Climate change impacts on ecosystem functioning and services provided by temperate benthic ecosystem

Dissertation

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A gente não se deixa dominar pelo medo, tem que levantar a cabeça e fazer acontecer. É nisso que acreditamos e por isso que lutamos

Paulino Guajajara

To Nilda and Mauro

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Summary/
Zussamenfasung

Summary

The world is going through severe climatic changes and this transition period is characterized by peculiar phenomena. Despite the mean global temperature increase, episodes of higher frequency and longer heatwaves will occur more often. Heatwaves have already disrupted resilience of macrophyte species, resulting in massive mortality of seagrasses and macroalgae. Macrophytes are responsible for considerable amounts of carbon storage and sequestration in marine coastal ecosystems. Many macrophytes are also considered foundation species since they harbor high species diversity, which results in large capacity to structure a community. Thus, heatwaves are able to cause shifts in biodiversity and ecosystem functioning. The goal of this thesis was to improve the understanding of the mechanistic effect of climate change on temperate coastal marine ecosystems based on macrophytes meadows. I performed experiments in indoor and outdoor mesocosm to trace energy flows (expressed as carbon) in a benthic ecosystem exposed to current and future temperature regimes. The experiments and analysis were designed to investigate (1) a simple trophic interaction of an isopod (*Idotea balthica*) feeding on a macroalgae (*Fucus vesiculosus*) under temperature gradient; (2) the effect of heatwaves on a benthic food web and (3) how the heatwaves affected the provision of ecosystem services by the benthic ecosystem. The first work showed that the increase of temperature linearly modulates the photosynthesis rate until 25 °C. However, grazing intensity (that also depends on temperature) contributed to control the amount of carbon stored on the macroalgae and modified the trend to a non-linear pattern. The lowest carbon storage capacity was found between 20 and 22 °C, following the consumption intensity of the grazers. Second, I participated of an outdoor mesocosm experiment that reproduced spring and summer heatwaves on benthic communities associated to macroalgae (*Fucus vesiculosus*) and seagrass (*Zostera marina*) ecosystems. Using the data collected (e.g. biomass, stable isotopes, photosynthesis and respiration rates) during the experiment, I was able to analyze the carbon circulation in the benthic ecosystem applying ecological network analysis (ENA). The ENA indices and attributes of the ecosystem demonstrated that three sequential heatwaves jeopardized the capacity of the ecosystem to store carbon, since photosynthesis declined and the size of the ecosystem decreased. Moreover, three heatwaves caused a simplification on the pathways of carbon circulation, which makes the ecosystem more vulnerable to further disturbances. Third, the impact of sequential heatwaves on the capacity of the ecosystem to deliver services was analyzed with a qualitative network model (loop analysis); such model is able to detect direct and indirect impacts caused by disturbances on specific nodes of the network. The analysis showed that the provision of water purification and climate regulation services was impaired, while the capacity of habitat provision remained the same on the ecosystem after the exposure to heatwaves. Therefore, the conclusions are that: (1) both changes in temperature regimes (i.e. average constant and heatwaves) have profound effects on single species physiological performance and modify trophic interactions, thus altering energy circulation in food webs; (2) three consecutive heatwaves during spring/summer represented a threat for the health of the benthic ecosystem studied due to the reduction of productivity and the lowered diversity of energy flows, which increased vulnerability of the system; (3) besides having affected the functioning of the ecosystem, the heatwaves also harmed the capacity of the ecosystem to provide water purification and climate regulation services. This thesis showed that more knowledge on ecosystem functioning and services can be generated by combining experimental and modeling approaches. Furthermore, focusing on whole ecosystems rather than on isolated responses of single organisms expands our comprehension on the effects of changes in temperature regimes, which may assist further climate change mitigation measures.

Zussamenfasung

Die Welt durchläuft schwere klimatische Veränderungen und diese Übergangsperiode ist durch eigenartige Phänomene gekennzeichnet. Trotz des mittleren globalen Temperaturanstiegs werden Episoden mit höherer Frequenz und längeren Hitzewellen häufiger auftreten. Hitzewellen haben bereits die Widerstandsfähigkeit von Makrophytenarten gestört und zu einer massiven Sterblichkeit von Seegräsern und Makroalgen geführt. Makrophyten sind für die Speicherung und Bindung beträchtlicher Mengen Kohlenstoff in marinen Küstenökosystemen verantwortlich. Viele Makrophyten gelten auch als Basisarten, da sie eine hohe Artenvielfalt beherbergen und folglich große Kapazitäten innehaben um Gemeinschaften zu strukturieren. So können Hitzewellen zu Verschiebungen in der biologischen Vielfalt und der Funktionsweise von Ökosystemen führen. Das Ziel dieser Arbeit war es, das Verständnis der mechanistischen Auswirkungen des Klimawandels auf die Ökosysteme der gemäßigten Küstenmeere, auf der Grundlage von Makrophytenwiesen, zu verbessern. Ich führte Experimente in Innen- und Außen-Mesokosmosmen durch, um Energieströme (ausgedrückt als Kohlenstoff) in einem benthischen Ökosystem zu verfolgen, das aktuellen und zukünftigen Temperaturregimen ausgesetzt ist. Die Experimente und Analysen waren darauf ausgerichtet, (1) eine einfache trophische Wechselwirkung zwischen einem Isopoden (*Idotea balthica*) und der Makroalge (*Fucus vesiculosus*) von der er sich ernährt, unter einem Temperaturgradienten zu untersuchen; (2) die Auswirkung von Hitzewellen auf ein benthisches Nahrungsnetz zu erforschen und (3) zu erörtern, wie Hitzewellen die Bereitstellung von Ökosystemdienstleistungen durch das benthische Ökosystem beeinflussen. Die erste Arbeit zeigte, dass der Temperaturanstieg die Photosyntheserate bis 25°C linear moduliert. Die Weideintensität (die auch von der Temperatur abhängt) trug jedoch dazu bei, die Menge des im Makroalgen gespeicherten Kohlenstoffs zu kontrollieren und veränderte den Trend zu einem nichtlinearen Muster. Der niedrigste Wert für die Kohlenstoffspeicherung wurde zwischen 20 und 22 °C gefunden, entsprechend der Verbrauchsintensität der Weidegänger. Für den zweiten Versuch nahm ich an einem Mesokosmos-Freilandexperiment teil, bei dem Frühlings- und Sommerhitzewellen auf benthischen Gemeinschaften, die mit Makroalgen- (*Fucus vesiculosus*) und Seegras- (*Zostera marina*) Ökosystemen assoziiert sind, reproduziert wurden. Mit den in diesem Experiment gesammelten Daten (z.B. Biomasse, stabile Isotope, Photosynthese- und Respirationsraten), konnte ich die

Zussamenfasung

Kohlenstoffzirkulation im benthischen Ökosystem mit Hilfe der ökologischen Netzwerkanalyse (ENA) analysieren. Die ENA-Indizes und -Attribute des Ökosystems zeigten, dass drei aufeinanderfolgende Hitzewellen die Kapazität des Ökosystems, Kohlenstoff zu speichern, gefährdeten, da die Photosynthese sowie die Größe des Ökosystems abnahm. Darüber hinaus verursachten drei Hitzewellen eine Vereinfachung auf den Pfaden der Kohlenstoffzirkulation, was das Ökosystem anfälliger für weitere Störungen macht. Für den dritten Teil dieser Arbeit, wurde der Einfluss von aufeinanderfolgenden Hitzewellen auf die Fähigkeit des Ökosystems, Dienstleistungen zu erbringen, mit einem qualitativen Netzwerkmodell (Schleifenanalyse) analysiert. Ein solches Modell ist in der Lage, direkte und indirekte Auswirkungen von Störungen auf bestimmte Knoten des Netzwerks zu erkennen. Die Analyse zeigte, dass die Bereitstellung von Wasserreinigungs- und Klimaregulierungsdiensten beeinträchtigt wurde, während die Kapazität der Bereitstellung von Lebensräumen auf das Ökosystem nach der Exposition gegenüber Hitzewellen gleichblieb. Die Schlussfolgerungen sind daher folgende: (1) beide Änderungen der Temperaturregime (d.h. durchschnittliche Konstante und Hitzewellen) haben tiefgreifende Auswirkungen auf die physiologische Leistung einzelner Arten und modifizieren die trophischen Wechselwirkungen, wodurch die Energiezirkulation in den Nahrungsnetzen verändert wird; (2) drei aufeinanderfolgende Hitzewellen im Frühjahr/Sommer stellen eine Bedrohung für die Gesundheit des untersuchten benthischen Ökosystems dar, da die Produktivität und die verringerte Vielfalt der Energieströme die Verwundbarkeit des Systems erhöhten; (3) Hitzewellen beeinträchtigen nicht nur die Funktion des Ökosystems, sondern auch die Kapazität des Ökosystems Wasserreinigungs- und Klimaregulierungsleistungen zu erbringen. Diese These zeigte, dass durch die Kombination von experimentellen und Modellierungsansätzen mehr Wissen über die Funktionsweise und die Dienstleistungen des Ökosystems generiert werden kann. Darüber hinaus erweitert die Konzentration auf ganze Ökosysteme, statt auf isolierte Reaktionen einzelner Organismen, unser Verständnis der Auswirkungen von Änderungen der Temperaturregime, was weitere Maßnahmen zur Abschwächung des Klimawandels unterstützen kann.

General Introduction

Costanza et al. (1992) defined a healthy ecosystem as an undisturbed system, which is capable to function maintaining the resilience through its organization and sustainability over time. There are three main pillars that sustain the health of ecosystems, according to Costanza and Mageau (1999): (1) vigor, (2) organization and (3) resilience. The authors related vigor of the ecosystem to activity, metabolism or primary production, i.e. the functioning of the system. The organization of the system is represented by how the energy flows driven by ecological interactions (e.g. trophic interactions) are organized. Moreover, the organization of the flows indicates how diverse and efficient is a system to transfer energy (Ulanowicz 2004). The resilience is the capacity of an ecosystem to maintain its properties (structural and functional) under disturbances (Holling 1986). Ecosystem's health, which is also called ecosystem integrity, depends on the combination of ecological structures and functioning (Duarte et al. 2018). The ecological structure is represented by the living and non-living compartments of an ecosystem. The biotic structural contribution is given by biodiversity while the abiotic structure of the ecosystems is related to habitat provisioning that can also influence the functioning of ecosystems (Kandziora et al. 2013). Thus, the structural integrity directly impacts the ecological processes or ecosystem functioning. The functional integrity relevant for the marine ecosystems is the energy and matter balance. The balance corresponds to the flows of energy and material that enter the system and are cycled in the food webs (Kandziora et al. 2013). The evaluation of health is related to the detection of distress; thus, the "check-up" of the ecosystem should determine whether there are ecological processes not properly functioning that could lead to a collapse of the system (Duarte et al. 2018).

The ongoing climate change has already harmed ecosystems. In 2019, the Intergovernmental Panel on Climate Change special report on the ocean and cryosphere in a changing climate (IPCC-SROCC 2019) confirmed the warming of the oceans in the last decade. Climate change has been increasing not only mean sea surface temperature but also the occurrence of marine heatwaves (Frölicher and Laufkötter 2018). Marine heatwaves are characterized by anomalous warming (increase of 90 % above the baseline period) with clear start and end period (Hobday et al. 2016). The amplification of the magnitude of marine heatwaves is expected since global heatwaves are predicted to increase in intensity, frequency and duration (Meehl and Tebaldi 2004).

Environmental parameters shapes biodiversity (Hutchinson 1959), both natural fluctuations (e.g. seasonality, day-night fluctuations) or anthropogenic disturbances (e.g. climate change) are responsible for selecting species based on their physiological, morphological and behavioral performance (Price et al. 2003). The increase of the extreme events like summer heatwaves in the last years (Oliver et al. 2019) profoundly affected marine biodiversity (Nowicki et al. 2017). Heatwaves have increased mortality of seagrasses and invertebrates (Kendrick et al. 2019) by decreasing their thermal tolerance (Seuront et al. 2019) and the recovery time could be long enough to destabilize the ecosystem (Caputi et al. 2019).

Temperature increase affects marine biota by accelerating biochemical reactions (Kordas et al. 2011). However, if temperature thresholds are surpassed, the enzymes are denatured and lose their functions (Kordas et al. 2011). Metabolic activity is temperature-dependent and determines consumption, growth, respiration and reproduction rates. Marine organisms present different tolerance ranges to temperature, which can increase the complexity of ecological interactions (Edwards and Richardson 2004). The responses of marine organisms to warming may lead to phenological variability, e.g. shifting reproductive cycle timing that anticipates or delays the peaks in biomass (Batten and Mackas 2009), impacting food webs.

The changes in ecological interactions affect not only interactions within living organisms but also with non-living compartments, resulting in modifications in the whole ecosystem that may feedback on biodiversity (Walther et al. 2002). Therefore, to understand biodiversity it is essential to study the functioning of food webs that compose the ecosystem. Interspecific ecological interactions, and changes in their type and magnitude, define the nature of ecosystem processes (Hooper et al. 2005). A pivotal ecological interaction is predation since it maintains higher levels of biodiversity by preventing one food chain to prevail over the others (Paine 1966). Species usually present different temperature tolerance range, which depends on the variance of the range, degree of thermal specialization and the asymmetry of the thermal performance curves (Martin and Huey 2008). Since the species present different tolerance thresholds, changes in environmental conditions (e.g. temperature) may cause non-linear shifts in the interspecific interaction strength (Hoegh-Guldberg and Bruno 2010). These responses propagate through ecological interactions and increase the complexity of food webs reaction to climate change, generating uncertainties in the predictions for ecosystem functioning.

Food web analyses describe the energy flows determined by “who eats whom” (Ulanowicz 2004) that embed food chains responsible for energy transfer from one trophic level to another.

Ecological network analysis (ENA) besides the trophic interactions also includes the quantification of energy flowing in the food webs (Ulanowicz 2004). According to Kay et al. (1989), energy flows may be expressed as several mediums (e.g. carbon, nitrogen, phosphorus, and sulfur) and there are four types of energy flow that must be considered for investigating food webs (a) import, (b) intercompartmental exchange, (c) respiration (i.e. loss) and (d) export. The imports are the entrance of energy in the system, in many cases represented by photosynthesis. The intercompartmental exchange refers to the flow of energy from one compartment (groups of organisms or non-living components of the ecosystem) to another, e.g. feeding interaction. Respiration is considered energy lost from the system and dissipated as heat, i.e. the energy that was degraded during metabolic activity of living compartments of the ecosystem. Exports are the portions of usable energy transferred from the boundaries of one system to another, e.g. parts of macrophytes that are detached and transported by water currents to the sea shore. Thus, ENA combines ecological interactions through quantitative energy transfer between biotic and abiotic components of an ecosystem. The connection of energy flows using network analysis reveals direct or indirect effects of perturbations on species composition of an ecosystem (Ulanowicz 2004).

Besides trophic interaction, there are other classes of ecological interactions (e.g., competition and symbiosis) responsible for shaping the structure and functioning of ecosystems (Hooper et al. 2005). A particular important non-trophic ecological interaction is featured by foundation species. Foundation species are species that provide habitat and facilitate ecological succession, leading to high biodiversity (Bruno et al. 2003). Habitat-forming species are essential for determining food web structure increasing the complexity of the food webs, which regulate the functioning of ecosystems (Borst et al 2018).

Ecosystem functioning, defined by De Groot et al. (2002) as “the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly”, has direct impact on the health of the ecosystems since it is related to ecosystem integrity (Rapport and Singh 2006). Ecosystem integrity is the basic conditions of a system to provide services (Kandziora et al. 2013). The basic conditions are the maintenance of ecological processes and structures needed for supporting the capacity of self-regulation of the ecosystems (Kandziora et al. 2013). Therefore, understanding the functioning of the ecosystem is essential before studying the ecosystem services provisioning and how climate change will impact them.

According to the Millennium Ecosystem Assessment (MA 2003), "Ecosystem services are the benefits people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational and cultural benefits; and supporting services, such as nutrient cycling, that maintain the conditions for life on Earth." The provisioning services are, usually, the most highlighted section since they are easier to quantify, while the regulating services are usually underrated because often, they do not affect people directly. Hereby I emphasize the importance to study regulating and supporting services in depth because studies that map them usually face difficulties to rate their relevance according to the documentation the scientific literature provides (Salomidi et al. 2012, Potts et al. 2014). There is a need to understand how the biotic and abiotic components interact in the ecosystems and provide those services mainly under the impacts of climate change.

Dee et al. (2017) recommended the operationalization of the ecosystem services, in order to determine not only direct and indirect effects but also feedbacks of disturbances caused by the prospective climatic changes. The authors propose that the use of single indicators for management of ecosystems can lead to inaccurate environmental protection measures. The method I adopted in this thesis for applying the operationalization approach was the qualitative network analysis loop analysis (LA). A loop can create positive or negative feedbacks through a closed circuit, i.e. a pathway that crosses the nodes of a network only once finishing on the same node where it started. LA is a democratic method since the nodes, pathways and feedbacks that compose the network can be determined even on literature information (Bodini 2000). The advantage of this analysis is that it requires simple information about the network to construct the model. The model relies on positive, negative, and absence of interactions between nodes (Levins 1974). The information collected is depicted as a signed directed graph originated from a matrix of interactions that is used to run the analysis and make predictions on the response of the nodes. The outcome of the LA is prediction of the increase, decrease or no change of each node included in the network after a disturbance episode (Bodini 2000). The predictions are sensitive to cascade effects of the disturbances; thus, LA embeds the propagation of the perturbation on one node along the network (Barboza et al. 2019). LA is a versatile model since it allows the connection of nodes from different nature (e.g. biology, economy and social). Therefore, this qualitative model has been used to study not only ecological interactions (Bodini et al. 1994) but also how ecological processes influence society (Martone et al. 2017).

The research field on ecosystem functioning and services can benefit massively from the use of multiple approaches ranging from experimental to modeling. The application of multiple methods to unravel the ecosystem functioning mechanisms impacted by climate change will prevent blind spots and may decrease uncertainties on environmental management. Therefore, it is essential to apply a diverse set of tools at our disposal to tackle ecological questions and incorporate ecology in socio-economic field.

Aim of the study

Climate change is an ongoing process that has been affecting biodiversity directly and indirectly. The latest IPCC report (2019) predicts that (due to warming, stratification, light, nutrients and grazing) primary productivity will decline by 4–11 % until 2100. The report also emphasizes that decline of net primary production will result in lower biomass of marine animals leading to the shift of structure of marine food webs. The hypothesis of this thesis is that the alterations on energy flow of food webs due to climate regime changes will impact the functioning of ecosystems, hindering the delivery of ecosystem services (Figure A.1).

This thesis combined experiments with different modeling approaches to unravel the mechanistic effects of climate change on the ecosystem functioning and services provided by temperate coastal marine communities supported by benthic macrophytes. The aim of this study was to use single species responses, trophic interactions and whole-system perspective for addressing changes in ecosystem functioning and services. I aimed at addressing the following questions in this thesis:

1. How do the physiological responses of species and ecological interactions, modulated by temperature, affect carbon balance in a food web?
2. Does the sudden increase of temperature (heatwaves) alter energy flow distribution and functioning of ecosystems?
3. Do heatwaves jeopardize the delivery of ecosystem services?

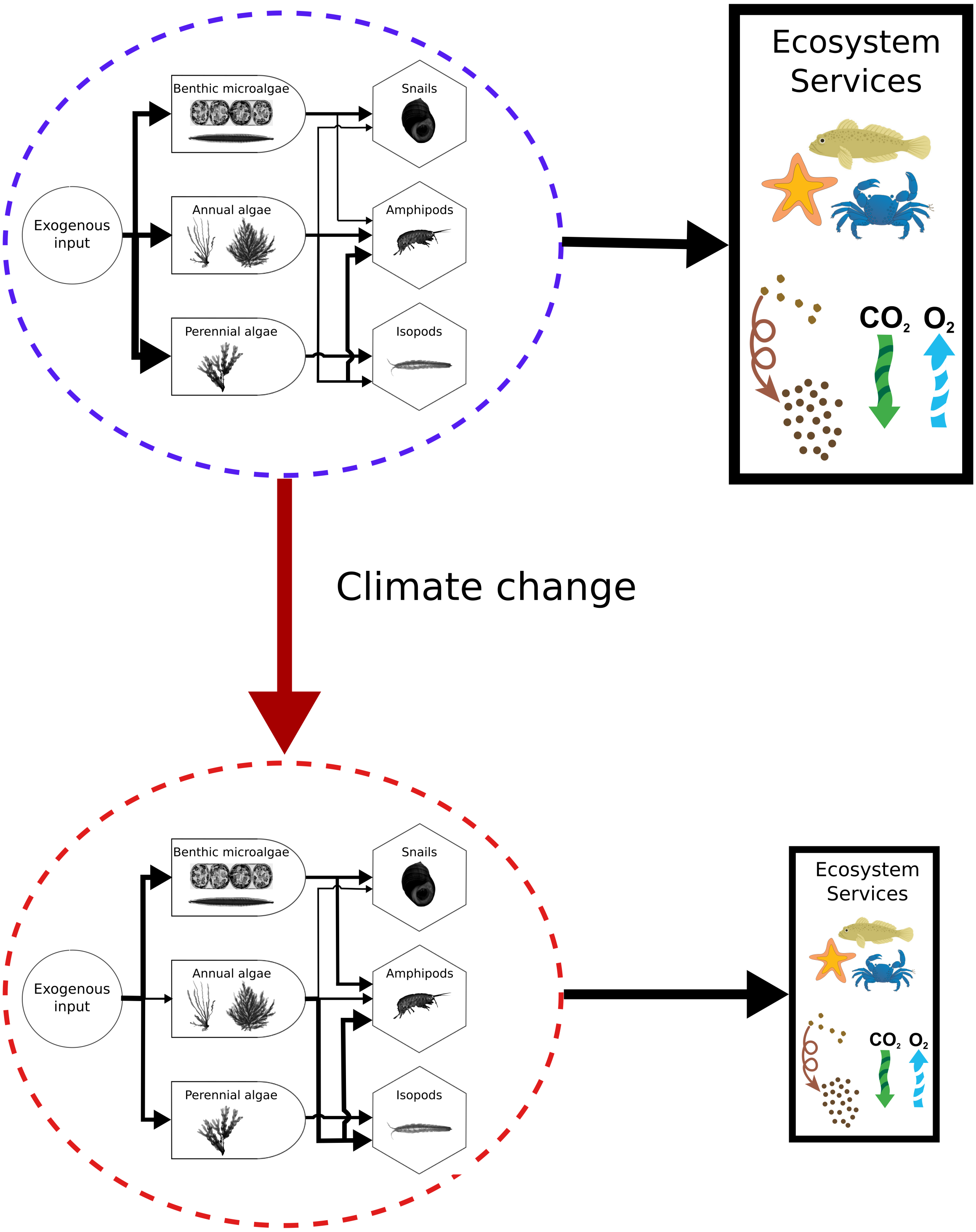


Figure A.1 – The energy flow of food webs is altered by climate change, i.e. some ecological interactions become stronger or weaker, modifying the functioning of the ecosystem and the provisioning of ecosystem services.

