spp., and *Pseudo/Paracalanus* spp., are the most dominant taxa recorded at Helgoland Roads since 1975 (Boersma et al., 2015, 2017) and key prey for *C. harengus* (Arrhenius, 1996). A contraction in their bloom due to MHWs could result in a mismatch between prey availability and herring larvae, potentially impacting herring recruitment (Alvarez-Fernandez et al., 2015). This issue could be further intensified by the observed earlier bloom of *Acartia* spp., during years of high MHW intensity and MHW days.

In spring, copepod nauplii exhibit a reduced bloom duration, indicating accelerated growth and shorter periods spent in the water column. In the North Sea, copepod nauplii are a dominant food source for cod larvae and juveniles during this season (Beaugrand et al., 2003). A reduction in their bloom duration could therefore have significant implications for cod recruitment.

An important aspect of changes in the bloom duration is that the potential for a mismatch will depends on which phase is affected. Since predator reproduction typically follows closely to peaks in food availability, a contraction in the overall duration or decline phase of the copepods' bloom could reduce the overlap between predator and prey availability (Fig. 7.2), increasing the likelihood of a mismatch. However, a contraction in the onset phase is unlikely to cause such a mismatch, as the overlap between predator and prey would remain unchanged if the decline duration remains consistent (Fig. 7.2).

On another note, the bloom contraction observed in copepod nauplii during spring, as well as in *Acartia* spp., and *Pseudo/Paracalanus* spp., during summer, could significantly impact the larval recruitment of *C. maenas* while having a lesser effect on *H. sanguineus*. Copepod nauplii and small copepods are generally of higher nutritional quality than phytoplankton, and many decapod crustacean larvae feed on them (Anger, 2001). Therefore, the contraction of these blooms could directly affect the larval recruitment of decapod species. Interestingly, studies have shown that for barnacles, native cold-adapted species were more sensitive to food limitation under elevated temperatures compared to their invasive counterparts (Griffith et al., 2021). Similarly, the lower performance of *C. maenas* larvae under increased temperatures was exacerbated by food limitation (Torres & Giménez, 2020), while this was not the case for *H. sanguineus* (Espinosa-Novo et al., 2023). Consequently, the contraction of copepod nauplii and small copepod blooms could influence *C. maenas* recruitment and potentially intensify the competition between the two species.

3.2. Biological invasion & competition

Chapter 6 of this thesis demonstrated that MHWs may be beneficial for *H. sanguineus* larvae as they can "rescue" them from the cold temperatures typically experienced at the beginning of summer. Under normal summer conditions, early-season hatching of *H. sanguineus* at around 15 °C involves a trade-off. Indeed, while around 20 % of the larvae developing at 15 °C can successfully reach the megalopa, lower temperatures will lead to reduced body mass at metamorphosis to megalopa. Interestingly, this early development can allow the larvae to settle in the benthos during warmer periods later in the season, promoting faster growth compared to larvae hatching in the late summer at higher temperatures, and settling in the benthos in autumn (Espinosa-Novo, 2023). The occurrence of a MHW during the larval stages of *H. sanguineus*, can lead to a disappearance of this trade-off, as the increased temperatures will also enhance larval growth.

Additionally, *H. sanguineus*' window of larval release, defined as the number of days during which larvae have sufficient time to successfully reach the megalopa stage (Giménez, et al., 2020), could be greatly extended if it coincides with or closely follows/precedes a MHW event. Since the window of larval release is directly influenced by temperature conditions, MHWs occurring in late spring or early summer can extend this period by providing extended favourable conditions for larval release and survival. For example, the 2018 summer heatwave notably lengthened this window in the Skagerrak region along the Norwegian coast (Giménez et al., 2020). Additionally, the contraction of the larval phase observed during MHWs could further increase the number of days available for complete development.

MHWs may also expand the range and establishment potential of *H. sanguineus* into areas further poleward than their current distribution. In regions where summer temperatures typically remain below 15 °C, biological invasions are usually constrained by limited spawning and larval survival. However, MHWs can create favourable conditions, opening new windows for larval release in cooler areas and facilitating the establishment of *H. sanguineus*, as observed during the 2018 heatwaves in Bergen, Norway (Giménez et al., 2020). This hypothesis holds true only if juveniles and adults can tolerate the lower temperatures at the invaded location once conditions return to normal. In the German Bight, *H. sanguineus* is present in the intertidal throughout the year (Jungblut, 2017), even during winter when temperatures drop to 5 °C (Amorim et al., 2023). Therefore, if MHWs can open new windows of larval release in an area where adults can survive the winter, MHWs could promote poleward range expansion of invasive species. For instance, Spyksma et al. (2024) demonstrated that MHW facilitated the range expansion of an invasive ascidian. The species survived the colder temperatures following the MHWs by entering a form of hibernation, enabling it to endure unfavourable conditions and quickly resume activity once conditions improved (Spyksma et al., 2024). With the increasing frequency and intensity of MHWs in the coming decades, more favourable conditions for the establishment of self-sustaining populations may emerge.

The hypothesis of MHWs facilitating range expansion could apply for other organisms with complex life cycles, associated with warmer temperature or located near the lower part of their thermal range. For example, during "The Blob" in the North Pacific Ocean, the abundance of *C. maenas* (invasive in this region and located in the lower part of it thermal range) increased and recently recruited juveniles were observed in the most northern point ever, suggesting that reproduction did take place on the study site, and not just temporary migration of adult (Yamada et al., 2022; Yamada et al., 2021).

It is important to acknowledge that this thesis focused only on these two model species. And while they are great models to study biological invasions, more laboratory and natural experiments are needed to conclusively validate the hypothesis of range expansion, and it cannot be assumed that MHWs will have the same effect on all invaders. For species situated at the cooler edge of their range, the extent to which MHWs can create opportunities for range expansion will depend on the species' ability to migrate into newly thermally suitable habitats (Harvey et al., 2022). This ability is closely tied to traits such as adult mobility (sessile *vs.* mobile) and the dispersal capacity of their young.

In environments where *H. sanguineus* has already established sustainable populations, such as the German Bight, the combined impact of MHWs negatively affecting *C. maenas* and benefiting *H. sanguineus* is likely to promote the dominance of *H. sanguineus*. MHWs occurring during a sensitive stage could potentially induce recruitment failure into the adult population for *C. maenas* through carry-over effects. For instance, high temperatures experienced during larval stages and pupal stages of a global insect pest reduced almost all aspects of the adult performance, such as longevity and female fecundity (Zhang, Rudolf, et al., 2015). Moreover, in the North Sea, the larval season of both *H. sanguineus* and *C. maenas* partially overlap. The huge contraction in the larval phase of *H. sanguineus* observed under MHWs conditions could increase this overlap, and by extension the interspecific competition between both species.

Up to this point, the MHW effect, whether positive or negative, have been discussed with a focus on specific traits such as growth, development, and survival. However, such traits are not always fixed. Phenotypic plasticity is often exhibited by species, and evolutionary adaptations can occur. Therefore, the impact of MHWs on organisms will also be influenced by their plasticity and capacity for adaptation. Since MHWs are discrete events, with temperatures generally returning to baseline conditions afterwards, the ability of organisms to cope with temperature changes will determine whether an invasive species can persist after expanding into a new environment made more suitable by the MHWs.

4. Phenotypic plasticity and adaptation

In the context of heatwaves, many organisms exhibit phenotypic plasticity as an adaptive response. For example, in fish, it has been demonstrated that sticklebacks show significant phenotypic plasticity during MHWs, with an increase in their upper thermal tolerance (Mottola et al., 2022). Similarly, in amphibians, heatwaves can influence the phenotypic sex ratio by triggering sex reversal from female to male, as seen in agile frogs (*Rana dalmatina*), where heatwaves push the sex ratio strongly toward males (Ujszegi et al., 2022). Reptiles, such as the turtle species *Trachemys scripta*, also experience shifts in sex ratios favouring females during heatwaves (Carter et al., 2023), with outcomes depending on the timing of heat exposure during embryonic development (Breitenbach et al., 2020).