Chapter I

In the first chapter, I investigated the energy budget of a simplified food web under temperature gradient. The first part of the study focused on single-species response variables to temperature. Therefore, I measured primary production, respiration and growth of the macroalgae *Fucus vesiculosus* and the respiration, growth and egestion of the mesograzer *Idotea balthica*. The hypothesis is that the response variables of the macroalgae were going to increase with temperature and the response variables of the grazer were going to collapse around 22 °C. In the second part of the study, I calculated the consumption rates of grazers based on their growth, egestion and respiration rates. The consumption was used for quantifying the proportion of carbon assimilated by photosynthesis that was grazed (GPP:C). This ratio should indicate the proportion of carbon that is mobilized by grazing activity instead of being stored as biomass.

Chapter II

In this study, I increased the complexity of the food web and the stressor. The experiment was conducted in the Kiel Outdoor Benthocosms (KOB), where communities based on the macroalgae *Fucus vesiculosus* and the seagrass *Zostera marina* were exposed to temperature variation. The near-natural condition of the experiment allowed the entry of plankton (i.e. phytoplankton, zooplankton and larval stages) inside the tanks, and daily and seasonal fluctuations (e.g. light and nutrients). The temperature treatments were: a control treatment that experienced no heatwave (0HW), one strong heatwave by the end of the summer (1HW), and three heatwaves along the spring and summer (3HW). I applied ecological network analysis (ENA) to investigate the energy flows of the food web, in order to comprehend the alterations in the functioning of the studied ecosystem. The hypothesis was that the system would go through a learning process after being exposed to successive heatwaves (3HW), thus the functioning of the ecosystem exposed to 1HW would be more harmed than the one exposed to 3HW after the last strong heatwave of the summer.

Chapter III

Using the same experimental ecosystem from the Chapter II, I investigated how ecosystem services changed when exposed to heatwaves events. The ecosystem services selected were climate regulation, waste regulation and habitat provision. From the analysis of Chapter II, it was possible to identify the groups of organisms that were essential for the ecosystem services selected. The groups of organisms and the ecosystem services were considered nodes of a network. The interactions were depicted in a matrix and classified in negative (-1), positive (1) or no effect (0). I used qualitative network analysis (loop analysis) for predicting the direction of the effect of heatwaves on the ecosystem services. The input that represented the impacts of the heatwaves was based on reaction of the metabolism of the organisms. The hypothesis was that the ecosystem services would follow the same direction as the functioning after the disturbance.

Chapter I

Chapter I

Effects of temperature on carbon circulation in macroalgal food webs are mediated by herbivores

Abstract

Warming is one of the most dramatic aspects of climate change and threatens future ecosystem functioning. It may alter primary productivity and, thus, jeopardize carbon sequestration, a crucial ecosystem service provided by coastal environments. *Fucus vesiculosus* is an important canopy-forming macroalga in the Baltic Sea, and its main consumer is *Idotea balthica*. The objective of this study is to understand how temperature impacts a simplified food web composed of macroalgae and herbivores to quantify the effect on organic carbon storage. The organisms were exposed to a temperature gradient from 5 to 25 °C. We measured and modelled primary production, respiration, growth and epiphytic load on the surface of *Fucus* and respiration, growth and egestion of *Idotea*. The results show that temperature affects physiological responses of *Fucus* and *Idotea* separately. However, *Idotea* proved more sensitive to increasing temperatures than the primary producers. The lag between the collapse of the grazer and the decline of *Fucus* and epiphytes above 20 °C allows an increase of carbon storage of the primary productivity at higher temperatures. Therefore, along the temperature gradient, the simplified food web stores carbon in a non-monotonic way (reaching minimum at 20 °C). Our work stresses the need of considering the combined metabolic performance of all organisms for sound predictions on carbon circulation in food webs.

Introduction

Future predictions on global carbon cycle estimate the rise of atmospheric carbon concentration due to anthropogenic CO_2 emissions, the magnitude of which increases even further when the ocean-atmosphere models are integrated with the responses of primary producers to climate change (Cox et al. 2000). The carbon fixation through photosynthesis and the release of carbon through respiration determine whether the system is a sink or a source of carbon (Valentini et al. 2000). Warming may decrease net primary production due to steeper increase of respiration than photosynthesis to rising temperature (Tait and Schiel 2013). This mechanism leads to a reduction in carbon fixation by primary producers thus jeopardizing global carbon sequestration (Mystakidis et al. 2016).

In coastal marine systems, canopy-forming seaweeds are responsible for a substantial proportion of total carbon storage (Golléty et al. 2008). For example, in the Australian coast, the estimated storage in living macrophytes biomass is $2200 \cdot 10^6$ grams of carbon per square kilometer (Hill et al. 2015). However, changes in the temperature regime (e.g. fluctuations and warming) threaten key macroalgae populations and their functioning (Wernberg et al. 2010; Wahl et al. 2015; Arias-Ortiz et al. 2018). In general, temperature-driven individual- and community-level shifts of physiological responses (Vasseur et al. 2014) and trophic interactions (Gilbert et al. 2014) can impact ecosystem functioning, such as carbon flow within the food web (Duarte and Cebrian 1996).

Under climate change scenarios, grazing plays an important role in maintaining balanced food webs. For instance, mesograzers consume epiphytic and free floating algae thus increasing light penetration and releasing habitat-forming macrophytes from competition (Alsterberg et al. 2013). Mesograzers also prey upon small herbivores that feed on benthic microalgae resulting in top-down control (Alsterberg et al. 2013). However mesograzers may pose a risk to primary producers (Gutow et al. 2016). Provost et al. (2017) demonstrated that besides direct effects of warming, indirect effects such as increase in herbivory represent additional threats to kelps exposed to higher temperatures. The strength of trophic interactions varies with temperature due to changes in physiological responses (Brown et al. 2004), e.g. consumers experience an increase in metabolic rates with rising temperature that results in individual and population growth and intensification of feeding rates (O'Connor et al. 2009).

Individual thermal performances are usually hump-shaped, indicating that biochemical reaction rates accelerate until the optimum temperature (Pörtner and Farrell 2008; Harley et al. 2012). The metabolic intensification, which occurs until the optimum temperature, increases loss of energy through respiration resulting in higher energy demand. All the organisms that compose a food web are vulnerable to the increase of energy demand resulting in the amplification of consumption in all trophic levels. Thus, the amount of energy produced by the lowest trophic level, which is already reduced by physiological response to temperature, becomes the limiting factor that determines the structure of the biological community (Kordas et al. 2011). The ensuing alterations of the food web structure depend on the specific tolerance to warming and the effective trophic level of the interacting organisms involved. A possible scenario is that herbivores cope with their rising energy demand by increasing grazing rates (O'Connor 2009). An alternative scenario is related to the loss of herbivores that do not tolerate warming. This loss might alleviate the pressure on the base of the food web, thus resulting in thriving primary producers (Petchey et al. 1999). The combination of both scenarios means that the rise in temperature enhances the metabolic activity of herbivores, thus triggering the top-down control on primary producers until the optimum temperature of the grazers is attained. If the temperature continues to rise above the optimal thresholds of herbivores, they will reduce their consumption (i.e. the declining part of the hump-shaped curve) until reaching their upper temperature tolerance limit, thus releasing the primary producers from top-down control (Mertens et al. 2015).

Fucus vesiculosus plays important roles in ecosystem functioning since it provides a habitat to numerous species (Wikström and Kautsky 2007) and contributes to nutrient binding, oxygen production and carbon fixation in coastal food webs (Worm et al. 2000). The *Fucus* populations in the Baltic Sea have already experienced steep decline since the 1970s, which was attributed mainly to high input of nutrients (Nilsson et al. 2004). The increase of nutrients may cause a phytoplankton bloom that, due to decreased water transparency, restricts the macroalgae population to shallower depths (Kautsky et al. 1986). Another side effect of nutrient load is the excessive growth of filamentous algae (Nilsson et al. 2004). The filamentous algae may affect *F.*

vesiculosus in different ways. The first one is the increase of competition for hard surfaces during the recruitment stage (Berger et al. 2003, Kraufvelin et al. 2007). The second one is that epiphytic filamentous algae may attract grazers that consume both epiphytes and host algae, i.e. "co-consumption", although they may also protect *F. vesiculosus* from direct predation, i.e. "protective coating" (Wahl and Hay 1995; Karez et al. 2000; Råberg and Kautsky 2008). In the Baltic Sea, the isopod *Idotea balthica* exerts strong control on primary producers and is the main consumer of *F. vesiculosus* (Engkvist et al. 2000).

In this work, we studied the impact of temperature on carbon fluxes together with the interaction between the macroalgae system, i.e. the *Fucus*-epiphytes assemblage (Thornber et al. 2016) and the mesograzer *I. balthica*. We aimed to (a) investigate how single physiological responses of the *Fucus*-epiphytes assemblage and *I. balthica* are modulated by different temperatures and (b) quantify the amount of carbon transferred through the trophic interaction between the grazer and the macroalgae assemblage along the temperature gradient. We expect temperature to regulate the carbon balance directly by affecting the physiology at individual-level and indirectly due to its effect on grazing rates. Modelling the carbon balance from a system perspective might challenge the interpretation based on the performance of single species.

Materials and methods

Material collection

Individuals of *F. vesiculosus* were collected in the Kiel Fjord (54°38'N, 10°20'E) on 17-Oct-2016 and transported within 20 minutes to the facilities of GEOMAR while maintained in the seawater from the sampling site. The algae were collected together with attached cobbles, as naturally occur in the field. The *Fucus* individuals were placed in tanks inside a climate chamber at field temperature (15 °C) for 24 hours with continuous flow through of seawater. The tanks were equipped with a combination of LED lights providing an irradiance level of 165 µmol photons m^{-2} s^{-1} (eco+ LED-Leiste SUNSET 3500K 34W and eco+ LED-Leiste DAY 5500K 34W, LEDAquaristik UG, Hövelhof, Germany). The organisms were kept under 12:12 hours light:dark cycle, which corresponded to field conditions when the material collection took place. After the initial 24 hours, all individuals of *F. vesiculosus* were submerged in freshwater for 20 seconds, a procedure ensuring the removal of all motile organisms associated with the thalli (Holmlund et al. 1990) and the *F. vesiculosus* were then placed in the experimental setup. The organisms removed with freshwater were retained in a sieve and 18 *I. balthica* individuals of approximately 1.2 cm were collected. Each individual was kept isolated inside a 200 mL glass jar with food ad libitum and continuous aeration for temperature acclimation.

Experimental design

The experiment was conducted in the climate chamber from 17-Oct to 30-Nov-2016. The macroalgae were kept in 10 L buckets that were maintained in thermobaths. The buckets were equipped with a mosquito net (mesh size 1.5 mm, installed vertically dividing each bucket into two equal sized halves). In each half of the bucket, one *F. vesiculosus* individual of comparable biomass (mean wet weight = 11.2 g, sd = 5.5 g) was placed. The buckets were supplied with continued aeration and received a flow through of 13 L sand-filtered seawater per day pumped from the Kiel Fjord. There were three replicate buckets per temperature treatment.

The target temperatures for the experiment were 5, 10, 15, 20, 22 and 25 °C. Since we expected *I. balthica* to decline at 25 °C, we added 22 °C for keeping a higher resolution of the hump-shaped curve of the thermal performance. These temperatures were reached by gradually increasing or decreasing 1 °C per day the initial temperature of the tanks (15 °C). In order to have identical rates of temperature change, the starting points of warming and cooling differed in time. After 10 days all tanks attained the target temperatures. Once the target temperatures were reached, in only one of the two halves of each bucket we introduced one individual of *I. balthica* in order to assess the effect of grazing on *F. vesiculosus*. The temperature treatment ran for four weeks. We started the experiment in October since field temperature matched the mean temperature of the selected gradient (15 °C). Moreover, carrying out the study during this month kept at minimum the amount of energy invested by *F. vesiculosus* for reproduction (Graiff et al. 2017).

Every week the macroalgae were separated from the grazers for two days. Both were maintained in thermobaths at the corresponding temperatures; the macroalgae were kept in the buckets and each isopod was transferred to a 200 mL-glass jar for egestion quantification before the respiration measurement. This separation process imposed transient starvation on the grazers. However, moderated starvation periods have little or no effect on lipid content and survival of adult *I. balthica* (Gutow et al. 2007).

Incubations

Every week we incubated the *Fucus*-epiphytes assemblage (i.e. the brown algae together with associated epiphytes) for photosynthesis and respiration measurements and each *I. balthica* individually for respiration measurements.

The photosynthesis and respiration of the *Fucus*-epiphytes assemblage were measured in 6 L gas-tight cylindrical chambers equipped with a stirrer and a non-invasive oxygen sensor spot PSt3 (PreSens Precision Sensing GmbH, Regensburg, Germany). The seawater used for incubations was filtered through a 1 µm polypropylene sediment filter. After sealing the chamber, the change in oxygen concentration was logged during one hour using the Multi-channel Fiber Optic Oxygen Meter Oxy-10 mini (PreSens Precision Sensing GmbH, Regensburg, Germany). The incubation chambers were kept in thermobaths respecting the corresponding temperatures. The photosynthesis (net primary production, NPP) incubations were performed under light conditions (165 µmol photons m^{-2} s^{-1}). The respiration measurements were performed in the dark after a black cover was temporarily placed over the tanks. During every incubation, a control chamber containing only filtered seawater was measured for correcting possible changes in oxygen concentration.

The respiration of *I. balthica* was measured in 100 mL Winkler bottles. The measurements were carried out with the PreSens system described above and logged during one hour, after sealing the bottle. The water used for incubation was filtered through 0.2 µm Whatman mixed cellulose ester filter (GE Healthcare Life Sciences, Germany) and kept in bottles inside thermobaths overnight to reach the temperature of the respective treatments before the incubations. Control incubations of filtered seawater were carried out for detecting possible changes in oxygen concentration due to reasons unrelated to the respiration of *I. balthica* (e.g. temperature compensation). All the respiration incubations were carried out in thermobaths, in order to maintain the experimental temperature conditions.

The oxygen consumed or produced was calculated as the difference between final and initial concentrations; this value was corrected by the control incubations and standardized by incubation time, biomass (wet weight - ww, g) of the *Fucus*-epiphytes assemblage or length (mm) of *I. balthica*.

Growth of the Fucus-epiphytes assemblage

The macrophyte biomass was quantified (ww) weekly. The relative growth rate (RGR) was calculated according to eqn I.1:

$$RGR\ (\%) = 100 \cdot \frac{ln(b_t) - ln(b_{t-1})}{\Delta t} \qquad \text{(eqn I.1)}$$

where b_{t-1} refers to initial biomass, b_t indicates final biomass and Δt is the number of days between the two measurements.

Biomass of epiphytes

In order to avoid disturbing certain properties of the *F. vesiculosus* surface, e.g. bacterial composition (Wahl et al., 2010), during the experiment we did not remove the epiphytic filamentous algae growing on the host brown algae. Therefore, biomass quantification and incubations for photosynthesis and respiration refer to both the host brown algae and epiphytes (i.e. *Fucus*-epiphytes assemblage). At the end of the experiment, the epiphytes were removed from a piece of *F. vesiculosus* with a cell scraper, washed with distilled water and kept in 20 mL glass vials. The samples were frozen at -80 °C. They were thawed and dried at 40 °C for 48 hours and the dry weight was quantified. The dry weight was normalized by the wet weight of the piece of *F. vesiculosus* from which the epiphytes were removed.

Egestion and growth rates of I. balthica

Weekly, the grazers were isolated from the *F. vesiculosus* for 48 hours (period in which the macroalgae incubations were carried out). After this period, we collected the fecal pellets produced with disposable transfer pipettes and froze them at -20 °C. For dry weight (dw) determination, the pellets were thawed, placed in pre-muffled and pre-weighed Whatman glass microfiber filters (GF/C - GE Healthcare Life Sciences, Germany), freeze-dried and weighed. After each incubation, the isopods were photographed and their body length (from cephalon to telson, excluding antennas) was measured using ImageJ software (Schneider et al. 2012). After all measurements were completed, the individuals were placed back in the buckets. The body length was converted to body mass according to the eqn I.2 (author's unpublished data; see Appendix I.1):

$$\log(m) = 2.56 \cdot \log(l) - 1.86 \qquad \text{(eqn I.2)}$$

where m is body mass in dry weight (mg) and l is body length (mm). Finally, using weekly measurements of body mass we determined growth rates (eqn I.3):

$$G = \frac{(m_t - m_{t-1})}{\Delta t} \qquad \text{(eqn I.3)}$$

where G is growth rate, m_t and m_{t-1} are final and initial body mass, respectively, and Δt is the time interval between initial and final measurements (in our case, 7 days).

Carbon consumption of I. balthica

The measurements of egestion (E), respiration (R) and growth (G) rates of *I. balthica* were converted to carbon (Appendix I.1 and Appendix I.2). The values were summed to determine the carbon consumption per individual per day (C), according to eqn I.4 (Crisp 1971).

$$C = G + R + E \qquad \text{(eqn I.4)}$$

In order to quantify the energy used from the carbon storage of the primary producers, we calculated the ratio between *I. balthica* consumption and the NPP of *Fucus*-epiphytes assemblage. The ratio presents the proportion of carbon mobilized from NPP of the assemblage, thus the higher the ratio the lower the amount of carbon stored in the primary producers. The oxygen production was converted to carbon using a photosynthesis quotient of 1.2 (Kotta et al. 2000) and a respiration quotient was 0.85 (Hawkins and Bayne, 1985) (Appendix I.3). NPP of the *Fucus*-epiphytes assemblage and consumption of *I. balthica* were expressed as milligrams of carbon per day. To obtain a more realistic outcome, we scaled experimentally quantified NPP and consumption with field data of *I. balthica* density in relation to 1 kg dry weight of *F. vesiculosus* biomass to the respective temperatures (Anders and Möller 1983) (Appendix I.4).

Assimilation efficiency of I. balthica

We calculated the assimilation efficiency of *I. balthica* after Lang et al. (2017). Assimilation efficiency (e) is obtained dividing the energy assimilated (respiration plus growth) by the total consumption:

$$\varepsilon = \frac{R+G}{C} \qquad \text{(eqn I.5)}$$

Assimilation efficiency is always included in the interval $0 \leq e \leq 1$; without knowing the relative importance of the three consumption components (i.e. egestion, respiration and growth) it can be calculated with the following equation:

$$\varepsilon = \frac{e^{E_\varepsilon \frac{(T-T_0)}{kTT_0}} \, m^{\alpha_\varepsilon}}{1+e^{E_\varepsilon \frac{(T-T_0)}{kTT_0}} \, m^{\alpha_\varepsilon}} \qquad \text{(eqn I.6)}$$

where E_ε is the activation energy for assimilation efficiency, T is the temperature in Kelvin (K) and T_0 the temperature normalized to 20 °C (293.15 K), k is the Boltzmann's constant ($8.62 \cdot 10^{-5}$ eV K^{-1}), m is the body mass in grams and α_ε is the allometric exponent for assimilation efficiency. Many studies report that the allometric exponent of various types of consumers (i.e. detritivores, herbivores and carnivores) is 3/4 while the activation energy ranges between 0.6 and 0.7 eV (Brown et al. 2004; Lang et al. 2017). Here we aimed at quantifying the exact values of these constant parameters for *I. balthica*.

Statistical analysis

The focus of our analysis was to assess the effect of temperature on the carbon transfer along the *Fucus*-epiphytes-grazer system. Therefore, the weekly repeated measurements obtained for every response variable were summarized in a single mean value per replicate and temperature level. Measurements obtained from the second week onwards were considered, excluding the first week when acclimation to the target temperatures took place. In case of growth of *I. balthica*, mean daily values as biomass were used along the three weeks to avoid stochastic variations due to the molting of single individuals, which occurred during different moments. The effect of the temperature gradient over the response variables of *Fucus*-epiphytes assemblage (i.e. NPP, respiration, growth and epiphytic load) was modelled using linear regression analysis. The adequacy of the selected models was evaluated through diagnostic plots of residuals. The models were selected according to the best fit provided by the Akaike Information Criterion (AIC). Respiration, growth, egestion, consumption and ratio consumption:NPP of *I. balthica* were modelled using nonlinear least squares. The Gaussian equation fitted to these *I. balthica* responses to temperature was based on Angilletta (2006). The assimilation efficiency was fitted using nonlinear least squares and it follows a logistic model (Lang et al. 2017). The analyses were performed with the R package *stats* (R Core Team 2017).