In **Chapter 4**, while the majority of copepod species were unable to shift their phenological timing in response to MHWs, *Acartia* spp., demonstrated a notable change. During years with intense and frequent MHW days, *Acartia* spp., exhibited an earlier occurrence, suggesting a capacity for phenotypic plasticity in response to MHWs.

In **Chapter 6**, the findings demonstrated that *H. sanguineus* generally exhibited better performance under MHW conditions. However, developmental plasticity emerged as another important mechanism explaining larval responses to these events. Depending on the timing of warm presses during development (and by extension the time spent in cooler conditions), *H. sanguineus* larvae exhibit the ability to follow two distinct developmental pathways. When cooler conditions preceding a warm press were short-lived, the larvae developed through a common pathway involving five zoea stages before metamorphosing to the megalopa. Conversely, when exposed to prolonged cooler temperatures prior to the warm period, the larvae followed a longer pathway, characterised by an additional zoea stage (Zoea IV). This longer pathway extended the larval development, allowing for an extended feeding period and therefore resulting in higher megalopa body mass. Although this plasticity provided the larvae with the ability to cope with stressful thermal conditions by increasing body mass, it came at the cost of lower survival rates. Nonetheless, the presence of a potential carry-over effect to later life stages, remains a strong possibility. Indeed, it is well known that environmental stress during larval development can affect post settlement performance (Anger, 2001; Giménez &

Torres, 2002). For instance, the crab *Neohelice granulata* can develop through an extra larval stage under food or osmotic stress (Giménez & Torres, 2002). The development through a long pathway can lead to megalopa with higher biomass as well as larger juveniles than those originating from the shorter pathway. Crabs are not the only organisms showing developmental plasticity; shrimp species like *Crangon crangon* can also undergo alternative developmental pathways in response to environmental factors such as temperature (Giménez, 2006)

For phenotypic plasticity to be effective, theory suggests that organisms must accurately predict environmental changes (Kroeker et al., 2020; Scheiner, 1993; Scheiner & Holt, 2012). By detecting environmental cues early, they can anticipate the optimal time to initiate specific behaviours and align their phenotype with the expected conditions. Therefore, the environment needs to be predictable (i.e., low variability) to support phenotypic plasticity (Fig. 7.3a). Generally, marine ecosystems, and specifically coastal areas, are more predictable than terrestrial ecosystems as the heat capacity of the water mass can buffer short-term variability in temperature and instead leads to relatively large amplitude variability over longer temporal scales (Kroeker et al., 2020; Steele, 1985; Vasseur & Yodzis, 2004). Nonetheless, what happens when the environment becomes unpredictable (i.e., high variability)? Predictability in this context, refers to the extent to which environmental conditions remain similar across successive time points and how long these conditions are likely to persist into the future, independent of the mean environmental state (Marshall & Burgess, 2015). In **Chapter 4**, the findings revealed that many copepod species experienced increasing variability in MHW components over time. According to theory, while low variability can support phenotypic plasticity, a shift toward higher variability in environmental conditions alters how organisms cope with such changes. In such cases, organisms may increasingly rely on bet-hedging strategies (Marshall et al., 2008) or adopt a generalist strategy (Gilchrist, 1995) (Fig. 7.3b). Interestingly, for some taxa, this increasing environmental variability is not consistent over time. A period with high variability does not necessarily predict similar variability in the preceding or following periods (Fig. 7.3c). In **Chapter 4**, the shift from low to high and high to low variability in MHW conditions appears to occur over a decade and suggests that organisms may experience shifts in the direction of selective pressures. Theory predicts that high genetic variation and short generation times can allow for rapid evolutionary change in response to environmental changes (Berteaux et al., 2004; Marcus, 1985). Given their short generation times (Mauchline, 1998), copepods are likely to respond rapidly to MHW variability. However, this is not true for all organisms, and species with longer generation times or lower genetic diversity, such as larger organisms, adapt slower and may be more vulnerable to MHWs variability.

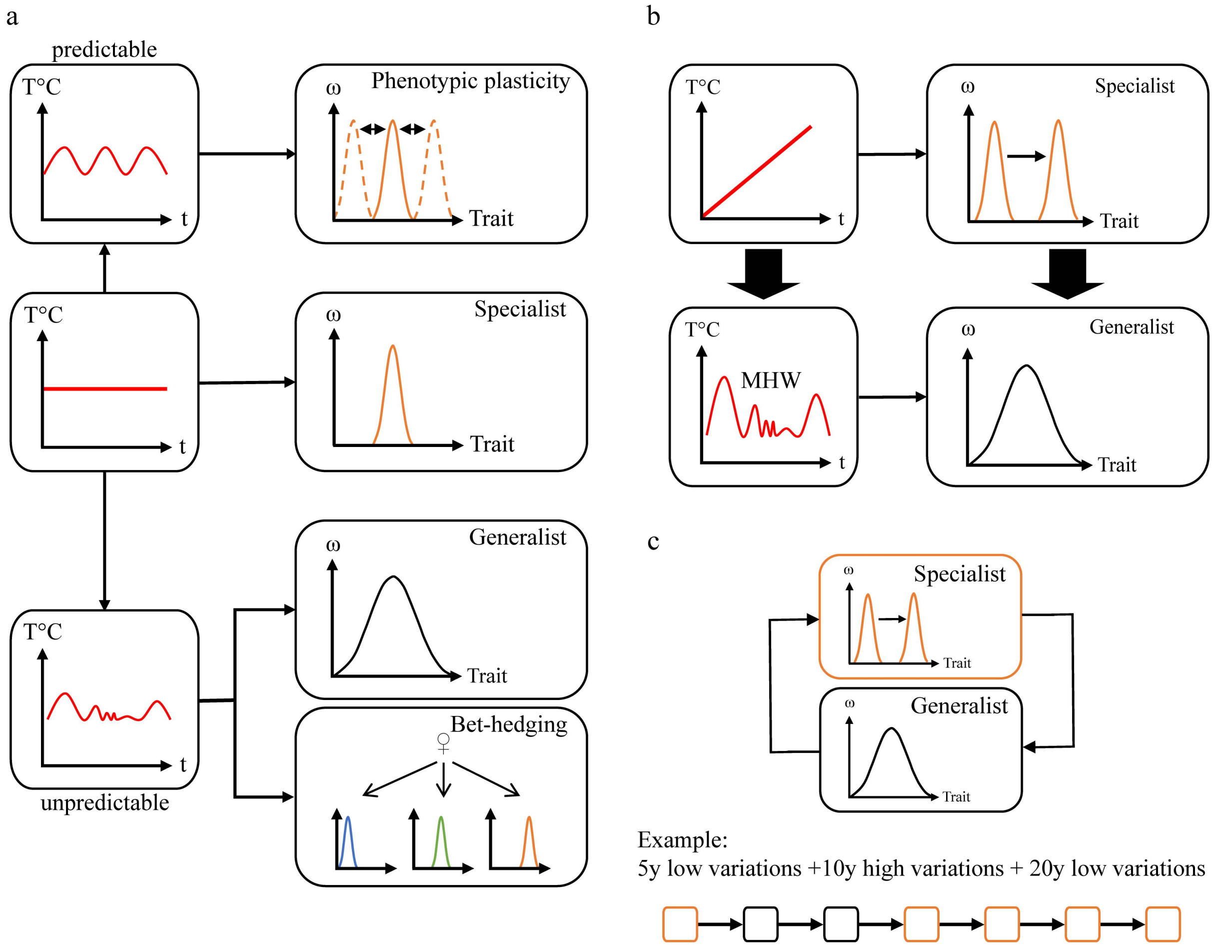

Figure 7.3. a. Strategy selections in response to changes in temperature (T°C) over time (t). **b.** Strategy selection in response to variations in the number of MHW days. As conditions shift from a constant increase to an unpredictable state, organisms' transition from a specialist strategy to a generalist or bet-hedging strategy. **c.** Strategy selection in a dynamic system. Some years will experience low variability in MHW days (see **Chapter 4**), while others will see higher variability. This fluctuation results in alternating selection pressures, favouring one strategy over the other. The orange box illustrates forces driving organisms toward a specialist strategy, while the black boxes depict forces promoting a generalist strategy.