Results

NPP, respiration and growth rates of Fucus-epiphytes assemblage

NPP and respiration increased linearly with temperature (Figures I.1a and I.1b; Table I.1). On average, the increase of NPP with temperature was marginally significant from 130.41 µmol $O_2 \cdot [\text{g ww } Fucus]^{-1} \cdot \text{day}^{-1}$ at 5 °C to 189.66 µmol $O_2 \cdot [\text{g ww } Fucus]^{-1} \cdot \text{day}^{-1}$ at 25 °C. Respiration increased from 63.27 µmol $O_2 \cdot [\text{g ww } Fucus]^{-1} \cdot \text{day}^{-1}$ at 5 °C to 158.28 µmol $O_2 \cdot [\text{g ww } Fucus]^{-1} \cdot \text{day}^{-1}$ at 25 °C. The best fit for growth rates was a quadratic polynomial (Figure I.1c) although the relationship with temperature was not siginificant (Table I.1). The modeled maximum growth rate occurred at 15 °C (2.05 % $\cdot \text{day}^{-1}$) and the minimum at 25 °C (-2.04 % $\cdot \text{day}^{-1}$).

Biomass of epiphytes

Biomass of epiphytes changed with temperature following a quadratic polynomial trend (Figure I.1d; Table I.1). The epiphytic load was low at 5 °C (average 6.15 mg dw epiphytes $\cdot [\text{g ww } Fucus]^{-1}$), reaching the highest fouling density at 15 °C (20.54 mg dw epiphytes · [g ww

Fucus]$^{-1}$). Beyond the peak, the epiphytes biomass declined to 3.79 mg dw epiphytes · [g ww *Fucus*]$^{-1}$ at 25 °C.

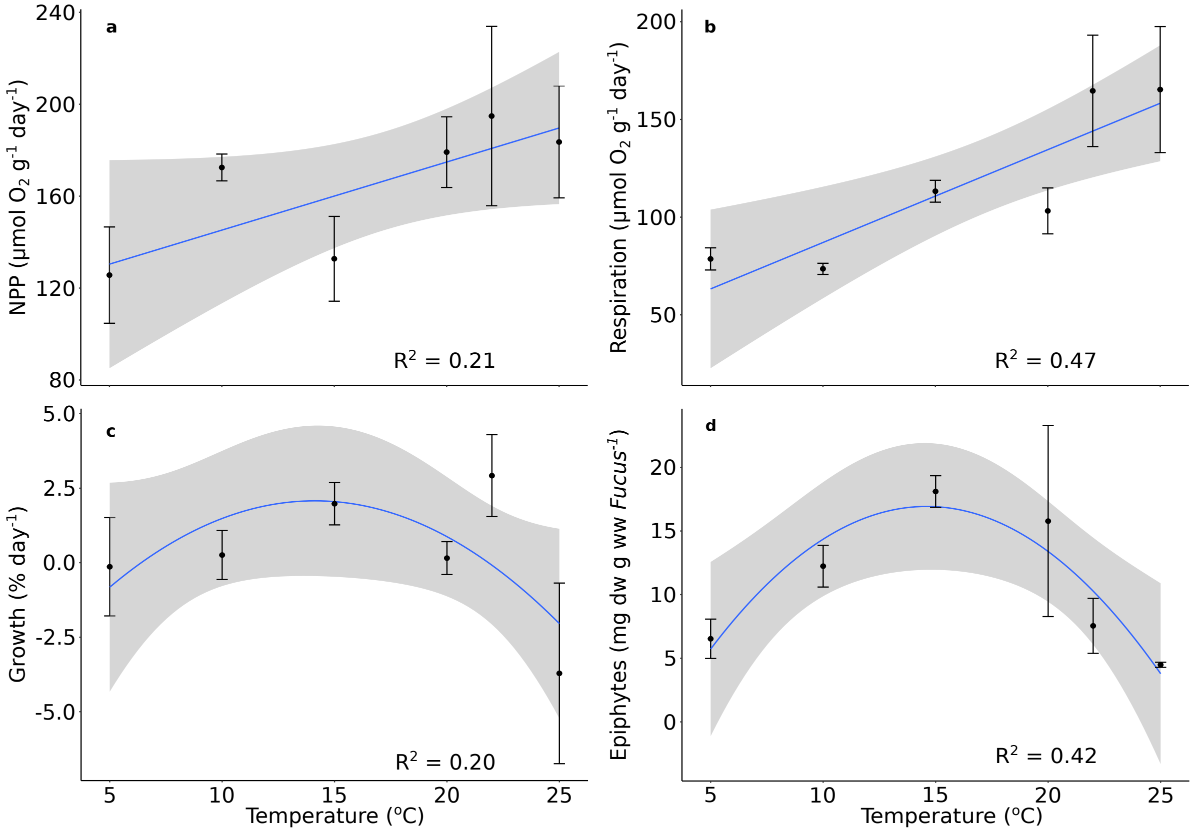


Figure I.1 – Relationship between temperature and net primary production (NPP) (a), respiration (b), growth (c) of the *Fucus*-epiphytes assemblage and macroepiphytes load on *F. vesiculosus* surface (d) (blue lines: mean trends, grey areas: 95% confidence intervals). The circles correspond to mean values and the bars to standard error of the mean (n = 3).

Respiration, egestion, growth and carbon consumption rates of I. balthica

The respiration, growth, egestion and carbon consumption rates of *I. balthica* were modelled with Gaussian fitting (Table I.2). Respiration increased from 5 to 20 °C (4.55 and 20.83 µmol O_2 · [mm *Idotea*]$^{-1}$ · day^{-1}, respectively), followed by a decrease reaching 15.29 µmol O_2 · [mm *Idotea*]$^{-1}$ · day^{-1} at 25 °C (Figure I.2a). Growth rates also increased from 5 to 20 °C (0.08 to 5.43 mg dw · day^{-1}, respectively), and decreased above this temperature to 2.45 mg dw · day^{-1} at 25 °C (Figure I.2b). Egestion rate observed at 5 °C was 0.15 mg dw · day^{-1}, followed by an increase towards the maximum value at 15 °C (0.32 mg dw · day^{-1}); after this peak, egestion decreased to 0.19 mg dw · day^{-1} at 25 °C (Figure I.2c). The amount of carbon consumed by the isopod was low at 5 and 10 °C (0.10 and 0.38 mg C · day^{-1}, respectively), increased and peaked at 20 and 22 °C (0.89 and 0.81 mg C · day^{-1}, respectively), followed by a final decline at 25 °C (0.59 mg C · day^{-1}) (Figure I.2d; Table I.2).

Table 1.1 Linear model results of the response variables of *Fucus*-epiphytes assemblage exposed to temperature gradient. The linear models follow the equation y = a + bx and the quadratic function follows the equation y = a + bx + cx^2. The element y corresponds to the response variable (NPP, respiration, growth and epyphites load), x is the temperature (independent variable) and the parameters a, b and c refer to the terms presented below.

Response variable	**Model**	**Term**	**Estimate**	**Std. Error**	**t-value**	**p-value**
NPP	Linear ($R^2 = 0.214$,	a	115.597	28.042	4.122	0.001
	$F_{1,14} = 3.803$,	b	2.962	1.519	1.950	0.071
	$p = 0.071$)					
Respiration	Linear ($R^2 = 0.465$,	a	39.514	25.129	1.572	0.138
	$F_{1,14} = 12.180$,	b	4.750	1.361	3.490	0.003
	$p = 0.003$)					
Growth	Quadratic ($R^2 =$	a	0.243	0.716	0.339	0.739
	0.202, $F_{2,15} = 1.897$,	b	-1.782	3.037	-0.587	0.566
	$p = 0.184$)	c	-5.641	3.037	-1.857	0.083
Epiphytic load	Quadratic ($R^2 =$	a	11.149	1.423	7.830	<0.001
	0.417, $F_{2,14} = 4.997$,	b	-0.614	5.871	-0.105	0.918
	$p = 0.023$)	c	-18.549	5.871	-3.159	0.006

Ratio consumption:NPP

The ratio of organic carbon consumed in relation to the NPP informs about how much useful carbon produced by *Fucus*-epiphytes assemblage is lost to grazing instead of being potentially available for growth, reproduction and exudate (e.g. as dissolved organic carbon) of the macroalgae. The ratio responded to temperature following a Gaussian trend (Figure I.3; Table I.2). From 5 to 22 °C the proportion increased from 0.001 to 0.024 decreasing at 25 °C to 0.017. Gutow et al. (2006) found that *I. balthica* is able to destroy algae patches rapidly due to sloppy feeding behavior, which we did not take into account for the proportion calculated. Thus, despite the low percentage we found in this study, this might be an underestimation of the carbon removal of the macroalgae assemblage by *I. balthica*.

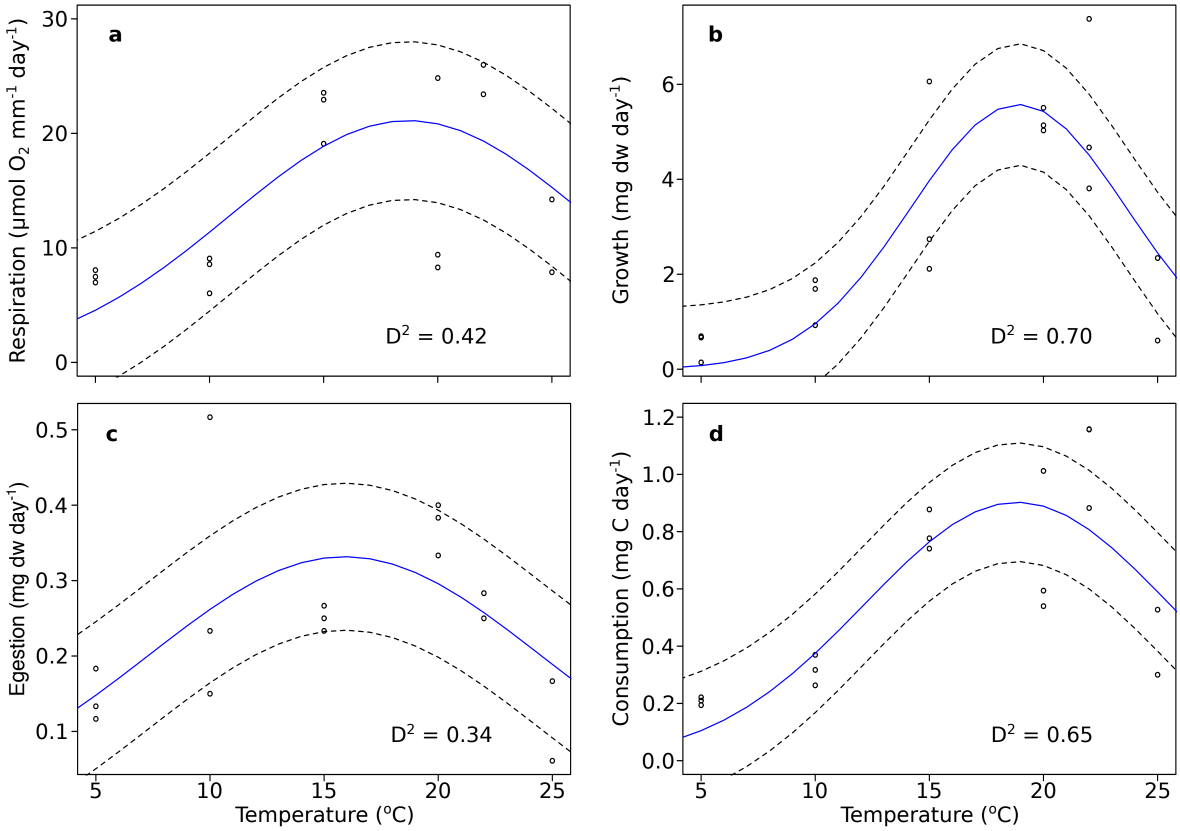


Figure I.2 – Relationship between temperature and respiration (a), growth (b), egestion (dw of fecal pellets produced per day) (c) and carbon consumption (d) rates of *Idotea balthica*. The circles correspond to the replicates (n = 3), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals.

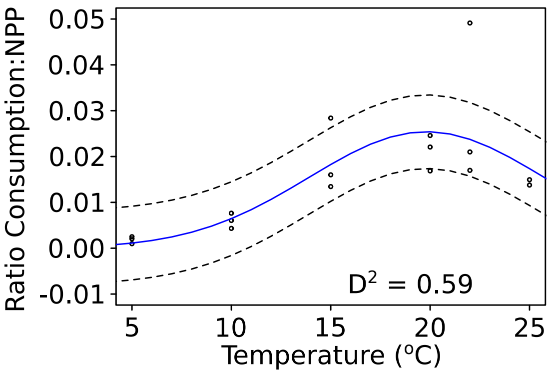


Figure I.3 – Relationship between temperature and ratio of *Idotea balthica* consumption to *Fucus vesiculosus* NPP. The circles correspond to the replicates (n = 3), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals.

Table I.2 – Gaussian model results summarizing the response variables from *I. balthica* exposed to temperature gradient. The term mu refers to mean value and the term sigma stands for standard deviation of the Gaussian distributions fitted.

Species	**Response variable**	**Term**	**Estimate**	**Std. error**	**t-value**	**P-value**
I. balthica	Respiration (D^2 = 0.42)	mu	18.710	1.729	10.821	<0.001
		sigma	7.828	2.089	3.747	0.002
	Growth (D^2 = 0.70)	mu	18.910	0.677	27.910	<0.001
		sigma	4.747	0.813	5.833	<0.001
	Egestion (D^2 = 0.34)	mu	15.899	1.302	12.204	<0.001
		sigma	8.579	1.961	4.374	<0.001
	Consumption (D^2 = 0.65)	mu	18.843	0.990	19.030	<0.001
		sigma	6.673	1.178	5.663	<0.001
Ratio Consumption:NPP (D^2 = 0.59)		mu	19.822	1.342	14.770	<0.001
		sigma	5.930	1.508	3.931	0.001

Assimilation efficiency

The assimilation efficiency of *I. balthica* followed a logistic trend that tends to saturation with increasing temperature (i.e. especially, starting from 15 °C; Figure I.4). By applying the eqns I.5 and I.6 to our data, we fitted a logistic curve and obtained the value of the constant parameters representing the allometric exponent ($\alpha_\varepsilon = 0.77$) and the activation energy ($E_\varepsilon = 0.74$ eV) for the assimilation efficiency of *I. balthica*. These values comply with those of the metabolic theory (Brown et al. 2004) as illustrated by Lang et al. (2017), i.e. $\alpha_\varepsilon = 0.75$ and $0.6 \text{ eV} \leq E_\varepsilon \leq 0.7 \text{ eV}$.

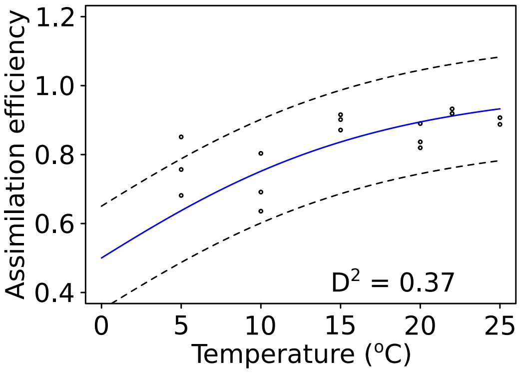


Figure I.4 – Relationship between temperature and assimilation efficiency of *Idotea balthica*. The circles correspond to the replicates (n = 3), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals.

Discussion

In this work we measured individual-level metabolic responses of two consecutive trophic levels exposed to a temperature gradient and combined them to quantify the potential carbon storage in the primary producers of this simplified food web. The NPP rate of *F. vesiculosus* presented an increase (marginally significant) and respiration rates of the macroalgae increased linearly under the temperature gradient to which they were exposed (Figure I.1). The respiration and growth rates of the mesograzers reached maximum values at ca. 20 °C, while egestion rate peaked at 15 °C (Figures I.2a, I.2b and I.2c). The proportion of carbon consumed by the isopods to the NPP of the *Fucus*-epiphytes assemblage (Figure I.3) followed the individual carbon consumption trend of *I. balthica* (Figure I.2d) with both peaking around 20 °C. The carbon balance of the trophic interaction between the *Fucus*-epiphytes assemblage and *I. balthica* was regulated by temperature. The combination of metabolic processes with different functional responses (i.e. the modelled trends) illustrates that conclusions on carbon balance differ when considering single species in isolation versus a system perspective.

F. vesiculosus is able to withstand a wide range of environmental changes, since the species is exposed to different temperatures along the seasons (Takolander et al. 2017). Graiff et al. (2015) demonstrated that the temperature for maximum photosynthesis capacity (expressed as maximum relative electron transport rate) was 24 °C. Takolander et al. (2017) found that temperatures beyond

26 °C jeopardize the photosynthetic activity of the macroalgae. In our study, the rates of NPP did not decrease along the temperature gradient and respiration of the *Fucus*-epiphytes assemblage increased linearly with temperature (Figures I.1a and I.1b). Our experimental temperature did not exceed 25 °C, which could be the reason we did not detect a collapse in NPP rates. In addition, we were not able to directly disentangle the contribution of *F. vesiculosus* to NPP and respiration from that of epiphytes. However, Binzer and Middelboe (2005) demonstrated that the photosynthetic performance per thallus surface area of *Fucus* in isolation is higher than that of epiphytic filamentous algae. Graiff et al. (2015) showed that the highest rates of *F. vesiculosus* growth ranged between 15 and 20 °C. In our work, although the growth rate trend (Figure I.1c) was comparable with the previous study, it did not respond significantly to temperature (Table I.1). In light of these results and the similiarities of our trends to those obtained by previous studies (Graiff et al. 2015; Takolander et al. 2017), we suggest that in our work *F. vesiculosus* was the main responsible for NPP changes. Noticeably, the NPP rate was relatively low at 15 °C, the temperature in which the epiphytic load peaked (Figure I.1d). This pattern could indicate that epiphytes negatively affected the photosynthetic activity of *F. vesiculosus* due to shading (Vogt and Schramm 1991; Rohde et al. 2008).

Differences in the trends displayed by the physiological responses of *I. balthica* in relation to temperature were detected. Our study shows that all metabolic variables considered for *I. balthica* responded to temperature following a non-monotonic curve, exhibiting increasing values up to the optimum (Strong and Daborn 1980). Respiration and growth rates peaked at ca. 20 °C, beyond which they decreased, showing considerably lower values at 25 °C (Figures I.2a and I.2b). Similarly, Panov and MacQueen (1998) observed that high temperatures are responsible for low growth rates of amphipods. In case of respiration, our model corroborates the findings of Gutow et al. (2016) between 10 and 22 °C. Our results demonstrate that beyond 22 °C, the respiration rate declines, revealing the upper limit for this response variable for *I. balthica*. Clarke and Fraser (2004) suggested respiration rates as an appropriate indicator for basal metabolism (i.e. energy necessary for maintaining essential metabolic activities) in invertebrates because the respiration is related to the synthesis of ATP. Therefore, a temperature of 20 °C can be regarded as the limit of *I. balthica* metabolism capacity since the respiration rates attain their maximum. Differently, egestion rate peaked at lower temperature (15 °C; Figure I.2c). Although the biomass of algae consumed directly by the grazer was not quantified in our experiment, Gutow et al. (2006) found that *I. balthica* egests about 90% of the ingested algae. The high percentage is attributed to the herbivore feeding, i.e. the algae are available in excess and such diet is poor in nitrogen and proteins thus the feeding rate must be intensified in order to supply the isopod's demands.

As an analogy to ecosystem functioning, the fitness of individuals should be considered as multidimensional (Laughlin and Messier 2015). Thus, in order to have a better perspective of how the grazers interfere in the carbon balance, we integrated the physiological response variables that result in energy expenditure (i.e. respiration, growth and egestion) for calculating carbon consumption. Our outcomes on the individual responses demonstrate that the carbon consumed by *I. balthica* was modulated by temperature (Figure I.2d). The *I. balthica* consumption changed very little at low temperatures (between 5 and 10 °C) and increased from 10 to ca. 20 °C, followed by a drastic decrease beyond this threshold. Respiration is usually the most important determinant of an individual's carbon budget (López-Urrutia et al. 2006) but our results show that both growth and respiration can mostly explain the changes of this response variable for *I. balthica*.

Allen et al. (2005) suggested that the carbon stored in the individuals can be scaled up to calculate the storage capacity of ecosystems. Therefore, we focused on the proportion of NPP consumed by *I. balthica* to understand how the carbon storage in the simplified food web of the experiment was modulated by the temperature gradient. Although the NPP rate increased linearly with temperature, the ratio of carbon consumed by *I. balthica* in relation to NPP increased up to 20 °C and decreased at 25 °C (Figure I.3). This outcome can be explained by the mesograzer's carbon consumption and is coherent with the increase of grazing on the primary producers that was previously found to occur in temperatures up to 20 °C (Gutow et al. 2016). The change in the ratio is due to the reduction of the metabolism of *I. balthica* (Figure I.2) at temperatures above 22 °C. Werner et al. (2016) also found that warming affected the metabolism of grazers at lower temperatures than that of the primary producers. This pattern confirms the finding of Mertens et al. (2015) that the daily interaction strength per capita increased up to 20 °C. Between 22 and 24 °C the strength declined significantly, i.e. the primary producers outperformed the grazers under higher temperatures. Our results show that the decline of potential carbon storage is driven by *I. balthica* within the temperature range of its maximum consumption (from 15 to 20 °C; Kotta et al. 2006). Therefore, the carbon storage in this simplified food web is regulated by top-down control only at temperatures between 15 and 20 °C, while above such interval the decline in the consumption of the grazers was severe enough to attenuate the effect on the NPP.