Another key point is that variability in the number of MHW days within the bloom changed not only by species but also by life stage over time. For instance, while most summer copepod taxa showed a temporal shift from high to low variability over the course of a decade, copepod nauplii exhibited a consistent increase. At Helgoland Roads, copepod nauplii are not identified at the genus or species level, but given that *Acartia* spp., and *Pseudo/Paracalanus* spp., are the most abundant taxa (Boersma et al., 2015), they are likely to be highly representative of the nauplii group. These findings suggest that responses to MHW conditions experienced by an organism can vary depending on its life stage, which means the selective pressures may also differ throughout their development.

Just as MHs conditions can vary over time, one could hypothesise that they may also fluctuate spatially. Migratory organisms or those with biphasic life cycles might experience different MHW conditions depending on their location. For instance, larvae of *C. maenas* may encounter different MHW conditions in the water column during their larval development compared to conditions experienced in the benthic environment by juveniles and adults. Given the sensitivity of the later larval stages of *C. maenas* to MHW conditions, it is likely that the strongest selective pressures will occur during these developmental stages. Apart from the findings presented in **4**, there is currently limited data on how spatial and temporal variability in MHW conditions affects organisms with complex life cycles. This highlights the need for further research to better understand how these variations might impact such species.

5. Careful definitions matter: MHWs and their impact on marine organisms

Previous chapters emphasised that MHWs can lead to varied outcomes in terms of phenology, species performance, and community structure, depending on the combination of components, the species, and the season studied, suggesting the need to reconsider the original definition of MHWs when applied to biological systems.

From a climatological perspective, a MHW is defined as an event lasting for five days or more, with temperatures exceeding the 90th percentile of the historical baseline (Hobday et al., 2016). However, applying this definition to a biological context can be challenging, as climatological MHWs may not always qualify as an extreme event for organisms. Indeed, an event is considered extreme for the organism when “climate or climate-driven conditions trigger a negative threshold-like biological response” (Bailey and van de Pol 2016). **Chapters 5** and **6** demonstrated that the same type of heatwave can have different outcomes on two species. Moreover, the impact will directly depend on the state of each component, which interact to influence the overall outcome. These effects vary not only in strength, ranging from weak to strong, but also in direction. The same MHW might have a positive effect on one species while negatively affecting the other. Therefore, the definition of a biological extreme event diverges from that of a MHW.

Another issue arises when considering the seasonal and ontogenetic timing of MHWs, as discussed in Section 2 of the discussion. The impact of a MHW can vary significantly depending on its timing. However, climatological definitions assume that the severity of MHWs remains the same, suggesting that a spring MHW would have the same effect as a winter one, or that a MHW occurring early in the larval stages would have a similar impact to one occurring later. Therefore, the reliance on the Q90 threshold to define a MHW event from a biological perspective might be a problem. Results from **Chapters 5** and **6** revealed that not all combinations of MHWs conditions are experienced as extreme events by organisms. For example, in *C. maenas*, early MHWs at low intensity had no impact on larval performance and thus would not be considered extreme from a biological perspective. These results emphasise that events that are classified as MHWs do not always match extreme conditions. However, according to the Q90 threshold for the North Sea at this season, all the intensities studied in **Block II** are classified as MHWs. This suggests that the definition of MHWs by Hobday et al. (2016) might overestimate the effect of MHWs as a biological extreme event as it does not consider the timing of the event in the ontogeny of the organisms. Therefore, the climatological definition of MHWs does not accurately categorise biological changes and there is a need for a more nuanced framework when studying the effect of MHWs on organisms.

An alternative approach to defining biological MHWs could involve the concept of the "region of existence," which represents a range of environmental fluctuations (i.e., SOFiA framework, where these fluctuations are characterised by specific MHW components) bounded by a threshold. Beyond this threshold, the performance of organisms begins to decline (Giménez, 2023). The SOFiA framework shares similarities with the thermal landscape concept (see **Chapter 1**), which is based on the idea that thermal tolerance decreases with prolonged exposure (Rezende et al., 2014). However, within the SOFia framework, the temporal aspect of fluctuations is defined by the timing of the event in relation to the studied organisms. Additionally, this framework can also be expanded to include more components, such as event duration or other environmental variables (Giménez, 2023). This concept could be an interesting approach to define biological MHWs in a more nuanced way. Building on the climatological definition of MHWs by Hobday et al. (2016) and the biological one by Bailey & van de Pol (2016) a MHW for organisms could be defined as:

"an episode of elevated temperatures where the combination of components results in a shift in the size of an organism's region of existence compared to what will be expected under natural conditions."