Although the grazer's consumption in relation to NPP may be regarded as negligible (up to 2.5%), the secondary production is a relevant link to higher trophic levels in the food web (Waters 1977). Secondary production is defined as the formation of biomass by heterotrophic organisms (Benke and Huryn 2010) and is directly dependent on assimilation efficiency, which is modulated by temperature (Lang et al. 2017). In our study, the assimilation efficiency increased with temperature (Figure I.4) and, according to the values of Lang et al. (2017), at higher temperatures the assimilation efficiency of *I. balthica* was comparable to that of carnivores. The authors detected differences in the assimilation efficiencies of detritivores, herbivores and carnivores, attributing the dissimilarities between the feeding modes to digestibility. Jormalainen et al. (2005) found that phlorotannin produced by *F. vesiculosus* was responsible for lowering assimilation efficiency in *I. balthica* since this compound decreases digestibility. However, temperatures higher than 20 °C inhibit the production of phlorotannins by brown algae (Cruces et al. 2012), which supports high assimilation efficiency of the grazers. In our study such pattern is further corroborated by the egestion rates of the isopod, which decreased at 20 °C thus suggesting higher digestibility. Therefore, the secondary production in the present work was a product of the synergistic response of autotrophs and heterotrophs to temperature.

Warming is expected to intensify the loss of carbon stored within the living systems (Allen et al. 2005). Here we show that at temperatures higher than 20 °C the *Fucus*-epiphytes assemblage presents higher capacity to store carbon while the grazers display a decline in all metabolic responses. The combination of the linear NPP trend of the macroalgae (Figure I.1a) together with the Gaussian distribution of *I. balthica* consumption (peak at 18.8 °C; Figure I.2d; Table I.2) resulted in a Gaussian response (ratio consumption:NPP; Figure I.3) that attains its maximum at 19.8 °C (Table I.2). These outcomes emphasize how integrating the study of the physiological responses of single species with herbivory is crucial to quantify functioning and services provided by primary producers under global warming scenarios.

Conclusions

In this work we showed that the strength of the interaction between the *Fucus*-epiphytes assemblage and *I. balthica* is modulated by species-specific physiological responses to temperature. The decline of the herbivore's physiological performance causes an increase in carbon storage at the level of the primary producers. Therefore, the interaction strength between primary producers and herbivore plays an important role in driving the carbon balance of the system in times of ocean warming. The inclusion of primary producers has been shown to be an essential feature to yield accurate carbon cycle estimates using ocean-atmosphere models (Cox et al. 2000). Here we demonstrate that trophic interactions should not be neglected if the goal is to generate realistic predictions of carbon storage and circulation in food webs.

Chapter II

Temperate benthic ecosystems become less productive and resilient when exposed to sequential heatwaves

Abstract

The world is going through severe climatic change. Besides the increase in mean global temperature, longer length and higher frequency of heatwaves will become more common. Marine heatwaves have already caused massive mortality of benthic macrophytes, which are responsible for high amounts of carbon storage. Moreover, a shift in biodiversity occurred in such areas since many of these primary producers are also foundation species. The objective of our work was to understand the effect of heatwaves on temperate coastal benthic communities, which in the Baltic Sea are mainly supported by the macrophytes *Fucus vesiculosus* and *Zostera marina*. Based on near-natural experiments in the Kiel Outdoor Benthocosms we analyzed the structure of energy flows in food webs exposed to different temperature regimes: without heatwaves (0HW), with one heatwave (1HW) and with three heatwaves (3HW) along spring/summer. We investigated the responses of the ecosystem to HW by applying ecological network analysis (ENA). A single HW enhanced redundancy of the flows but at the same time reduced food web connectance. After 3HW the size of the ecosystem (i.e. the amount of energy flowing within the system) diminished due to the decline of biomass and photosynthetic activity of primary producers. Moreover, 3HW decreased ecosystem stability since the pathways for energy circulation became less diversified. The contradiction of the responses to 1HW might be an early sign of stress while 3HW treatment was clearly detrimental for the ecosystem. This work shows that sequential heatwaves cause negative impacts to ecosystem integrity (that is the basis for ecosystem services provisioning) as demonstrated mainly by the ENA indices.

Introduction

Climate change has modified temperature regimes and ocean circulation, causing shifts in species' phenology, displacement or extinction and altered ecological dynamics (Walther et al. 2002). In marine ecosystems, climatic extreme events have already compromised primary and secondary production resulting in cascading effects through food webs affecting economically important species (Walther et al. 2002). As one consequence of climate change, heatwaves are supposed to increase in intensity and duration all over the globe (Meehl and Tebaldi 2004) and marine heatwaves are becoming more common already (Frölicher and Laufkötter 2018). Marine heatwaves were reported from the Mediterranean Sea in 2003 (Garrabou et al. 2009), the coast of western Australia in 2011 (Nowicki et al. 2017), northeast Pacific Ocean in 2014/15 (Di Lorenzo and Mantua 2016) and Baltic Sea in 2018 (Humborg et al. 2019).

Heatwaves may severely impact resilience (i.e. the ability of an ecosystem to bounce back to the state previous to the disturbance; Pimm et al. 2019) of marine ecosystems. The resilience of the seagrass *Amphibolis antarctica* (which is considered a habitat-forming species) meadow was affected in Australia by the 2011 heatwave (Nowicki et al. 2017). The macrophyte experienced massive mortality, which subsequently led to a reduction in biodiversity and a shift in ecological dynamics (Wernberg et al. 2013). The seagrass meadows were replaced by a tropical species of seagrass (e.g. *Halodule uninervis*) and other macroalgae (Nowicki et al. 2017). The new assemblage of macrophytes species was not able to completely substitute the functions of the former seagrass meadow (e.g. carbon fixation, habitat provision to other species) resulting in a decrease of ecosystem services, e.g. closure of fisheries and decline in tourism (Kendrick et al. 2019). In northern Europe, the Baltic Sea has also experienced a massive heatwave in 2018 that caused the abnormal release of carbon dioxide and methane from the marine ecosystem (Humborg et al. 2019) and it is not yet known how this heatwave impacted the ecosystem as a whole. Therefore, there is an urgent need to understand in depth the effects of heatwaves on the functioning of ecosystems.

The functioning of ecosystems depends on the modulation of ecological interactions, which are highly impacted by temperature (Alsterberg et al. 2013, Raddatz et al. 2017). The performance of organisms (Wahl et al. 2019) and their interactions responds differently according to the temperature they are exposed to (Ito et al. 2019a), resulting in the propagation of the metabolic effects along the food web (Baird et al. 2019). The food webs embedded in ecosystems can be analyzed by combining the qualitative structure of the network ("who interacts with whom") and the quantitative dimension of these interactions ("how much they interact") through ecological network analysis (ENA; Ulanowicz 2004). The construction of weighted networks enables quantifying the amounts of energy exchanged between ecosystem compartments (e.g. species, trophic groups, particulate organic matter); furthermore, ENA provides a set of indices that assist the evaluation of the ecosystem status. Whole-system indices are sensitive to disturbance and may, for example, detect early signs of stress (Bondavalli et al. 2006), the impact of invasive species introduction (Baird et al. 2012) and effects of climate change (Schückel et al. 2015, Baird et al. 2019) on ecosystems. The study of ecological interactions is able to provide us a wider perspective of how the ecosystem reacts to different environmental conditions (Goldenberg et al. 2017).

The Baltic Sea is considered an ideal region for studying climate change effects since environmental parameters (e.g. temperature, salinity and dissolved oxygen) oscillate between extreme levels (Franz et al. 2019a). Reusch et al. (2018) compared the Baltic Sea to a "time machine" since other coastal ecosystems are supposed to experience the same range of oscillations in the future. The benthic ecosystems of the Baltic Sea are supported by foundational species such as macroalgae, seagrass and mussels. The decline of these species alters patterns of biodiversity (Wikström and Kautsky 2007) and ecosystem functioning (Franz et al. 2019b, Reusch et al. 2005). In this work, we are going to focus on an ecosystem composed mainly by two habitat-forming macrophytes. The first species is the macroalgae *Fucus vesiculosus* that represents important biodiversity harbor (Wikström & Kautsky 2007) and has already experienced severe decline (Nilsson et al. 2004). The second macrophyte is the seagrass *Zostera marina*, which also enhances biodiversity (Boström and Bonsdorff 1997) and has shown high mortality rates after a heat stress (Reusch et al. 2006). The macrophytes are responsible for increasing complexity of habitat structure, boosting the provision of food availability and providing shelter against predators. These characteristics are important for the maintenance of biodiversity and energy transfer within ecological interactions (Borst et al. 2018), which in turn reverberates along the whole food web (Baeta et al. 2011).

The objective of this work is to improve the understanding of effects of heatwaves on coastal benthic ecosystem. We exposed the benthic ecosystem to simulated heatwaves of natural amplitude and duration in a mesocosm experiment and collected data on biomass, primary production, respiration rates and stable isotopes. The dataset was combined with literature information and used to construct food webs applying ENA, in order to model energy flow along the ecosystem. This study aimed to detect changes in the activity and stability of the ecosystem (Ulanowicz 2001). The insights obtained allowed us to discuss the impacts of heatwaves on ecosystem structure and functioning.

Material and Methods

Kiel Outdoor Benthocosms and temperature treatments

The study was carried out in the Kiel Outdoor Benthocosms (KOB; Wahl et al. 2015) from 6 May to 20 August 2015. The KOB is equipped with 12 tanks of 1500 liters capacity each. The tanks are computer-controlled by ProfiLux 3.1T (GHL GmbH, Germany) allowing the regulation of temperature in the tanks. The temperature regime without heatwaves was defined based on 15 years of data (from 2000 to 2014) analyzed by a GAMM model that revealed the seasonal temperature cycles for the southwestern Baltic Sea (more details in Pansch et al. 2018). The model obtained allowed us to identify 2009 as the year with the smoothest temperature profile. We used the temperatures of the referred year as the baseline to apply the heatwaves events. The amplitude and duration of the heatwaves treatment of the experiment were also based on the patterns detected on the15-years temperature regime data analysis. The treatments applied in this experiment were (1) no heatwaves (0HW) that corresponded to the temperature of 2009, (2) one heatwave at the end of the summer (1HW) and (3) three heatwaves along end of spring and through summer (3HW) (Figure II.1). The first two heatwaves of 3HW treatment were characterized by an increase of 1.2 °C per day during four days in June and July 2015. The plus 3.6 °C temperature was kept for four days followed by a two-days cooling period until reaching the same temperature as 0HW and 1HW. In August 2015, the last heatwave was applied to treatments 1HW and 3HW. This heatwave differed from the ones before in intensity, the temperature increased 1.7 °C in average per day during three days and reached 5.2 °C above the temperature of 0HW. The peak of the heatwave was kept for four days and the cooling phase lasted two days. The values of warming and cooling phases of the heatwaves respected realistic boundaries and more details about the models used for determining the heatwaves intensity and duration are found in the supplementary material of Pansch et al. (2018).

Material collection

The organisms introduced in the tanks were collected at the Kiel fjord (54.39 N, 10.19 E) between 4 and 6 May 2015. The experimental community was composed by two main habitat-forming macrophytes the seagrass *Zostera marina* and the macroalgae *Fucus vesiculosus*. The individuals of *Z. marina* were collected and planted in beakers filled with sieved sediment (2000 µm), which was collected at the same site. Individuals of *F. vesiculosus* were collected and kept attached to the stones. In addition, the associated biota (*Littorina littorea*, *Idotea balthica*, *Gammarus sp.*, *Mytilus edulis*) was added to the tanks at densities comparable to in situ habitats. Since the tanks were supplied continuously with unfiltered seawater from the Kiel Fjord, other species settled inside the tanks during the execution of the experiment, e.g. filamentous algae and sediment in- and epifauna.

Data collection for network construction

The data used for network construction was mainly generated during the experiment; such data were verified and sometimes integrated with information retrieved from the literature. The collection of data for determining energy flows (expressed as carbon flows in mg C · m^{-2} · day^{-1}) in the food web was carried out after the last heatwave. Data collection included measurements of photosynthesis and respirations, biomass, stable isotopes, exports from primary producers, dissolved organic carbon (DOC) and particulate organic carbon (POC). Literature information was used to select the subset of resources considered to determine the feeding preferences of each trophic group (see Appendix Table II.1), in addition to their consumption, production and egestion ratios (Appendix Table II.2). We constructed one network per tank resulting in a total of 12 networks, i.e. each treatment had four replicates (n = 4).

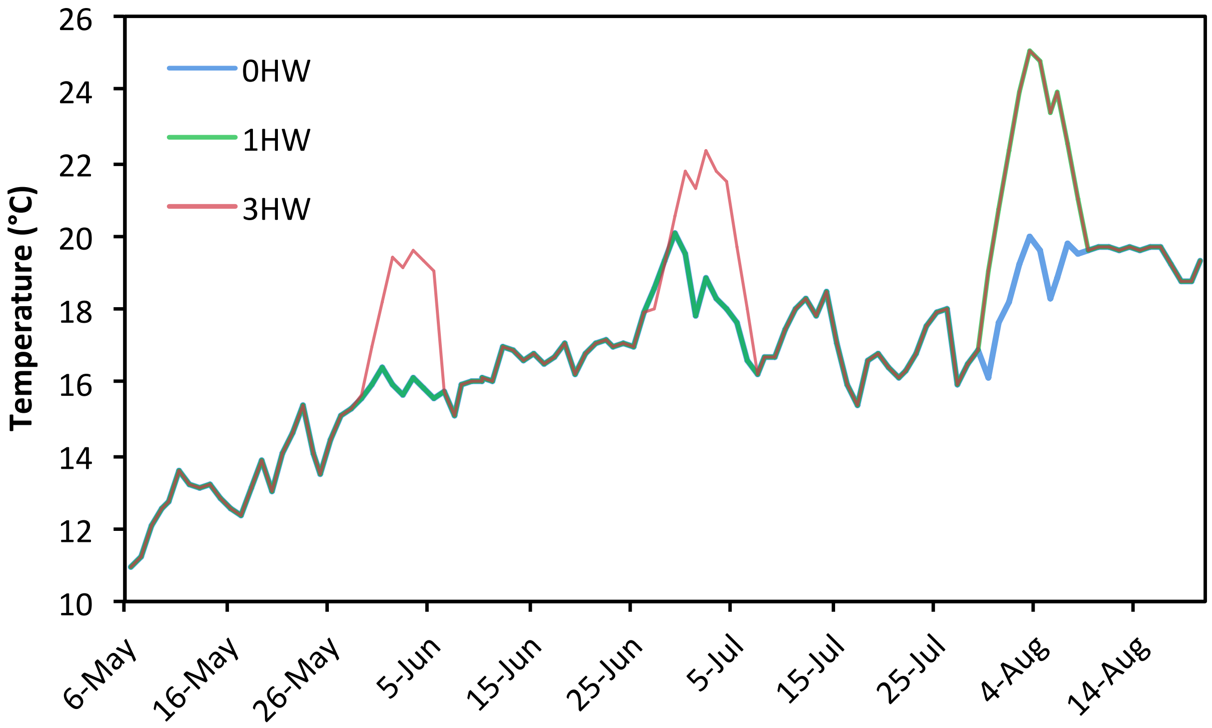


Figure II.1 – Temperature profile applied for no heatwave (0HW, blue line), one heatwave (1HW, green line) and three heatwaves (3HW, red line) treatments along spring/summer 2015

Photosynthesis and respiration measurements

The photosynthesis and respiration measurements were carried out one week after the third heatwave (10 to 14 August 2015). The primary producers (*F. vesiculosus*, *Z. marina* and filamentous algae) were incubated in gas-tight cylindrical chambers equipped with a stirrer and a non-invasive oxygen sensor spot PSt3 (PreSens Precision Sensing GmbH, Regensburg, Germany). We obtained measurements of the oxygen concentration change right after the chamber was sealed and after one (*F. vesiculosus* and filamentous algae) or four hours (*Z. marina*) using the fiber optic oxygen meter Fibox 4 (PreSens Precision Sensing GmbH, Regensburg, Germany). The photosynthesis (net primary production, NPP) incubations were performed under natural light conditions. The respiration measurements were performed in the dark after a black cover was placed around the chambers. Each incubation also had a reference chamber containing either only seawater (*F. vesiculosus* and filamentous algae) or seawater and a sediment beaker (*Z. marina*), in order to correct possible changes in oxygen concentration that were unrelated to the macrophytes activity (e.g. bacterial activity). The oxygen values were converted to carbon (Appendix II.3).

We collected organisms (*I. balthica*, *Gammarus* sp., *Nereis* sp., *M. edulis*, *Limecola balthica*) from each tank and carried out respiration measurements in laboratory using thermo baths for maintaining the temperature that corresponded to the one of the KOB. The respiration was measured in sealed 100 mL Winkler bottles and logged for one hour using the Multi-channel Fiber Optic Oxygen Meter Oxy-10 mini (PreSens Precision Sensing GmbH, Regensburg, Germany). The water used for the incubations was filtered through 0.2 µm Whatman mixed cellulose ester filter (GE Healthcare Life Sciences, Germany) and kept in bottles inside the thermo baths overnight to reach the temperature before the incubations. Control incubations of filtered seawater were carried out for detecting possible oxygen concentration changes due to reasons unrelated to the respiration (e.g. bacterial activity). The respiration values were converted from oxygen to carbon (Appendix II.3).

Biomass quantification

The biomass in wet weight of the macrophytes was estimated based on growth measurements that were carried out regularly during the experiment. The conversion wet to dry weight of *Z. marina* was based on Kraemer and Alberte (1993). While the wet weight of *F. vesiculosus* was converted to dry weight using the conversion factor of Küppers and Kremer (1978).

By the end of the experiment (20 August 2015), we collected all the heterotrophic organisms of the tanks and stored them in -40 °C for further analysis. These organisms were identified and their body size was measured using ImageJ (Schneider et al. 2012). The biomass of the organisms (*I. balthica*, *Gammarus* sp., *Littorina* sp. and Polychaeta) was inferred using size-dry weight regressions from organisms collected in the same KOB experiment (Appendix Table II.3). In addition, sediment of four 1.4 L beakers was sieved (1000 µm mesh) to collect epi- and infauna organisms (more details in Pansch et al. 2018). The organisms were identified to the lowest taxonomic level possible and the biomass was quantified.

The conversion of dry weight to carbon was based on the data acquired in parallel through stable isotopes analysis (Appendix Table II.3) of some species (i.e. *Z. marina*, *F. vesiculosus*, filamentous algae, *Gammarus* sp., *I. balthica*, *Littorina* sp., *M. edulis*, *Nereis* sp., *Limecola balthica* and *Scoloplos* sp.). The biomass of each species was standardized by area of the tanks (dimensions: 2 x 1 x 0.9 m - Wahl et al. 2015). The conversion factor from dry weight to carbon was used according to the similarity of the species (Bondavalli et al. 2006); i.e. the conversion factor for *Nereis* sp. was used for *Polydora* sp. and *Harmothoe* sp.; *Gammarus* sp. for *Corophium* sp. and *Microdeutopus* sp.; *Littorina* sp. for *Hydrobia* sp., *Scoloplos* sp. for *Marenzelleria* sp. and *Pygospio* sp.; *Limecola balthica* for *Mya* sp. and *Mysella* sp. (Appendix Table II.4).

Primary producers export quantification

The organic material from macrophytes detached and floating in the tanks were considered exports. In natural ecosystems, water currents would have transported this material to outside the studied ecosystem's boundaries where they would represent a potential source of energy. For quantification of exports, we collected leaves and thalli of primary producers (*Z. marina*, *F. vesiculosus* and filamentous algae) that were found detached and floating in the tanks. We obtained their dry weight and converted these values to carbon according to Appendix Table II.4.

POC, DOC, microalgae and zooplankton quantification

Water samples were taken from each tank plus the fjord and 180 ml were filtered through pre-muffled GFF filters. The filters were stored in -20 °C for particulate organic carbon (POC) quantification.

Filtered water samples were collected in pre-combusted 25 mL glass vials closed with Teflon washer and plastic cap. The samples were maintained in -20 °C for dissolved organic carbon (DOC) measurement. The water samples were measured using a Shimadzu TOC analyzer (TOC-VCSN). The instrument uses the high temperature catalytic oxidation (HTCO) method modified from Sugimura and Suzuki (1988). The samples were acidified and sparged with a CO_2 free gas to remove any dissolved inorganic carbon before it was then injected in 150 µL increments (3 – 5 injections per sample) on the catalyst (2% Pt on Al2O3), which was flushed with high purity oxygen (99.9995%). Organic carbon was converted in CO_2, which was detected using an infrared detector. The DOC values were obtained in µmol L^{-1}, thus the eqn. II.1 was applied to convert the values to mg C per tank.

$$y = DOC \cdot V \cdot M \cdot 1000 \div 10^6 \qquad \text{(eqn. II.1)}$$

where V is the volume of the tank (1500 L), M is the molar mass of carbon (12 g · mol^{-1}), 1000 corresponds to the conversion from g to mg and 10^6 is the conversion from µmol to mol.

The POC of the fjord was used as baseline for the dataset and the relative amounts of phytoplankton, zooplankton and water column detritus were estimated from data collected in the fjord. These parameters were proportionally quantified for each tank using the POC data collected during the experiment.

The biomass of phytoplankton was calculated based on the data from the fjord (Annegret Stuhr unpubl. data). The phytoplankton data was measured in chlorophyll a, thus it was converted to carbon based on eqn. II.2.

$$\log C = \log A + \beta \cdot \log Chla \qquad \text{(eqn. II.2)}$$

where $A = 25$ and $\beta = 0.98$ for estuarine stations, with salinity similar to the Kiel Fjord (Jakobsen & Markager, 2016).

Biomass of microphytobenthos was calculated based on the data of an experiment carried out in 2016 during the same season in the KOB (unpublished data). The dataset showed that the phytoplankton to benthic microalgae ratio was 2.25. Thus, we used the phytoplankton biomass from each tank to determine the biomass of microphytobenthos.

The zooplankton was estimated based on number of individuals in Kiel Fjord (Catriona Clemmesen unpublished data). The POC of each tank was used as baseline for the biomass of zooplankton. We considered the POC of the Kiel Fjord equivalent to the mean POC of 0HW treatment and the proportion of zooplankton per POC was calculated and estimated for each tank. The values were converted into carbon based on Appendix Table II.3.