Compared to the definitions by Bailey & van de Pol (2016), this definition acknowledges that the impact of a MHW can be bidirectional, meaning an extreme event is not necessarily detrimental to organisms as seen in **Chapter 3** and **Chapter 6**. An expansion of the region of existence suggests improved performance, while a contraction indicates impaired performance. The region of existence could be either survival or functional traits linked to the fitness. In this thesis, the region of existence was built using two MHW components, namely the intensity and timing. However, one could increase the dimensionality of the space of fluctuations to include other components such as the duration, frequency, or the temperature increase and decrease rate. Indeed, as explained above, MHW components must be studied together, and adding one component to the framework will create new interactions and change the overall response. This framework will also enable the identification of biological effects from MHWs lasting less than five days, which are classified as heat spikes under the Hobday et al. (2016) definition, but may still significantly impact biological processes (Villeneuve & White, 2024). By incorporating more MHWs components into the analysis, one could deepen the understanding of how a specific MHW will influence organisms.

6. Multi-methods to study MHW impacts on marine organisms

The integration of field observations and laboratory experiments in this thesis addressed several gaps and methodological limitations commonly found in MHW research. First, this thesis revealed the distinct effects of MHWs and long-term warming, demonstrating that a constant temperature cannot always predict an organism's response to MHWs. While larval performance in two species of decapod crustaceans was used as the focal response variable, it is likely that these findings extend to broader biological systems, from individual organisms to communities and entire ecosystems.

Second, results of this thesis expressed the need to study MHWs as a whole, integrating multiple MHW components, and not only the intensity, to properly understand the effect of a specific MHW event on biological systems. Key components, related to the temporal pattern of the event, such as the timing and the duration should be included in all future studies. Using wider frameworks such as the thermal tolerance landscape or the SOFiA which integrate the temporal patterns of events into the analysis (Giménez, 2023; Rezende et al., 2014), should now be a standard practice. To date, only two studies have applied the thermal landscape approach to assess biological responses to MHWs and explore the potential mismatch between the MHWs definition and the extreme events experienced by organisms, both of which support the findings of this thesis. Bertolini & Pastres (2021) used the thermal landscape to predict clams mortality, revealing that heatwaves, as defined by Hobday et al. (2016), did not always result in mortality, while some events not classified as MHWs did lead to significant mortality. This "mismatch" was directly attributed to the incorporation of duration and frequency of the MHW event into the framework, similar to the observations made in **Chapters 5** and **6** of this thesis. Villeneuve & White (2024) reached the same conclusion, attributing the mismatches between methods to the focus on MHWs intensity, rather than the interaction between duration and intensity, in the MHWs definition by Hobday et al. (2016).

Third, while laboratory experiments provide valuable insights into the mechanisms by which MHWs affect species, they do not reveal whether the species' overall abundance is impacted as shown by field observations. A major challenge in using current field observations to understand MHWs impacts on biological systems is the lack of replication and control units. Many studies rely on long-term time series data that focus on a single extended MHW event (often "The Blob" or the Ningaloo Niña), using a Before-After (BA) design to assess the event's impact. This approach makes causal inference difficult, as trends in environmental data are common and may or may not be directly attributable to the MHW event (Smith, 2002). Additionally, many of those designs do not consider the seasonal timing of the event as they compare the state of the ecosystem usually during the same year as the event. **Chapter 3** suggests that to better assess the general impact of MHWs on biological systems while accounting for natural variability, an effective approach would be to pair each MHW event with an appropriate control where no MHW was recorded. Careful selection of the control is essential; to account for global warming and environmental changes over time, the control should be chosen from a time period not too distant from the actual MHW event. Furthermore, selecting a control from the same seasonal period in a different year would offer a clearer understanding of the seasonal-specific effects of MHWs.