Compartments and intercompartmental exchanges

Species classification was conducted according to taxonomic criteria and feeding behavior, with both aspects driving species aggregation in compartments (Appendix Table II.1). Benthic macrophytes were classified as *Z. marina* (ZM), *F. vesiculosus* (FV) and filamentous algae (FA). The microphytes were divided into microphytobenthos (MPB) and phytoplankton (PP). The consumers were zooplankton (ZO), bivalve-filter feeders (BF) (*M. edulis*, *Cerastoderma* sp., *Limecola balthica*, *Mya truncata*), amphipod-deposit feeders (AD) (*Microdeutopus* sp. and *Corophium* sp.), amphipod-omnivores (AO) (*Gammarus* sp.), isopod-omnivores (IO) (*I. balthica* and *Jaera albifrons*), gastropod-herbivores (GH) (*L. littorea*, *Hydrobia* sp. and *Rissoa* sp.), Polychaeta-deposit feeders (PD) (*Marenzelleria viridis*, *Polydora cornuta*, *Pygospio elegans* and *Streblospio* sp.) and Polychaeta-omnivores (PO) (*Eteone longa*, *Harmothoe imbricata*, *Nereis* sp., *Scoloplos armiger* and *Phyllodoce mucosa*). Particulate organic matter and bacteria were considered components of detritus, which it was divided into water column (WD) and sediment (SD) detritus. A last node was then considered for the dissolved organic carbon (DOC).

The intercompartmental exchanges (carbon flows) were determined based on stable isotopes analysis (Appendix Table II.4). For this purpose, we collected individuals of *Z. marina*, *F. vesiculosus*, filamentous algae, *I. balthica*, *Gammarus* sp., *Nereis* sp., *L. littorea* and *Scoloplos* sp. They were washed with distilled water and frozen at -80 °C until processing. The samples were thawed and dried at 40 °C for at least 48 hours. They were ground with agate mortar and pestle and kept in glass vials. The ground material was subsampled, weighed and placed into tin capsules (3.2 X 4.0 mm, Hekatech, Wegberg, Germany). They were analyzed by measuring simultaneously $\delta^{15}N$ and $\delta^{13}C$ using an elemental analyzer system (NA 1110, Thermo, Milan, Italy) connected to a temperature-controlled gas chromatography (GC) oven (SRI 9300, SRI Instruments, Torrance, CA, USA) that was connected to the isotope ratio mass spectrometer (Delta^{Plus} Advantage, Thermo Fisher Scientific) as described in Hansen et al. (2009). The isotopes ratios are expressed in δ values following the calculation (eqn II.3):

$$\delta X = \{(Rsample \div Rstandard - 1) \times 1000\} \qquad \text{(eqn. II.3)}$$

where X corresponds to ^{13}C or ^{15}N and R represents the ratio of the heavy isotope to the light isotope.

The set of plausible prey items was defined based on literature data for each species (see SI.2 – Table S1) and was used for modeling the stable isotopes (see Appendix Table II.2) with MixSIAR (Stock and Semmens, 2013). Feeding preferences obtained from the analysis were used as reference for the carbon flows between the compartments. The combination of these elementary details resulted in the matrices of interactions for each tank (Appendix Tables II.5, II.6 and II.7). Feeding preferences of species that were not sampled for stable isotopes analysis were retrieved from the literature (Baird et al. 2004). Consumption, egestion and production rates of each species were calculated based on respective ratios in relation to biomass (Appendix Table II.2).

The DOC excretion by macrophytes was estimated based on literature data. The dissolved carbon excretion of seagrass and filamentous algae was estimated in percentage of carbon imported by photosynthesis (gross primary production). According to Penhale and Smith Jr (1977), the DOC excreted by *Z. marina* and filamentous algae is 1.5 % and 2.1 % of the carbon fixated by photosynthesis, respectively. The DOC released by *F. vesiculosus* was estimated as 2.5 % of the carbon fixation (Carlson and Carlson 1984). Net DOC released by microalgae was considered 3.7 % of the net primary production (Lignell et al. 1993).

The flow from phytoplankton to sediment detritus (sedimentation rates) was estimated as 69.89 % of the net primary productivity - NPP (Lignell et al. 1993). From phytoplankton to water column detritus (i.e. DOC exudate to bacteria embedded in detritus) and to copepods (zooplankton) the estimations were 10.5 %, and 2.7% of the NPP, respectively (Lignell et al. 1993). For the estimations of the carbon transferred from microphytobenthos to detritus and zooplankton, we applied same parameters as those of phytoplankton. The energy transfer of zooplankton to sediment and water column was considered 25 % (Sandberg et al. 2000).

In our work, detritus refers to living and non-living particulate organic matter. Living POM includes heterotrophic bacterioplankton and protozoa (Bondavalli et al. 2006). The net productivity of bacteria was estimated as 13.45 % of the biomass, it was calculated for determining respiration rates. The ratio between bacterial net production and respiration was 1.4 (Jensen et al. 1990).

Balancing procedure

After determining all the flows, we reviewed the total input and output of each compartment to certify that the difference between them would not surpass 10 %. In order to keep this threshold, whenever the differences of input and output flows were above 10 %, we considered extra export and import. The extra export and import are important information that could provide insights on growth and biomass mobilization of the compartments, respectively (Ulanowicz 2004).

The ENA requires the system to be at steady-state (i.e. the total amount of energy entering each compartment must equal the energy leaving the compartment). All networks were constructed by manually attaining the best level possible of balancing through the use of experimental data. Therefore, in presence of deviations ≤ 10 % from steady-state, we used the *averaging input-output and output-input coefficients* (AVG2) algorithm described by Allesina and Bondavalli (2003) to balance the matrices (see Appendix Tables II.5, II.6 and II.7). The ENA was finally carried out using the software tool WAND (Allesina and Bondavalli 2004).

Information theory indices and attributes of the ecosystem

The ENA provided a set of information theory indices that are described in Appendix Table II.8, in this section we are going to provide a summary of each ENA index. We quantified growth (total system throughput, TST) and development (average mutual information, AMI) of the ecosystems, with a single index embedding both components (ascendency, A). The upper limit of ascendency is the development capacity (DC) while its counterpart is the overhead (O_t). The overhead is also categorized in (1) overhead on imports (O_i) that depicts the disorganization of the energy flows that enter the ecosystem (e.g. photosynthesis), (2) overhead on exports (O_e) disorganization of the energy exported to other ecosystems, (3) dissipative overhead (O_r) that characterizes the disorganization of the energy lost as respiration, and (4) redundancy (Re) is related to the disorganization of the internal flows. The disorganization shows that the architecture and the intensity of energy flows are homogeneously distributed, when the indices become lower they indicate that the energy flows are depending on more specific nodes and links. Some indices quantify the growth (internal capacity, DC_i) and the development (internal ascendency, A_i) of the network that excluded external exchange of energy (i.e. imports, exports and respiration). The connectance of the network was quantified for the whole ecosystem perspective (overall connectance, CC_o) that included internal and external flows, the biotic and abiotic compartments exchange (intercompartmental connectance, CC_i), and the biotic compartments only (food web connectance, CC_{fw}).

In addition, we analyzed various attributes of the ecosystem, which included total biomass, total biomass of consumers, total biomass of macrophytes, total primary productivity (total photosynthesis of macrophytes), total respiration (total energy lost from the system), total export (energy flow that leaves the system but is still usable elsewhere), ratio between respiration and primary productivity, carbon recycled (quantified with the Finn cycling index, FCI; i.e. the ratio between amount of carbon recycled and total carbon circulating in the system), carbon storage in the sediment (i.e. the amount of carbon that was retained in the sediment), carbon circulation in detritus, herbivory, detritivory, grazing chain efficiency (energy transfer efficiency from primary producers to the herbivores) and Lindeman spine efficiency (energy transfer from the first to second trophic level, without discriminating whether the first trophic level is occupied by primary producers or detritus).

Data analysis

We used the log response ratio (Hedges et al. 1999) as effect index on information theory indices and attributes of the ecosystem, in order to obtain the magnitude and direction in which the treatments (1HW or 3HW) changed compared to the control (0HW). As a validation of the significance of the test, the p-values were obtained by the permutation analysis using ad hoc R scripting.

We applied linear mixed effects models for analyzing the parameters (i.e. biomass, primary production, consumption and respiration rates) of the living compartments to test the differences between the treatments using nlme R package (Pinheiro et al. 2019). For the post hoc analysis we used the Tukey test for multiple comparison purpose using the multcomp R package (Hothorn et al. 2008)

Results

Parameters of the nodes

The 3HW treatment jeopardized the biomass of filamentous algae (FA) and *F. vesiculosus* (FV). FA declined 94.1% in relation to 0HW ($p = 0.02$; Figure II.2a) and FV decreased 18.7% in comparison to 0HW ($p = 0.06$; Figure II.2a). The biomass of FV was 29.9% lower in 3HW in comparison with 1HW treatment ($p = 0.02$; Figure II.2a). The biomass of *Zostera marina* was not significantly affected by 3HW ($p = 0.79$) or 1HW ($p = 0.41$) in comparison to 0HW (Figure II.2a). Respiration rates of the macrophytes did not change significantly ($p > 0.10$; Figure II.2b). The photosynthesis of filamentous algae was 73.8% marginally significantly lower in 3HW treatment in comparison to 0HW ($p = 0.10$; Figure II.2c) while the *F. vesiculosus* and *Z. marina* did not change significantly ($p > 0.10$). The exports from filamentous algae (i.e. usable energy that leaves the system) severely declined in 3HW treatment almost reaching no export ($p = 0.04$ in comparison to 0HW; Figure II.2d).

Although the Polychaeta compartments composed most of the biomass of the consumers (Figure II.3a), other compartments contributed to display pervasive physiological responses (amphipods omnivores, bivalves and isopods omnivores Figures II.3b and II.3c). The biomass of bivalves decreased 41.2% after 3HW ($p = 0.05$) in relation to 0HW (Figure II.3a). Interestingly, heatwaves affected the respiration rates (i.e. loss of energy from the system) of bivalves but also those of amphipods omnivores, isopods and Polychaeta detritivores (Figure II.3b). Respiration rates of amphipods omnivores significantly increased at 1HW in comparison to 0HW (44.1%; $p = 0.01$) and 3HW (62.8%; $p < 0.01$). The bivalves had the respiration rates significantly lowered in both 1HW (60.5%; $p < 0.01$) and 3HW (63.1%; $p < 0.01$) treatments in relation to 0HW. The respiration rates of isopods in the 1HW treatment amounted to 89.5% ($p = 0.15$) higher compared to 0HW and 91.4% ($p = 0.05$) in relation to 3HW treatment (Figure II.3b).

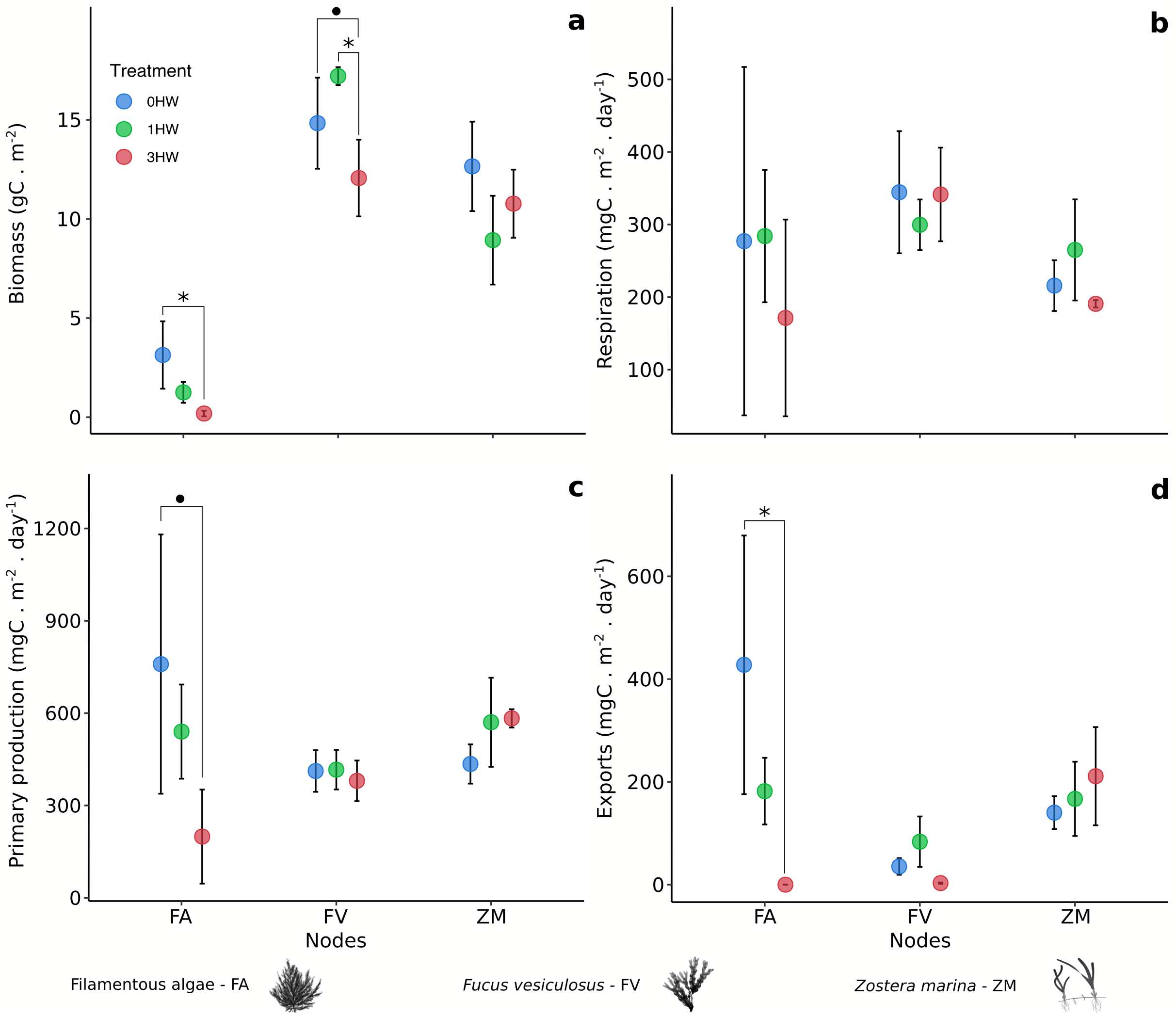


Figure II.2 – Responses (mean ± std. error) of the macrophytes in the whole ecosystem under 0HW (blue), 1HW (green) and 3HW (red). The parameters considered were biomass (a), respiration (i.e. loss of carbon from the system) (b), primary production (c) and exports (i.e. transfer of usable energy from system) (d); p-value: '**', 0.01; '*', 0.05; and '•', 0.10

The consumption rates changed in amphipods omnivores, bivalves, gastropods, isopods and Polychaeta detritivores under the effect of heatwaves (Figure II.3c). The consumption rate of amphipods omnivores exposed to 1HW increased 46.1% ($p = 0.01$) in relation to 0HW and 65.2% ($p < 0.01$) compared to 3HW. The feeding rates of bivalves decreased 59.4% ($p < 0.01$) in 1HW and 50.7% ($p < 0.01$) in 3HW treatments in comparison to 0HW. The 1HW treatment enhanced feeding rates of gastropods by 67.4% ($p = 0.11$) compared to 0HW and 112.2% ($p = 0.02$) in relation to 3HW. The isopods presented 125.4% (p = 0.05) increase of feeding rate at 3HW in comparison to 1HW but the consumption did not change (p = 0.24) in relation to 0HW. The consumption rates of Polychaeta detritivores compartment lowered by 41.5% (p = 0.10) at 3HW compared to 0HW treatment.

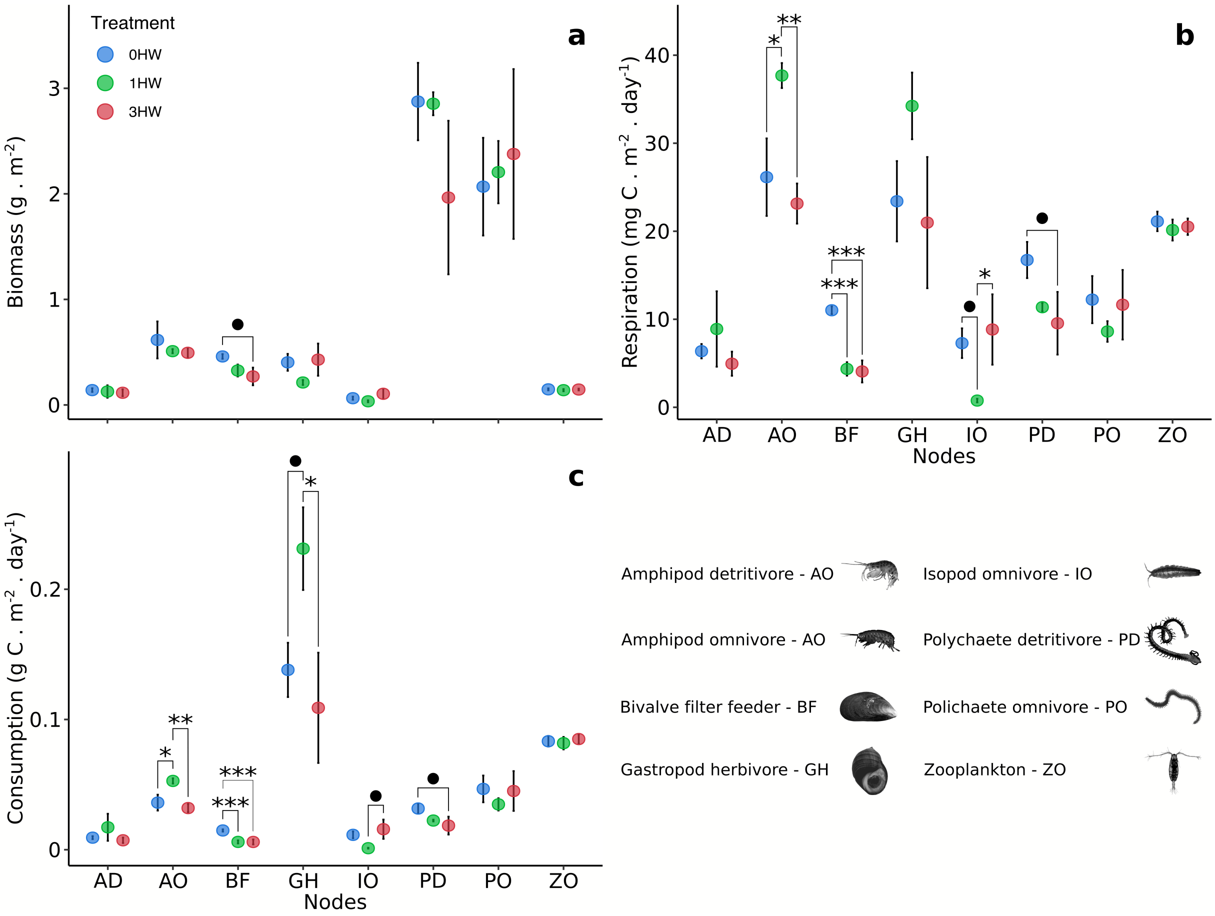


Figure II.3 – Responses (mean ± std. error) of the consumers in the whole ecosystem under 0HW (blue), 1HW (green) and 3HW (red). The parameters considered were biomass (a), respiration (i.e. loss of carbon from the system) (b) and consumption (c); p-values: '**', 0.01; '*', 0.05; '•', 0.10

Attributes of the ecosystem

The **total biomass** (Figure II.4) of the whole community (i.e. sum of all primary producers and consumers' biomasses) decreased 7% after 1HW (p = 0.12) and 10.8% after 3HW (p = 0.04). The **total macrophytes biomass** (sum of *Z. marina*, *F. vesiculosus* and filamentous algae) decreased by 10.6% ($p = 0.21$) after 1HW and 24.8% after 3HW ($p = 0.02$; Figure II.4). The **total biomass of consumers** declined non-significantly at 1HW and at 3HW ($p = 325$ and $p = 128$ respectively; Figure II.4).

Primary productivity was lower compared to 0HW in both heatwave treatments (decrease of 5.1% in 1HW and 18.8% in 3HW) but this decline was only significant for the 3HW treatment ($p = 0.32$ and $p = 0.04$ respectively; Figure II.4). The **total respiration** of the whole community (primary producers and consumers) was not significantly different than 0HW after 1HW and 3HW ($p = 0.53$ and $p = 0.19$ respectively 0.10; Figure 4). The **exports of macrophytes** (i.e. the material transported to another system) decreased by 21.0% non-significantly after 1HW ($p = 0.29$) and presented a significant 54.7% decline after three sequential heatwaves ($p = 0.03$; Figure II.4). The **ratio total respiration of the community per primary productivity** (R/P ratio representing the metabolism of the ecosystem) increased in 1HW and 3HW treatments (4.9% and 3.9% respectively) but the changes were not significant ($p = 0.37$ and $p = 0.40$ respectively; Figure II.4).

The carbon cycling, represented as **Finn Cycling Index**, was not different between both heatwave treatments and 0HW (increase of 21.1% at 1HW and decrease of 11.9% at 3HW; $p = 0.10$ and $p = 0.19$ respectively). The **total amount of carbon recycled** within the ecosystem increased 20.5% at 1HW and decreased 16.1% after 3 HW in comparison to 0HW, although both trends were not significant ($p = 0.13$ and $p = 0.13$ respectively; Figure II.4). The **carbon stored** in the sediment increased 24.5% non-significantly after 1HW ($p = 0.12$) and marginally significantly intensified 27.3% after 3HW ($p = 0.09$). The **circulation in detritus** did not change significantly in both treatments ($p = 0.35$ for 1HW and $p = 0.44$ for 3HW; Figure II.4).

Herbivory increased by 36.5% after 1HW and declined by 19.6% after 3HW, but in both cases the responses were not significant ($p = 0.17$ and $p = 0.25$). **Detritivory** increased 5.8% non-significantly ($p = 0.31$) at 1HW and decreased 13.3% after 3HW ($p = 0.09$). As a consequence, the same tendency was verified in the trophic efficiency of the **grazing chain** and **Lindeman spine** in both treatments (Figure II.4). The trophic efficiencies were not significant however there was an increase in the 1HW treatment (35% of grazing chain efficiency and 15.1% of Lindeman spine efficiency; $p = 0.14$ and $p = 0.21$ respectively) and a decrease in the 3HW treatment (18% of grazing chain efficiency and 11.8% of Lindeman spine efficiency; $p = 0.28$ and $p = 0.22$; respectively).

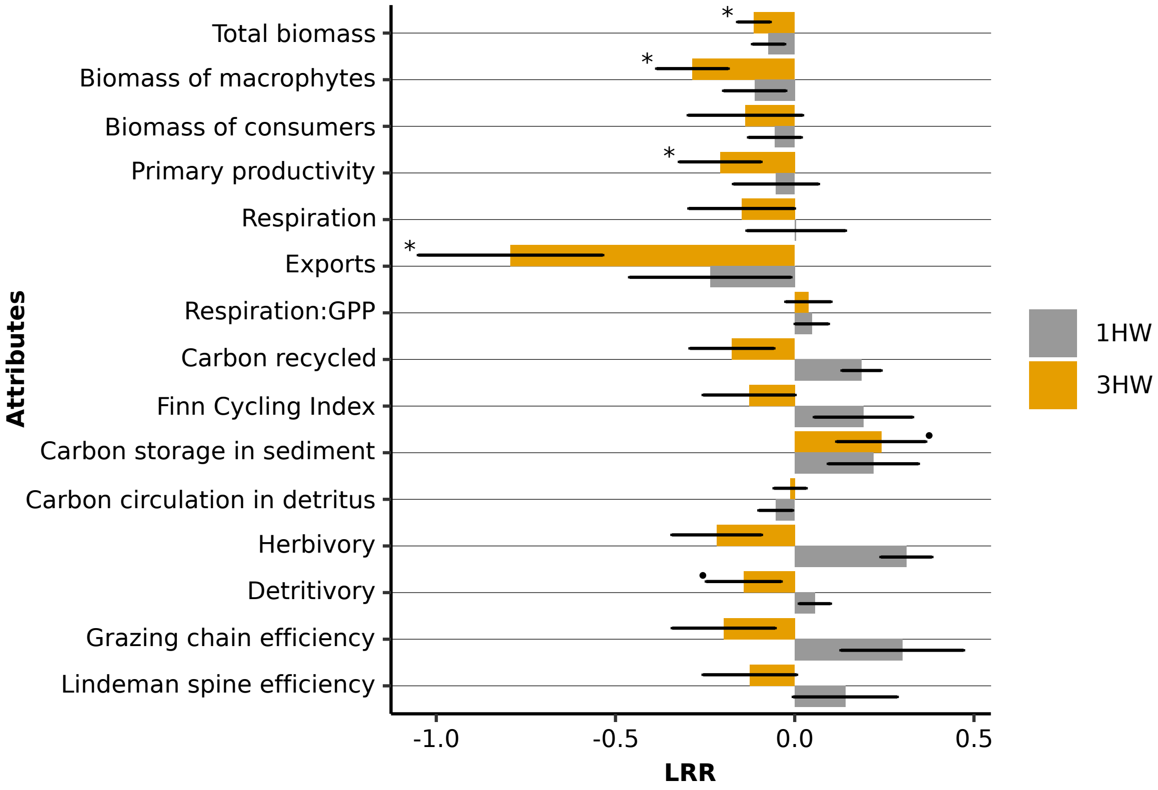


Figure II.4 – Attributes of the ecosystem in log response ratio 1HW/0HW (grey bars) and 3HW/0HW (yellow bars), the error bars correspond to std. error; p-value: '**', 0.01; '*', 0.05; and '•', 0.10

Information theory indices

The size of the ecosystem, which was represented by **total system throughput (TST)**, decreased in both heatwave treatments compared to 0HW (2.6% in 1HW and 14.5% in 3HW), which means that the heatwaves had detrimental consequences on ecosystem activity (Figure II.5). However, this decrease was only significant at 3HW (p = 0.04). The **average mutual information (AMI)** decline 1.4% after 1HW and increased 2.6% after 3HW, although the changes were not significant (p = 0.31 and p = 0.20 respectively). The **ascendency (A)** of the ecosystem was not significantly different at 1HW and 3HW treatments (decrease of 3.4%, p = 0.36 and 10.6%, p = 0.13 respectively) when compared to 0HW. The **development capacity (DC)** of the ecosystem was not different after 1HW (increase of 0.5%; p = 0.51), while at 3HW it was significantly lower (decreased by 14%; $p = 0.04$) when compared to 0HW. The decrease of DC means that 3HW treatment impaired the potential of the ecosystem to develop. The ratio **A/DC** (i.e. the growth proportion of the ecosystem in relation to the maximum threshold) was 3.9% marginally significantly higher in the 3HW treatment ($p = 0.09$) and 3.4% non-significantly lower in the 1HW treatment ($p = 0.10$). The increase of the ratio A/DC in the 3HW treatment means that the ecosystem moved towards a configuration of the network with fewer pathways responsible for energy circulation in comparison to the 0HW network; which could make the ecosystem more brittle.

Overhead refers to the disorder of energy flows of the ecosystem, which is related to the redundancy regardless the types of flows. The **total overhead (O_t)** that quantifies disorder of the whole ecosystem flows decreased 15.7% at 3HW ($p = 0.03$) and increased 2.5% non-significantly at 1HW ($p = 0.40$) in comparison to 0HW. The **overhead on imports (O_i)** did not change significantly at 1HW (increase of 1%; $p = 0.53$) while there was marginally significant decrease of 18.2% at 3HW ($p = 0.06$). The decrease of O_i means that the flows of energy entering the ecosystem were jeopardized (e.g. as photosynthesis), i.e. the 3HW treatment reduced the sources of carbon that were supplying the system. The **overhead on exports (O_e)** was not significantly impacted after 1HW (decrease of 1.8%; $p = 0.47$) however the index significantly decreased 30.9% after 3HW ($p = 0.01$) in comparison to 0HW. Less compartments contributing to usable carbon flowing outside the boundaries of the system explains the negative impact on O_e. The **dissipative overhead (O_r)** that is related to loss of carbon through respiration was not significantly different at 1HW and 3HW when compared to 0HW (increase of 6.7%, $p = 0.28$ and decrease of 13.1%, $p = 0.13$ respectively). **Redundancy** did not change in systems exposed to heatwaves in comparison to 0HW, increase of 3.7% at 1HW ($p = 0.36$) and decrease of 5.1% at 3HW ($p = 0.28$). The **ratio O:TST (H_c, residual or flow diversity)** increased 3.6% marginally significantly ($p = 0.06$) in 1HW treatment in comparison to 0HW (Figure II.5). The 1HW treatment had a positive impact on the diversification of energy flows. After 3HW, H_c significantly decreased 3.4% ($p = 0.04$), i.e. the three sequential heatwaves jeopardized the even distribution of energy flows on the ecosystem. The **internal capacity (DC_i)** index increased 2.8% non-significantly at 1HW treatment ($p = 0.39$) and decreased 5.9% at 3HW treatment ($p = 0.27$) in comparison to 0HW. The **internal ascendency** (A_i) of both heatwaves treatments was not different to 0HW ($p > 0.01$).

Overall connectance (CC_o) was not affected by heatwaves treatment in comparison to 0HW ($p > 0.10$). **Intercompartmental connectance (CC_i)** non-significantly decreased in average 2.9% at the 1HW treatment ($p = 0.13$) and significantly lowered 7.2% at 3HW ($p < 0.01$). The connectance of living and non-living compartments within the ecosystem was impaired by the three sequential heatwaves. **Food web connectance (CC_{fw})** was marginally significantly lower at 1HW (8.6%; $p = 0.07$) and marginally significantly lower at 3HW (9.8%; $p = 0.05$) compared to 0HW. The latter index shows that both heatwave treatments harmed the connectance within the living compartments of the ecosystem (Figure II.5).

Discussion

The use of energy flow analysis in ecosystems is considered a powerful tool for understanding the complexity of ecosystem functioning (Barnes et al. 2018). This work presents an alternative to the single-species effects of climate change by providing an ecosystem-wide analysis of energy flows among biotic and abiotic compartments. The response at the ecosystem level is a combination of the metabolic responses of each species, which demonstrate how the impacts on the populations spread across the food web. In general, thermal performances of species are hump-shaped (Angilletta 2006) with species-specific optima and comfort zones (Woodin et al. 2013). As a consequence, shifting temperatures usually leads to shifts in interspecific interactions (Kordas et al. 2011, Ito et al. 2019a). Thus, although individually the heatwaves affect only some macrophytes and consumers (Saha et al. 2019, Pansch et al. 2018), an analysis at the community-level provides further insights on the real consequence in terms of ecosystem functioning, providing further insights on the real consequences on ecosystem functioning (Alsterberg et al. 2013).

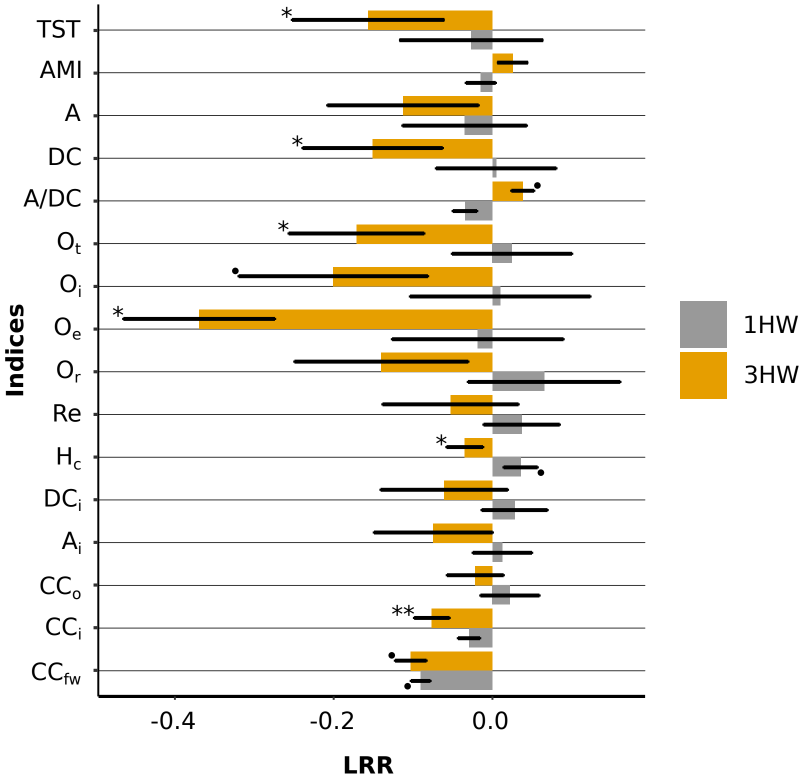


Figure II.5 – Information theory indices from ecological network analysis in log response ratio 1HW/0HW (grey bars) and 3HW/0HW (yellow bars), the error bars correspond to std. error; the indices illustrated are total system throughput (TST), average mutual information (AMI), ascendency (A), development capacity (DC), ascendency:development capacity ratio (A/DC), total overhead (O_t), overhead on imports (O_i), overhead on exports (O_e), dissipative overhead (O_r), redundancy (Re), residual diversity (H_c), internal capacity (DC_i), internal ascendency (A_i), overall connectance (CC_o), intercompartmental connectance (CC_i), food web connectance (CC_{fw}); p-value: '**', 0.01; '*', 0.05; '•', 0.10

Effects of one heatwave treatment on general features of the ecosystem

After one heatwave the attributes of the ecosystem were not affected and the majority of the indices obtained from the ENA did not respond either. There were two indices that were marginally significant but changed in different directions (1) the residual diversity (H_c) increased and (2) the food web connectance (CC_{fw}) decreased (Figure II.5). The increase in H_c indicates that the overall connections between all the compartments (living and non-living compartments) became more diverse. It means that energy flows are more homogeneously distributed among the different links, which lowers the chances of disrupting interactions between compartments under stress. Considering that the definition of stability is the ability of an ecosystem to resist disturbance (Odum 1969) and resilience the capacity of recovery in a short time following disturbance (Pimm et al. 2019), ecosystems benefit from the increase of H_c because the multiplicity of pathways for energy circulation make them more resistant to disturbance. The disturbance applied in the ecosystem may alter biomass or interactions strength, thus in case the alterations result on the disruption of some links the energy transport is guaranteed by the presence of multiple pathways. The high diversity of flows increases the presence of redundant paths, which function as a disturbance buffer to the ecosystem. However, the connectivity among the living compartments (food web connectance, CC_{fw}) responds in the opposite direction, with a decrease of the average, weighted number of links per trophic group. Food web structure became more efficient (i.e. the transfer of carbon along the food web became more specific) and the flows between living compartments were more unevenly distributed, which could lower the stability of the food web. Indeed, the consumption rates of some compartments changed after 1HW treatment, explaining the decrease of CC_{fw}. The feeding rates of amphipod-omnivores and gastropods increase while the consumption of bivalves decreased. The contradiction in the patterns displayed by the indices demonstrates that the ecosystem as a whole increased its resilience in response to a single heatwave but the food web resulted to be threatened. The living compartments responded faster than the abiotic ones to the disturbance; mainly the consumers were affected by 1HW treatment as we detected from respiration and feeding rates (Figures II.3b and II.3c). An alternative explanation is that this response might be a demonstration of early signs of stress of the ecosystem, therefore further studies should be carried out to confirm whether this trend would lead to a more vulnerable ecosystem or not. Moreover, in some cases, the effects of heatwaves (e.g. increase of mortality) may be delayed and appear after several days or even months (Edwards 2004, Takolander et al. 2017).

Three heatwaves impact on ecosystem structure and activity

Spring and summer heatwaves are responsible for increasing mortality rates in marine ecosystems (Garrabou et al. 2009) and can thus threaten ecosystem functioning. Our results demonstrate that 3HW lowered **total biomass** in comparison to 0HW (Figure II.4). By separating the **biomass into macrophytes** and **consumers** we found that mainly macrophytes declined after

3HW (Figure II.4), with *F. vesiculosus* and filamentous algae being the most affected (Figure II.1). Heatwaves are known to cause decline on populations of macroalgae (Smale et al. 2013) and seagrasses (Arias-Ortiz et al. 2018). Although the macroalgae (*F. vesiculosus* and filamentous algae) are exposed throughout the year to temperatures varying between 0 and 25°C, sequential heatwaves in spring/summer proved detrimental to these macrophytes. Another factor that contributed to the decline of macroalgae biomass could be grazing activity. The quantity and biomass of the main mesograzers in this experiment (*Idotea balthica*, *Gammarus* sp. and *Littorina littorea*) did not change after 3HW treatment (Pansch et al. 2018). However, the feeding of mesograzers intensifies during the exposure to higher temperatures (Ito et al. 2019a). Our results showed that grazing of isopods and amphipod-omnivores strengthened mainly on *F. vesiculosus* (Appendix Tables II.5 and II.7).

Disturbed ecosystems may respond with lower primary production, which leads to lower activity levels in the whole food web (Baeta et al. 2011). The decline of macrophytes biomass in our experimental ecosystem was followed by lower **primary productivity** after experiencing three sequential heatwaves in comparison to 0HW treatment. The size or activity of the ecosystem (i.e. the quantity of energy flowing in the ecosystem) expressed as **total system throughput (TST)** and the **development capacity (DC)** also declined in the 3HW treatment (Figure II.5). Wulff and Ulanowicz (1989) detected higher TST and DC in Chesapeake Bay than in the Baltic Sea and attributed this difference to higher productivity in the Chesapeake Bay, which was boosted by the higher mean temperature. This result indicates that the response of the ecosystem to heatwaves may not be the same compared to studies that consider increase of mean temperature directly. Temperature variability might cause severe changes in the metabolism of organisms decreasing the temperature threshold tolerated and increasing mortality rates (Seuront et al. 2019).

Since macrophytes are considered habitat-forming organisms (Wikström and Kautsky 2007, Byrnes et al. 2011, Githaiga et al. 2019), it is natural to expect the **biomass of some consumers** to decline with the macrophytes. The loss of habitat combined to metabolic changes that we can observe in respiration and consumption rates contributed to the decline of some species. The compartment with highest decline in biomass, consumption and metabolic activity after 3HW was the bivalve filter-feeders (Figure II.3); this result was expected since heatwaves are affecting mostly low mobility species (Pansch et al. 2018).

Both compartments of Polychaeta (detritivore and omnivore) were responsible for a substantial portion of the biomass of consumers in this study (Figure II.3a). However, the compartment with higher activity within the consumers was the group of gastropods, as it can be observed from the values of total consumption and respiration (Figures II.3b and II.3c). Loss through respiration was also relatively high for amphipods omnivores, which mainly included *Gammarus* sp. Our results are in line with Goldenberg et al. (2017) that detected that secondary productivity of food webs is negatively affected by warming even under the positive effects of acidification.

Regarding feeding traits, Niquil et al. (2014) found that detritivory is higher in seagrass meadows than in bare sediment since the meadows are able to retain large quantities of detritus, boosting the use of this resource. Our results are compatible with the findings of these authors, since detritivory decreased after 3HW (Figure II.4), which could be associated to the decline of the macrophytes (Figures II.2a and II.4).

Although there was no change in the overall connectance, the intercompartmental connectance decreased after three sequential heatwaves. This decrease is explained mainly by change in the organization of energy flow associated mainly to the connectivity of the living compartments since also the food web connectance decreased. These indices demonstrate that the structure of the energy flow became less food web-like and more linear (food-chain-like). Therefore, the changes in secondary productivity, activity of the consumers and feeding behavior intensified some interaction strengths while others were significantly reduced, which caused the uneven distribution of energy flow in this ecosystem.

Three heatwaves impact on efficiency versus stability of the ecosystem

The total overhead quantifies the degrees of freedom for energy circulation in ecosystems (Ulanowicz 2001). Its increase is associated with the prevalence of unorganized, incoherent and inefficient energy circulation. Despite the negative perception provided by such description of the overhead, under disturbance an unorganized ecosystem (i.e. with multiple and redundant paths for energy circulation) is able to reallocate disrupted energy flows by modifying the strength of unaltered ecological interactions (Ulanowicz 2001), boosting resilience of the ecosystems. In this study, the sequential heatwaves decreased the total overhead. The heatwaves were able to lower the disorder of the ecosystem by leaving a few alternatives for the energy to flow since the residual diversity (H_c) also decreased. Moreover, the distribution of carbon flows (i.e. the interaction strengths) was reduced and not reallocated after the sequential disturbance. These results indicate that the efficiency of energy transfer increased since the flows organization reinforcing that the energy flow configuration became closer to a food chain than food web. The resilience of the ecosystem decreased due to the decline of diversity of the links that transfer energy, which resulted in an ecosystem more vulnerable to disturbances since the linkages could be easily disrupted. The indices analyzed demonstrate that respiration was not the main factor driving the overhead trend (Figure II.5, dissipative overhead). The main components that caused the disorganization of the system were the imports and exports (Figure II.5, overhead on imports and exports). These outcomes indicate that the whole ecosystem photosynthetic activity became more dependent on a few primary producers, i.e. *Z. marina* and *F. vesiculosus* exceeded the contribution of filamentous algae that was dominant in 0HW. Thus, in this study, the ecosystem did not go through a learning process after the sequential heatwaves treatment.

Carbon storage - Functioning of the ecosystem

In our study, we focused on carbon cycling and storage using the outcomes of the network analysis to explain changes in ecosystem functioning. We found that the amount of energy that entered the system through photosynthesis decreased after 3HW, although the proportion of carbon recycled in the ecosystem did not change with the heatwaves as indicated by the Finn cycling index (Figure II.5). The storage of carbon in the sediment increased after sequential heatwaves, such response might be associated with bacteria activity. The dissolved organic carbon concentration (DOC) in the tanks was significantly higher at 3HW in comparison to 0HW ($p = 0.04$) and 1HW ($p < 0.01$) (Appendix II.5). DOC concentration is one of the parameters regulating bacterial activity (Šimek et al. 2003), thus the bacteria from 3HW treatment may have processed and stored larger amounts of carbon in the sediment.

Therefore, despite the positive impact on carbon storage, 3HW affected negatively the import of carbon mainly due to the decline in biomass and photosynthetic activity of filamentous algae and *Fucus vesiculosus* (Figure II.2a, II.2b). In the long term this could have serious consequences since the macroalgae are responsible for substantial amounts of carbon storage beside the pivotal role as foundation species (Duarte 2017).

Conclusions

Previous studies about mean warming predicted the increase of ecosystem activity (i.e. TST), which indirectly determined higher values for most of the information indices (Baird et al. 2019). Our work demonstrates that heatwaves have negative impacts on the indices depending on the frequency at which they occur. The experimental ecosystem was not strongly affected by one summer heatwave (1HW), although two of the ENA indices showed different responses to the treatment with residual diversity improving the integrity of the ecosystem and other illustrating stressed conditions (food web connectance). This uncoherent set of responses can correspond to an early sign of stress. Sequential heatwaves (3HW treatment) were instead clearly detrimental to the functioning of the ecosystem. Biomass production and primary productivity were lower and such declines compromised the transfer of carbon to higher trophic levels. The ecosystem lost stability due to decline of redundancy in the architecture of flows, which lowered the likelihood of finding alternative ways for energy circulation in case some links are disrupted (Barnes et al. 2018). Hereby, we emphasize the importance of assessing the functioning of the ecosystems using a holistic perspective by combining biomass and metabolic responses of living (i.e. primary producers and consumers) and non-living compartments together with structural descriptors of energy circulation. Our experiment is a current scenario approach since we used conservative temperatures and duration of heatwaves, i.e. the heatwaves were based on 15 years (2000 to 2014) of data analysis (Pansch et al. 2018). Therefore, in case a more extreme heatwave (higher magnitude and longer duration) occurs the ecosystem may go through a shift of equilibrium state as the one observed in Australia (Nowicki et al 2017).