In the same way as laboratory experiments cannot reveal changes in community dynamics, field experiments or observations do not isolate the specific effects of MHWs on the performance of individual organisms (Diamond, 1986). A multi-method approach integrating both field observations and laboratory experiments is therefore essential for addressing MHWs impact on biological systems. In this thesis, while the organisms studied are part of the same community, the choice of the model species varied across the two sections, since not all species can be conveniently examined using the same methods (Diamond, 1986). For example, using copepods in the laboratory experiments of **Block II** would have been an effective way to assess MHW impacts on this group beyond just abundance and phenology changes, allowing for a detailed evaluation of individual performance and developmental plasticity. However, including copepods posed methodological challenges related to their life history traits. The complete larval development of *C. maenas* under the 15 °C baseline was already so short that it was difficult to manipulate MHW intensity, timing, and duration. During short MHWs, late timing led to moulting into the megalopa stage before the MHW concluded. Copepods in the North Sea, like *Acartia* spp., have an even shorter development time. Although *Acartia* spp., which show significant changes in abundance and phenology in response to MHWs, would have been an ideal model to bridge laboratory experiments and field observations, its development time of around 19 days at 15 °C (Mauchline, 1998) is too short to simulate the frequently occurring MHWs effectively (i.e., 10 days; Giménez et al., 2024) and assess individual performance. As for linking decapod crustacean larval performance with abundance in field observation studies, the Helgoland Roads long-term time series does include data on zoea and megalopa stages (Boersma et al., 2017). However, their low densities in the dataset (even when combined) categorises them as rare taxa, making it difficult to conduct robust statistical analyses or meaningful assessments of community structure.

Nonetheless, the combination of field observations and laboratory experiments resulted in a more convincing study compared to those relying on a single method. Indeed, conclusions supported by different methodologies (e.g., the importance of studying MHW components together, or the importance of the MHW timing) are more robust, as each method provides complementary insights that the other cannot access (Diamond, 1986). In a conservation context, the use of a single approach might create management failure or risk policy (Dawson et al., 2011). Therefore, assessing biodiversity response to MHWs, and in a broader way, climate change, requires the use of different approaches to understand all aspects of species/population vulnerability (i.e., sensitivity, adaptive capacity, exposure). For example, while field observations can be used to assess sensitivity, they alone cannot explain how key ecological and evolutionary processes (e.g., phenotypic plasticity) allow species to persist or adapt in a given environment (Dawson et al., 2011).

7. Perspectives

Building on this, a future perspective emerging from this thesis would be to implement a field experiment using mesocosms to evaluate the effects of MHWs on the marine community. This approach would enhance the realism of laboratory experiments while allowing for greater control over the studied variable than it is possible in field observations (Diamond, 1986). By manipulating MHW conditions according to realistic scenarios, field experiments can surpass the limitations of tightly controlled laboratory experiments, which often lack realism. Therefore, they could address the issue of unrealistic temperature increase and decrease rates by simulating temperature rates more representative of the real world. Moreover, mesocosms can also facilitate the study of trophic interactions. Testing the match/mismatch hypothesis between zooplankton and their predators, including fish larvae and decapod crustacean larvae in response to MHWs, must remain a subject of future research. If the phenology of the predator and the phenology of the copepods were to respond similarly to temperature, it is unlikely that warming would lead to a desynchronization in the food web (Durant et al., 2019), nor would a MHW.

The second block of this thesis involved an experimental design using a complex combination of different MHW components. However, there is still room for improvement. First, it would be beneficial to simulate more realistic MHWs, particularly by including temperature increase and decrease rates that are representative of natural environments. Second, it is crucial to recognise that MHW frequency can lead to drastic changes in the responses of the organisms (Bertolini & Pastres, 2021) and should also be considered in future frameworks. Finally, MHWs can also occur alongside fluctuations in other environmental drivers, leading to different responses, including additive, antagonistic, and synergistic effects (Gunderson et al., 2016). Additional environmental factors such as salinity or food limitation may interact with MHWs and intensify (or mediate) their effects (Smith et al., 2023). In *C. maenas*, it has been shown that short heatwaves (six days) at mild temperatures (15-18 °C) can impair larval performance under food limitations (Giménez et al., 2021). Another study investigating the combined effect of salinity and temperature showed that late zoea stages of the shore crab *Hemigrapsus takanoi* were unable to metamorphose to megalopa under heatwave scenarios (Nour et al., 2022). Therefore, future studies should prioritise examining how the multiple components of MHWs interact with other environmental variables to better understand the full range of impacts on biological systems.