Chapter III

Chapter III

Sequential heatwaves decrease regulating and maintenance ecosystem services

Abstract

The rapid ecological shifts caused by climate change have been subject of concern for human well-being. Nature provides numerous ecosystem services that benefit people directly or indirectly. The ecosystem services are under threat and some of them have already been reported as lost due to the ongoing rise in temperature. Extreme events, e.g. heatwaves, are also becoming more frequent and intense as a consequence of climate change and in some cases exceeding thresholds of resistance of ecosystems. This study aims to meet the urgent need for understanding not only the direct effects but also the indirect effects and feedbacks that heatwaves can cause on the complexity of ecological interactions and ecosystem services. Our work used experimental data for predicting how the supply of ecosystem services responds to sequential heatwaves. We identified three services from regulating and maintenance category: (1) water purification, (2) climate regulation and (3) habitat provision. We applied qualitative approach (loop analysis) for investigating the effects of inputs caused by the heatwaves on the network of a temperate ecosystem. The results showed that water purification and climate regulation services decline in this ecosystem due to decrease of bivalves and macroalgae mainly, while habitat provision did not respond to the disturbance. The sensitivity analysis confirmed the robustness of our findings and also the vulnerability of water purification and climate regulation to heatwaves. This study is a contribution to move ecosystem services assessment toward operationalization for predicting the impacts of climate change and assist environmental management. Moreover, this work demonstrates the importance of including experimental data into ecosystem services analysis for decreasing uncertainties regarding the predictions made.

Introduction

Climate change has already impacted different levels of organization; the individual-level effects can alter ecological interactions that propagate through food webs affecting the delivery of ecosystem services (Prather et al. 2013). Mean global temperature has increased approximately 1 °C since the pre-industrialized period (IPCC 2018). However, not only mean temperature has been increasing. The magnitude of extreme events, such as heatwaves, has also risen (Oliver et al. 2018). In the last 30 years, the heatwaves increased 54% in intensity and duration (Oliver et al. 2018). Marine organisms are susceptible to change in temperature regimes (Wahl et al. 2019) and the heatwaves have already caused loss in biodiversity (Garrabou et al. 2009). In addition to mortality, the changes in temperature regime affect the individual physiological responses of the surviving organisms altering the strength of ecological interactions, e.g. intensification of feeding (O'Connor 2009). Changes in the interactions driven by temperature modify ecological processes impacting the functioning of ecosystems (Ito et al. 2019a). In Australia, heatwaves exceeded resistance thresholds in kelp ecosystems and shifted whole ecosystem dynamics by changes in ecological structure and interactions (Wernberg et al. 2016).

In Europe, the Marine Strategy Framework Directive (MSFD, Directive 2008/56/EC) was adopted to pursue Good Environmental Status of European marine ecosystems. The framework aims at the sustainable use of marine ecosystems recognizing the relevance of biodiversity for sustaining the resources that contribute to human well-being. The benefits that ecosystems provide for human well-being are represented by ecosystem services (Costanza et al. 1997). Ecosystems have the capacity to generate a wide range of services (ecosystem services supply) that in different proportions are demanded (ecosystem services flow) and used by humans (benefits) (Dee et al. 2017). Liquete et al. (2013) proposed three main categories of ecosystem services (1) provisioning, (2) regulation and maintenance and (3) cultural services.

Climate change is predicted to negatively impact the supply of many ecosystem services (Runting et al. 2017), which will lead to detrimental economic impacts (Shaw et al. 2011). The supply of ecosystem services depends on the quality of ecosystem functioning (De Groot et al. 2002), which in turn relies on biodiversity and the species interactions (Duffy and Stachowicz

2006MA 2005). Marine heatwaves have already caused massive mortality (including foundation species) that resulted in loss of ecosystems services (Smale et al. 2019). However, the role of ecological interactions and their feedbacks on ecosystem services remains unclear. Dee et al. (2017) recommended the operationalization of the ecosystem services analysis. The authors proposed that ecosystem services assessment should consider the use of network approaches for predicting indirect effects and feedbacks of environmental management actions.

Research on climate change related to ecosystem services has focused mainly on warming trends neglecting fluctuating temperature regimes. This study aims to investigate the mechanistic impacts of heatwaves on ecosystem services provided by marine ecosystems. This Chapter is based on the dataset described on Chapter II, which investigated the ecosystem network analysis of experimental treatments: no heatwave (0HW), one heatwave and three consecutive heatwaves (3HW). In the Chapter II, the responses of the ecosystem to 3HW treatment were more evident than one heatwave treatment, thus the focus of this Chapter is on the comparison of the ecosystem's capacity to provide services after the exposure to 0HW and 3HW treatments. The heatwaves in the experiment mimicked the heatwaves pattern (in duration and amplitude) that has already occurred in the Baltic Sea from 2000 to 2014 (Pansch et al. 2018). We selected three ecosystem services, based on Liquete et al. (2013): (1) water purification (removal of particles and nutrients from the water column decreasing turbidity), (2) climate regulation (carbon capture, storage and sequestration; blue carbon) and (3) habitat provisioning (or life cycle maintenance). The services belong to regulating and maintenance services category, thus they were selected due to their importance to support other ecosystem services. We applied qualitative network analysis (loop analysis) for tackling the effects of ecological interactions on the provisioning of services. Such approach is important for assisting ecosystem management since it sheds light on ecological feedbacks between species and ecological processes. The following questions motivated this study:

1. Do heatwaves impact ecosystem services? If so, in which direction?
2. Is it possible to employ experimental dataset in models for advancing the operationalization of the ecosystem services analysis?

Material and Methods

The experiment was performed from 6 May to 20 August 2015 in the Kiel Outdoor Benthocosms (KOB, Wahl et al, 2015). The KOB is composed by twelve tanks of 1500 L capacity each that are computer-controlled by ProfiLux 3.1T (GHL GmbH, Germany), allowing the regulation of the water temperature. The temperature treatment was selected based on the analysis of 15 years of temperature data of the southwestern Baltic Sea. A GAMM model was applied to determine the seasonal temperature regime and 2009 was identified as the year without heatwaves (see Pansch et al. 2018). The spring and summer temperature regime of 2009 was used as no heatwave treatment of the experiment (0HW; Figure 1). In addition, the analysis of the temperature dataset led to the identification of heatwaves pattern in the Kiel Fjord (Pansch et al. 2018). The sequential heatwave treatment (3HW) was composed by three heatwaves along spring and summer (Figure 1). The first two heatwaves were applied in June and July 2015, they were characterized by an increase of 1.2 °C per day during three days. The peak of temperature (3.6 °C) was maintained for four days followed by a cooling period (two days) until it reached the same temperature as 0HW. The third heatwave was reproduced in August 2015 and it was more intense than the first ones, the temperature increased 1.7 °C per day in average for three days reaching 5.2 °C above the temperature of 0HW. Such temperature was maintained for four days and the cooling phase lasted 2 days (Figure III.1).

The organisms that composed the experimental biological community were collected in the Kiel Fjord (54.39 N, 10.19 E) and they were introduced in the tanks between 4 – 6 May 2015. The community introduced in the tanks included the macroalgae *Fucus vesiculosus*, the seagrass *Zostera marina*, the mussels *Mytilus edulis* and the main mesograzers present in the Baltic Sea (*Littorina littorea*, *Gammarus* sp. and *Idotea balthica*). The tanks received non-filtered water from the Kiel Fjord, which allowed the establishment of other species of filamentous algae, bivalves, amphipods and Polychaeta.

Collection of data

The data collection was carried out after the third and last heatwave (18-20 August 2015). We measured photosynthesis and respiration rates using incubations. The incubations were carried out in 6 L gas-tight chambers equipped with a stirrer and non-invasive oxygen sensor spots PSt3 (PreSens Precision Sensing GmbH, Regensburg, Germany). The primary producers were enclosed in the chambers and the dissolved oxygen concentration was measured before and after the closure of the chamber (*F. vesiculosus* and filamentous algae – 1 hour, *Z. marina* – 6 hours) using the Fibox 4 (PreSens Precision Sensing GmbH, Regensburg, Germany). The incubations were carried out under natural light conditions for photosynthesis rates and under dark conditions by deploying a dark cover around the chambers for respiration rates quantification. The incubation chambers were kept in the tanks for temperature maintenance.

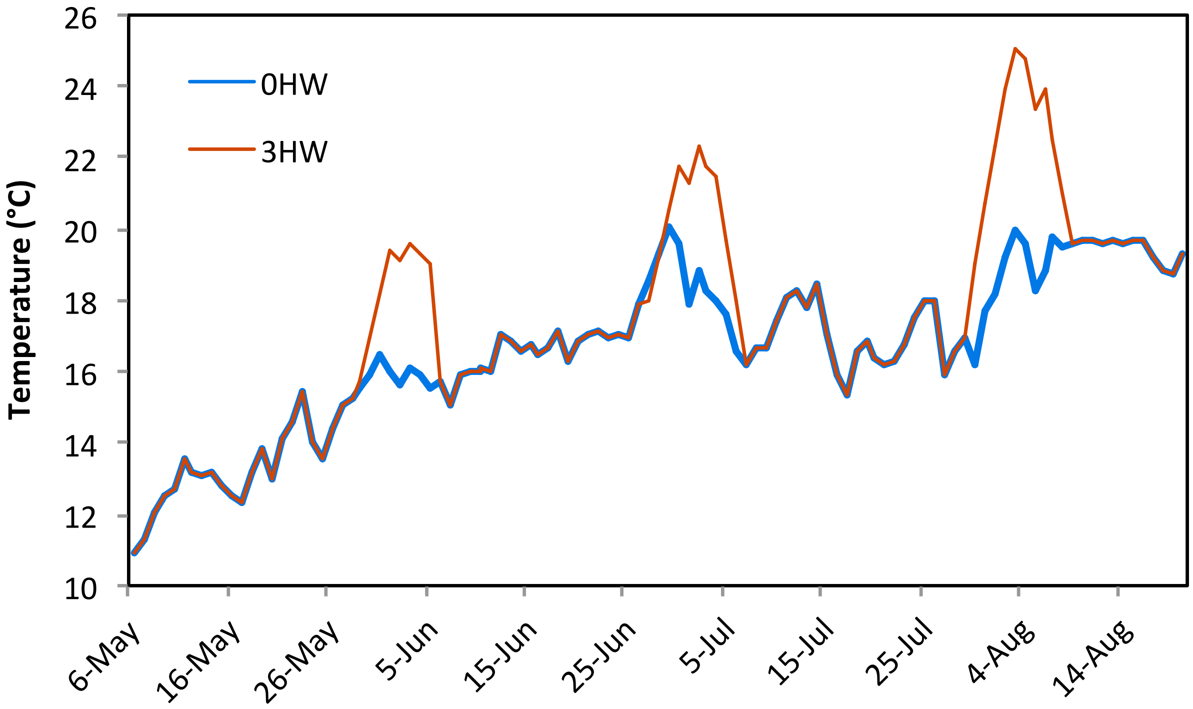


Figure III.1 – Temperature applied to no heatwave (0HW, blue line) and three sequential heatwaves (3HW, red line) treatments in the experiment performed during spring/summer 2015

The incubation of the consumers for measuring respiration rates were carried out in sealed 100 mL Winkler bottles using the non-invasive sensor spots and the Multi-channel Fiber Optic Oxygen Meter Oxy-10 mini (PreSens Precision Sensing GmbH, Regensburg, Germany). The oxygen concentration was logged for 1 hour and the respiration rates were extracted from the regression analysis.

For biomass quantification, the organisms that were in the tanks were collected at the end of the experiment. All the organisms were frozen at -40 °C until further analysis. The species were identified to the lowest taxa possible and separated, the samples were dried for 48 hours at 80 °C and the dry weight was quantified. The biomass of the consumers was used for calculating the consumption rates, which were based on consumption per biomass ratio (CB ratio, see Appendix Table III.1). The biomass was also used as benchmark to validate the outcome of the loop analysis.

Description of the selected ES and selection of the species

The analysis of ecosystem services started with the selection of the services of interest in this ecosystem (Dee et al. 2017). The ecological configuration of the biological community studied led to three main services provided by this ecosystem (1) water purification (removal of nutrients and particles from the water column decreasing turbidity), (2) climate regulation and (3) habitat provisioning.

In this study, we defined water purification service as the ability of the biotic component of the ecosystem to remove nutrients and particles from the water column, decreasing water turbidity (Maes et al. 2016). In the Baltic Sea, the main organisms that provide this service are the bivalves (mainly *Mytilus* sp.) that filter the suspended particles and nutrients removing them from the water column, which decreases eutrophication (Kotta et al. 2019a). Eutrophication increases turbidity since it promotes the excessive growth of phytoplankton hindering the light penetration in the aquatic environment. Thus, we designated water turbidity (Tb) as part of the matrix of interaction, since turbidity has already been pointed as one of the reasons for the decline of macrophytes (e.g. *F. vesiculosus*) in the Baltic Sea (Nilsson et al. 2004). Turbidity also affects seagrasses by impairing their growth and survival (Moore et al. 1997). However, primary producers from temperate regions have been declining not only because of water quality deterioration but also due to the ongoing climate change (Wernberg et al. 2011).

Climate regulation (cr) is the contribution of an ecosystem to avoid climatic changes by regulating chemicals that contribute to greenhouse effect, e.g. CO_2 (Costanza et al. 1997, Hattam et al. 2015). The parameters that indicate cr service can be carbon biding through photosynthesis, carbon storage and sequestration as blue carbon (Hattam et al. 2015, Maes et al. 2016). Vegetated coastal ecosystems have already been suggested as climate mitigation tools due to the amount of carbon they are able to store and sequester (Duarte et al. 2013). Marine macrophytes are able to store carbon either as biomass or by retaining it or in the soil; the carbon is then buried in the sediment and maintained over large time scale, i.e. carbon sequestration (Duarte et al. 2013, Krause-Jensen et al. 2018). In our study, we identified seagrass (Röhr et al. 2018) and macroalgae (Trevathan-Tackett et al. 2015) as actors of this particular service. If climate regulation is able to prevent or minimize climate change (e.g. warming and extreme events as heatwaves), this service has positive effects on organisms with a low range of temperature tolerance and low mobility capacity. Climate regulation would benefit the seagrass *Z. marina* and the macroalgae *F. vesiculosus* since warming is able to jeopardize the metabolism and increase the mortality of these primary producers (Reusch et al. 2005, Wahl et al. 2019). Primary producers are not the only group affected, sessile or low mobility organisms are also negatively impacted by increase in temperature (Wernberg et al. 2013) causing a decrease of foundation species responsible for habitat provisioning ecosystem service.

Habitat provisioning (hp) is related to the capacity of the ecosystem to harbor high biodiversity and biomass (Hattam et al. 2015). The species that contribute to habitat provisioning are also known as foundation species due to their importance in creating structures that shelter other species (Möller et al. 1985, Norling and Kautsky 2008). In addition to habitat, some species are targeted as prey item representing the basis of food webs, i.e. macroalgae (Wikström and Kautsky 2007), increasing the importance for sustaining biodiversity. Seagrass, *F. vesiculosus* and bivalves are known to facilitate the survival of other species creating biodiversity hotspots in the Baltic Sea (Möller et al. 1985, Wikström and Kautsky 2007, Norling and Kautsky 2008).

The organisms included in the analysis were selected based on their importance on the ecological interactions relevant for the selected ecosystem services. The division of the organisms into nodes (Table III.1) was also based on the food web analysis (Chapter 2).

Data analysis

Loop analysis is a qualitative network model that uses signed digraphs (directed graphs), which represent networks of linked variables (Bodini et al. 2018). The variables correspond to nodes that may consist not only of biological components, as species or group of species, but also of abiotic, social, economic variables (Reum et al. 2015). The links depicted in the matrix of interactions corresponds to diverse types of interactions (e.g. trophic interactions, competition, facilitation). The linkages denote signs that indicate changes such as growth.

Table III.1 – Biotic compartments selected for the analysis and the description of the species composing each node

Node	**Species**
Phytoplankton (PP)	All the phytoplankton species
Filamentous algae (FA)	All filamentous algae species
Fucus vesiculosus (FA)	*Fucus vesiculosus*
Zostera marina (ZM)	*Zostera marina*
Bivalves (BF)	*Mytilus edulis*, *Limecola balthica*, *Mya arenaria*, *Cerastoderma* sp.
Amphipods (AO)	*Gammarus* sp.
Isopod (IO)	*Idotea balthica*

For constructing the matrix of interactions (Figure III.2), the interactions within the biotic compartments were based on feeding interactions (“who eats whom”) that were established in Chapter II. The detailed description of the interactions between all the nodes (i.e. biotic nodes and the ecosystem services) was established based on literature search and feeding preferences (Appendix Table III.2).

Whenever press perturbations are applied the predictions will show alterations in biomass resulting from direct impact or the propagation of such stress through the network connections. The predictions indicate the direction of the changes: increase (+), decrease (-) or no effect (0).

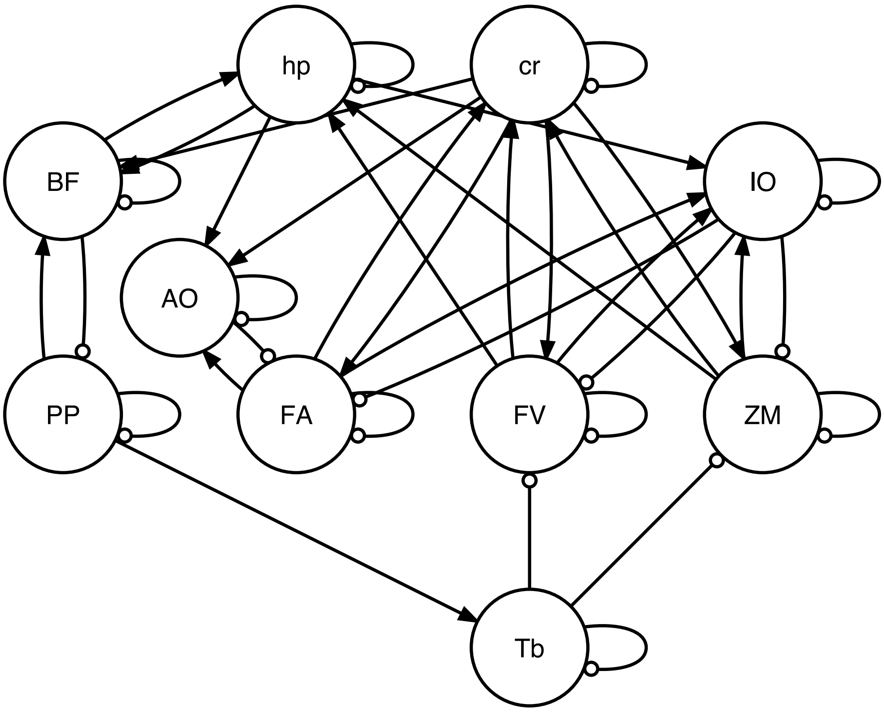


Figure III.2 – Signed directed graph of the interactions between biotic nodes and the ecosystem services, where the arrow indicates positive input on the node and the empty circle indicates negative input on the node. Note that each node has a negative self-loop that represents the self-regulation of the nodes due to intraspecific competition, carrying capacity or cannibalism, for example. Tb: turbidity, cr: climate regulation, hp: habitat provisioning, PP: phytoplankton, FA: filamentous algae, FV: *Fucus vesiculosus*, ZM: *Zostera marina*, BF: bivalves, AO: amphipods, IO: isopods

Therefore, for this study, we used metabolic activity as a representation of the press perturbation caused by heatwaves due to the capacity of combining distinct but complementary variables, i.e. respiration and photosynthesis or consumption. We used the data on gross primary production (GPP), respiration (R) and consumption (C) rates to calculate ratios (GPP:R for macrophytes and C:R for consumers). We applied generalized linear mixed models for analyzing the metabolic parameters of the nodes that were compiled using nlme R package (Pinheiro et al. 2019). The post hoc analysis was carried out with Tukey test for multiple comparison purpose using the multcomp R package (Hothorn et al. 2016). Whenever the metabolic activity of the node exposed to 3HW treatment was significantly different from the node exposed to 0HW (either positive or negative), they were used as input to the node.

The outcomes of each input and the global prediction given by the model are in percentage of the positive and negative percentage (i.e. the relative amount of times the simulation resulted in positive and in negative effect over the node). In order to present a single value, we applied the equation $x = a - b$, where a represents the percentage of the positive outcomes and b is the percentage of the negative outcomes of the simulation for each node. In the results, we present the x, i.e. the net percentage prevalence of the simulation outcome that ranges from 100 to -100, for indicating the direction of the press disturbances effect.

Sensitivity analysis

Additionally, we tested the effects of the strength of ecological interactions on the selected ecosystem services. The objective of this test was to find how sensitive the ecosystem services are to interaction strength. The premise followed for carrying out this analysis is that the system is at equilibrium state, i.e. it is resilient and can return to its original state after disturbance (Hughes and Roughgarden 1998). We referred to uncertainty analysis (Hines et al. 2018) to perform sensitivity analysis. Uncertainty analysis has been used to demonstrate the robustness of model outcomes, i.e. the analysis tests how the variability of the parameters of the model affects the results (Hines et al. 2018). We simulated the strength of each ecological interaction (Table III.2) with sequential increase from 1e-6 to 1 using 0.1 increments to evaluate the robustness of loop analysis outcomes. The threshold of the interaction strength was selected according to the first premise, i.e. the intensity of the interaction must be not higher than 1 otherwise the condition of stable equilibrium is not met (Hughes and Roughgarden 1998). The simulations consisted in crossing each interaction with the interactions strength and each scenario constructed yielded specific tables of prediction. Finally, since we were interested in understanding the conditions that jeopardize the ecosystem services, we selected the simulations that resulted in negative provisioning of each ecosystem service. The analysis would enable us to detect which ecological links or even nodes were most relevant for the maintenance of the selected services.