General conclusion

This thesis employed field observations and laboratory experiments to explore how MHWs affect community dynamics and species performance in a coastal region that has experienced frequent MHWs in recent decades. The findings of both **Block I** and **II** revealed that MHW impacts vary depending on the seasonal and ontogenetic timing of the biological system studied, underscoring the need for time-specific studies when assessing MHWs impacts. Using field observations and laboratory experiments, this thesis also revealed that MHWs could cause a contraction in the bloom duration of key copepod taxa in the North Sea as well as in the larval development of *H. sanguineus* and, to a lesser extent, *C. maenas*. These contractions could potentially lead to a mismatch situation between prey and their predators, with repercussions for higher trophic levels. **Block II** demonstrates that MHW effects on species performance differ from those caused by general warming. It highlights the importance of studying the combination of different MHW components (timing, intensity, and duration) to fully understand organismal responses. Species with higher thermal tolerance or invasive species are likely to thrive during MHWs, often at the expense of native species that may face increased stress and eventual competitive exclusion. Given the varying impacts across species, it is essential to carefully consider how climatological definitions of MHWs apply to biological systems. Further investigation is still needed, particularly to explore how other environmental stressors, such as salinity, food availability, or ocean acidification, may interact with MHWs. Additionally, studying trophic interactions remains crucial for understanding how MHWs could disrupt predator-prey dynamics. As MHWs become more frequent, intense, and prolonged, understanding the relationship between their components, other stressors, and their ecological and socio-economic consequences will be increasingly critical for predicting and managing future impacts on marine ecosystems.

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Declaration on the contribution of the candidate to a multi-author article/manuscript which is included as a chapter in the submitted doctoral thesis

Chapter 3: Responses of the mesozooplankton community to marine heatwaves: challenges and solutions based on a long-term time series

Deschamps M. M., Boersma M., Giménez L.

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 50%

Experimental work and/or acquisition of (experimental) data: no collection of data

Data analysis and interpretation: ca. 100%

Preparation of Figures and Tables: ca. 100%

Drafting of the initial manuscript: ca. 100%

Chapter 4: Beyond warming: copepods face marine heatwaves during blooms due to unchanged phenological timing

Deschamps M. M., Boersma M., Giménez L.

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 50%

Experimental work and/or acquisition of (experimental) data: no collection of data

Data analysis and interpretation: ca. 100%

Preparation of Figures and Tables: ca. 100%

Drafting of the initial manuscript: ca. 100%

Chapter 5: Responses of larvae of the European shore crab *Carcinus maenas* to marine heatwaves: disentangling the effect of duration, intensity and timing

Deschamps M. M., Giménez L., Astley C., Boersma M., Torres G.

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

Experimental concept and design: ca. 33%

Experimental work and/or acquisition of (experimental) data: ca. 60%

Data analysis and interpretation: ca. 100%

Preparation of Figures and Tables: ca. 100%

Drafting of the initial manuscript: ca. 100%

Chapter 6: Heatwaves to the rescue: Responses of larvae of the invasive crab *Hemigrapsus sanguineus* to marine heatwaves

Deschamps M. M., Giménez L., Boersma M., Torres G.

Contribution of the candidate in % of the total work load (up to 100% for each of the following categories):

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Data analysis and interpretation:	ca. 100%
Preparation of Figures and Tables:	ca. 100%
Drafting of the initial manuscript:	ca. 100%

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Hiermit betätige ich gemäß §7, Abs. 7, Punkt 4, dass die zu Prüfungszwecken beigelegte elektronische Version meiner Dissertation identisch ist mit der abgegebenen gedruckten Version.

Ich bin mit der Überprüfung meiner Dissertation gemäß §6 Abs. 2, Punkt 5 mit qualifizierter Software im Rahmen der Untersuchung von Plagiatsvorwürfen einverstanden.

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Unterschrift

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