Table III.2 – Ecological interactions considered for the analysis of interaction strength based on literature information (see supplementary information – Table S2)

Node	Link	Node
PP	→	BF
BF	⊸	PP
ZM	→	IO
IO	⊸	ZM
FV	→	IO
IO	⊸	FV
FA	→	IO
IO	⊸	FA
FA	→	IO
IO	⊸	FA

The nodes represent the organisms that compose the network, PP: phytoplankton, BF: bivavles, ZM: *Zostera marina*, FV: *Fucus vesiculosus*, FA: filamentous algae, IO: isopods and AO: amphipods. The links represent feeding interactions, where '→' represents positive interaction and '⊸' represents negative interaction

Results

Metabolic responses

The results of metabolic responses exhibited great variability (Figures III.3a-f). The ratio GPP:R of *Zostera marina* was 47.8% significantly higher when exposed to the heatwaves ($p < 0.01$; Figure III.3a), thus we considered a positive input on the ZM node. The metabolism (GPP:R ratio) of *Fucus vesiculosus* did not respond significantly to the disturbance (decreased 3.7%, p =

0.28; Figure III.3b). The ratio GPP:R of filamentous algae responded negatively to the heatwaves (decreased 94.7%, $p < 0.01$; Figure III.3c), which led to a negative input on FA node. The metabolism of amphipods and bivalves (Figures III.3d and III.3f, respectively) expressed as Consumption:R ratio was not influence by heatwaves ($p = 0.68$ and 0.16, respectively). The metabolism of the isopods increased 9.2% significantly ($p < 0.01$) when exposed to 3HW treatment (Figure III.3e), therefore it was considered a positive input on the IO node. The metabolic variables that responded significantly were used as the inputs, representing press perturbation caused by sequential heatwaves.

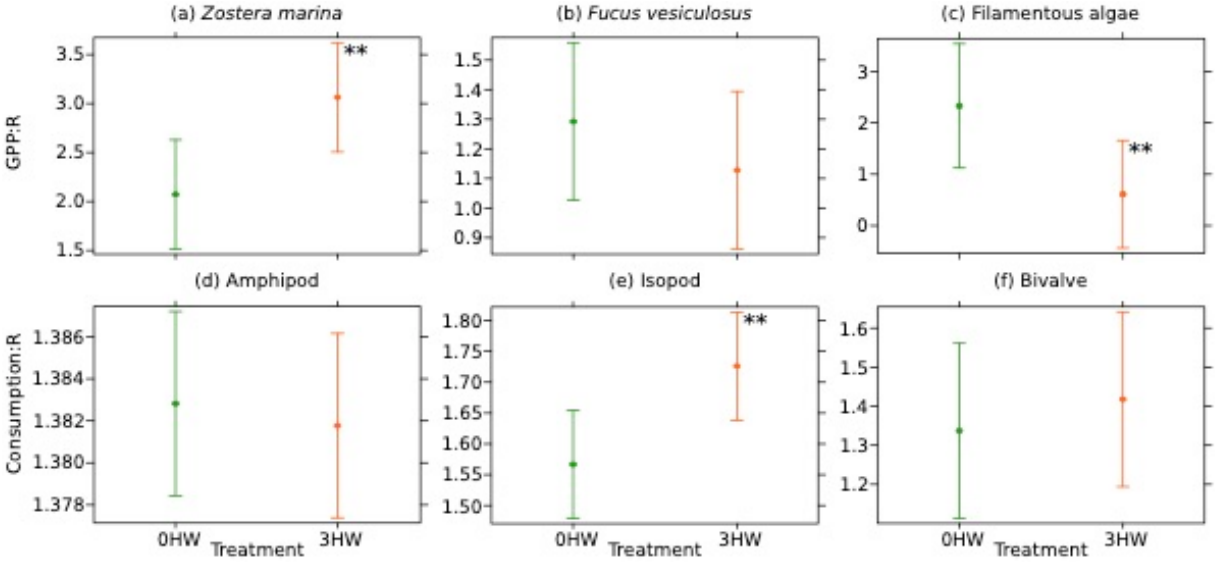


Figure III.3 – Metabolic responses (mean, 95% confidence interval) of *Z. marina* (a), *F. vesiculosus* (b), filamentous algae (c), amphipod (d), isopod (e) and bivalve (f) exposed to 0HW and 3HW treatments ('**' represents p-value lower than 0.01)

Biomass

The biomass was used to validate the predictions of the effect of sequential heatwaves on the network. Not all the nodes presented significant difference of biomass between no heatwaves and three heatwaves. The biomass of *Z. marina* did not change significantly with heatwaves treatment (decreased 14.9%, $p = 0.50$; Figure III.4a). The biomass of *F. vesiculosus* declined 18.7% marginally significantly after sequential heatwaves ($p = 0.07$; Figure III.4b). Filamentous algae significantly decreased 90.4% after 3HW compared to 0HW ($p = 0.02$; Figure III.4c). As for the consumers, the biomass of amphipods and isopods was not affected by 3HW in comparison to

0HW (p = 0.50 and 0.41; Figures III.4d and III.4e, respectively). The biomass of bivalves significantly decreased 41.2% after 3HW (p = 0.02; Figure III.4f).

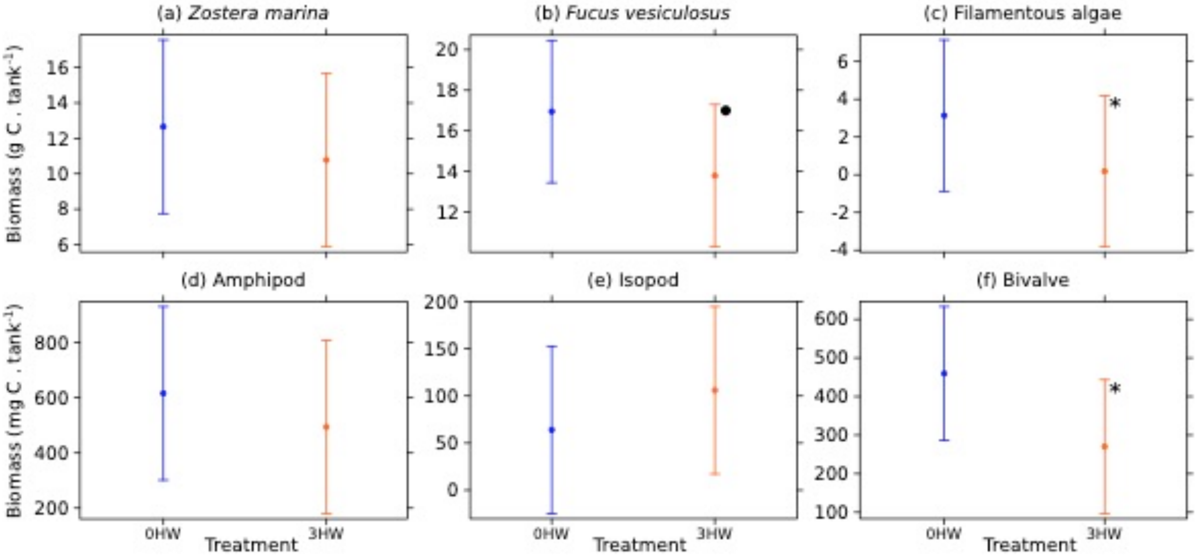


Figure III.4. Biomass (mean, 95% confidence interval) of *Z. marina* (a), *F. vesiculosus* (b), filamentous algae (c), amphipod (d), isopod (e) and bivalve (f) exposed to 0HW and 3HW treatments (p-values: '*', 0.05; '•', 0.10)

Model predictions

The metabolic responses that responded significantly to the 3HW treatment in comparison to 0HW were used as input on the nodes representing the effect of sequential heatwaves. The signal of each input was considered (1) positive when the metabolism of the node responded positively (*Z. marina* and isopod) or (2) negative when the metabolism responded negatively (filamentous algae) to the 3HW (Figure III.3).

Positive input on *Zostera marina*

The positive input on the node *Z. marina* (Figure III.5) led to strong positive response of isopods and slightly negative on amphipods. The filamentous algae and *F. vesiculosus* nodes responded negatively to this scenario. The decline of the macroalgae resulted in the decrease of climate regulation service. Since there was a strong positive response on *Z. marina*, the maintenance of habitat provisioning was positively impacted. The bivalves responded positively having a negative impact on phytoplankton, as a consequence there was a decrease in turbidity.

Positive input on isopods

The positive input on isopods (Figure III.5) had a negative impact on *Z. marina* and *F. vesiculosus*, leading to a decrease in habitat provisioning for other species and climate regulation service. There was a negative response of amphipods and bivalves. Interestingly, the isopods node also slightly decreased despite the positive input, this could be a response to the decline in habitat since *Z. marina* represents important shelter for these organisms. The bivalves responded negatively and the phytoplankton node responded positively, resulting in increased turbidity.

Negative input on filamentous algae

The negative input on filamentous algae node (Figure III.5) resulted in negative response of amphipods, isopods and bivalves. There was positive effect in *Z. marina*, *F. vesiculosus* and phytoplankton and negative response of filamentous algae. Turbidity increased and habitat provisioning as well, while climate regulation decreased.

Global prediction

The combination of the inputs (Figure III.5) resulted in low sign determinacy (i.e. decrease) of *F. vesiculosus* and filamentous algae biomass. Amphipods and bivalves also responded negatively. *Z. marina* and isopods did not respond to the combination of inputs. Phytoplankton and, as a consequence, turbidity responded with high sign determinacy, implicating in lower water purification service. Climate regulation responded negatively and habitat provisioning was not affected.

The combination of the inputs yielded 5 out of 6 correct predictions. The random graphs generated demonstrated that the pattern obtained by the experimental dataset was significant (pseudo p-value = 0.03).

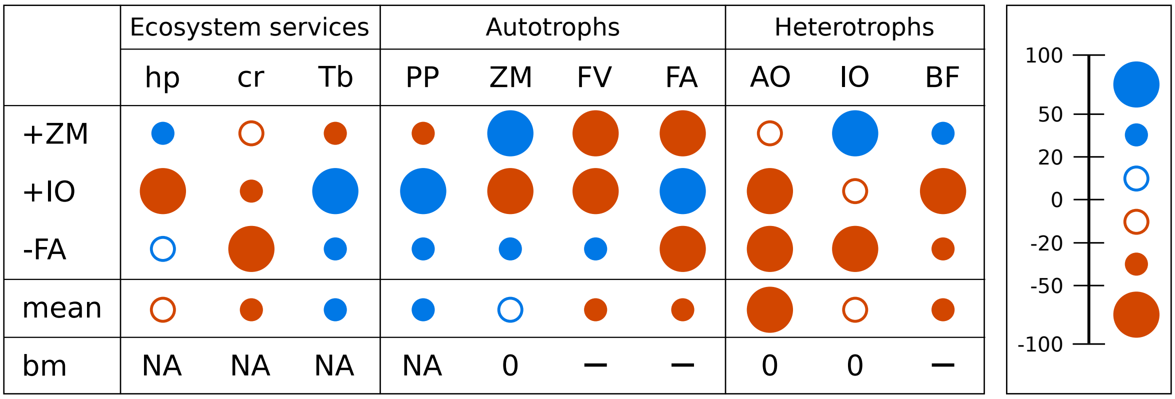


Figure III.5 – Loop analysis predictions of the ecosystem to heatwaves represented as a positive input on *Zostera marina* (+ZM), and isopod (+IO) and a negative press perturbation on filamentous algae (-FA). Outcomes reported in the table concern the response to such inputs of habitat provisioning (hp), climate regulation (cr), water purification as turbidity (TB); the autotrophs phytoplankton (PP), *Z. marina* (ZM), *F. vesiculosus* (FV), filamentous algae (FA); and the heterotrophs amphipods (AO), isopods (IO), bivalves (BF). The mean corresponds to the combination of the inputs' effects on the nodes. The scale on the right side of the figure represents the net percentage prevalence of the simulation outcome; the size of the circles indicates the intensity of the change, blue circles correspond to increase of the node, the red circles mean that the nodes decreased and the empty circles indicate no effect on the node. The benchmarks (bm), i.e. the baseline as change in biomass showed in the Figure 4, are represented as not available (NA), no effect (0) and negative impact (-).

Sensitivity analysis

Climate regulation was the most sensitive service to the strength of the ecological interactions. The service responded negatively (Figure III.6a) to all of the 11 simulations of interaction strength tested over the10 links that represented the network (Table III.2). This result reinforces the robustness of the predictions that show the decline of this service under 3HW treatment.

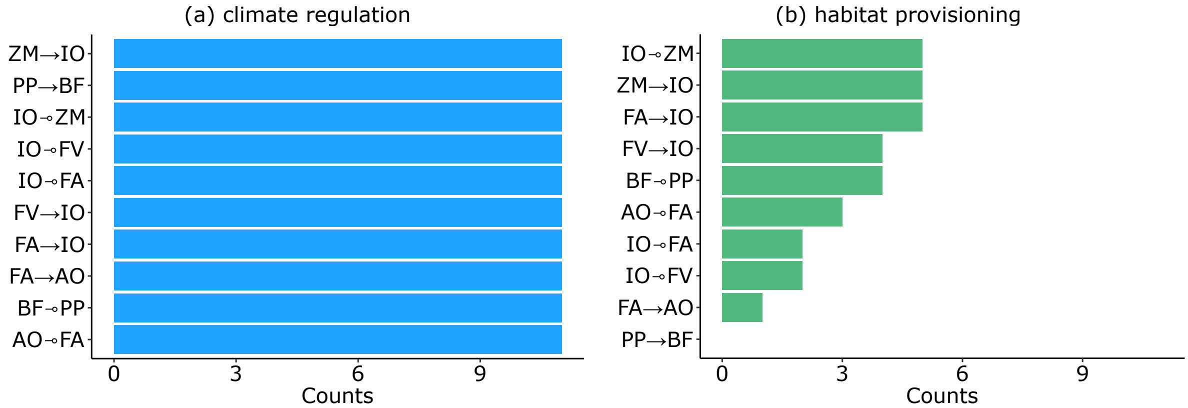
Habitat provisioning was the sturdiest service (Figure III.6b). The service responded negatively in 5 out of 11 simulations for the prey-predator interactions between isopods and *Z.*

marina and positive interactions from filamentous algae to isopods. The positive interaction from *F. vesiculosus* to isopods and the negative interaction from bivalves on phytoplankton had a negative influence on habitat provision in 4 out of 11 simulations. In case of the predator interaction between amphipod to filamentous algae, 3 out 11 simulations resulted in decline of habitat provisioning service. The predator interaction between isopod and filamentous algae and *F. vesiculosus* affected negatively habitat provisioning in 2 out of 11 simulations. The prey interaction between filamentous algae and amphipods caused negative effect on the service in 1 out of 11 simulations. The prey interaction between phytoplankton and bivalves did not result in negative impacts on the service in any of the simulations.

The water purification, represented as increase in turbidity, was sensitive to interaction strength (Figure III.6c). All interactions (except for prey interaction of filamentous algae and *Z. marina* with isopods) resulted in negative impacts on the service in 100% of the simulations. The positive interaction between filamentous algae and isopods resulted in negative provision of the service in 10 out of 11 simulations, while between *Z. marina* and isopods this value decline to 8 out of 11 simulations. The sensitivity of the service to the interactions strength confirms the negative response of the service that we obtained in the predictions (Figure III.5).

Discussion

The evaluation of ecosystem services based on the qualitative network approach is relevant since the models enable the detection of direct and indirect effects and feedbacks of the ecological interactions that can yield unexpected outcomes (Dee et al. 2017). This study used a mechanistic framework for investigating the connection of ecological interactions with ecosystem services provisioning under climate change. We found that climate regulation and water purification (represented as turbidity) services were jeopardized by heatwaves, while habitat provisioning was not impacted. The services negatively affected showed more vulnerability to changes in ecological interaction strength and the habitat provisioning was, indeed, more robust.


(a) climate regulation

(b) habitat provisioning

(c) water purification

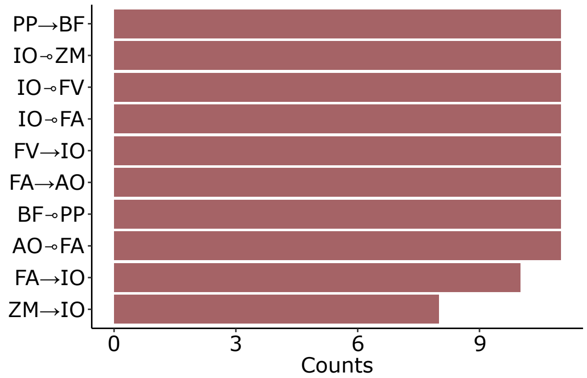


Figure III.6 – Results of the simulation on interaction strength of each ecological interaction that resulted in negative provisioning of climate regulation (a), habitat (b) and water purification represented as increase of turbidity (c). The y-axis represents the interactions tested and the x-axis shows in how many simulations of interaction strength the outcome was negative for the ecosystem services targeted

The first step to analyze the impact of heatwaves on the network was the identification of the inputs, in this case the metabolic response of the living nodes. The responses of metabolic rates to climate change might be variable, since each organism tolerates specific ranges of environmental fluctuations (Pansch et al. 2018, Wahl et al. 2019) that are determined by activation energy at individual level (Yvon-Durocher et al. 2010). The experiment generated three main inputs that represented the impacts of the sequential heatwaves treatment (3HW): (1) negative metabolic response of filamentous algae (Figure III.3a), (2) positive effects on the metabolism of *Z. marina* (Figure III.3e) and (3) positive input on isopods (Figure III.3d). These inputs were applied to the matrix of interactions that combined biotic nodes and ecosystem services nodes.

The second step was to identify how the biomass of the nodes that compose the ecological network would respond to validate our predictions. We found that there was a decline in *F. vesiculosus* (Figure III.4b), filamentous algae (Figure III.4c) and bivalves (Figure III.4f). These results were discussed in Chapter II; thus, we will focus on the outcomes of the loop analysis regarding the ecosystem services and the relation with the ecological interactions. Finally, the following discussion is going to focus on the capacity of the system to supply ecosystem services, i.e. the service generated independently of the direct demand or use by the people (Dee et al. 2017).

Water purification – turbidity

The turbidity increased indicating that the heatwaves may negatively affect water purification capacity of the ecosystem (Figure III.5). The loop analysis paths (Appendix Table III.3) showed that bivalves, which were feeding on phytoplankton, mediated all the effects on turbidity. Thus, the result on the decline of water purification service is related to the decline in abundance and biomass of bivalves (*Mytilus edulis* and *Limecola balthica*; Pansch et al. 2018) affected directly or indirectly by sequential heatwaves, which impaired the filtration capacity of the ecosystem. The heatwave exceeded the temperature tolerated by the filter-feeders (24 °C; Jansen et al. 2007) during the third heatwave (Figure III.1). Since sessile or low mobility organisms are unable to escape the increase of water temperature, bivalves are more vulnerable to heatwaves than high mobile taxa (Wernberg et al. 2013, Smale et al. 2019). Moreover, the high frequency of heatwaves may decrease the tolerance of *M. edulis* to warm temperatures (Seuront et al. 2019), which was detected in this experiment through the decline abundance of this species' abundance in comparison to one and no heatwave (Pansch et al. 2018). The sensitivity analysis revealed that the water purification service is consistent under different interactions strength (Figure III.6a), confirming the robustness of our results. The sensitivity analysis also indicates the high vulnerability of the service to sequential heatwaves.

Climate regulation

The capacity of the ecosystem to provide climate regulation (i.e. carbon storage) declined (Figure III.5) as we expected from the decrease of total macrophytes biomass, mainly macroalgae.

Macroalgae presents high potential for climate mitigation (Krause-Jensen et al. 2018) due to carbon binding function and the capacity of carbon storage and sequestration (Trevathan-Tackett et al. 2015). However, the increase in frequency extreme climate events, e.g. heatwaves, increases the mortality of macroalgae mainly species from temperate regions (Wernberg et al. 2013).

Seagrass ecosystems are known for their high carbon sequestration capacity (Arias-Ortiz et al. 2018). Although the seagrass did not present change in biomass and the metabolism was positively affected by heatwaves, there is a concern about their vulnerability to heatwaves (Arias-Ortiz et al. 2018, Nowicki et al. 2017). In the Baltic Sea, *Z. marina* was able to resist temperatures beyond the lethal threshold thanks to genotypic diversity (Reusch et al. 2005), however it is not yet known whether they will be able to cope with the predicted climate change.

The analysis of the paths (Appendix Table III.4) showed that grazers indirectly controlled the climate regulation service. Thus, whenever isopods and amphipods were either supported by feeding interaction or benefited from another service (i.e. habitat provisioning), climate regulation declined. Climate change may cause an amplification of grazing activity, which can cause a devastating effect on primary producers (Vergés et al. 2016).

Sensitivity analysis showed that climate regulation service was highly sensitive to interaction strength (Figure III.6a), which corroborates the results of the global prediction (Figure III.5) and demonstrates the fragility of such service to sequential heatwaves disturbances in this system.

Habitat provision

According to the loop analysis predictions, the capacity of the ecosystem to provide habitat may not change (Figure III.5). The sensitivity analysis showed that habitat provisioning was less robust to changes on ecological interaction strength compared to the other ecosystem services (Figure III.6b). The sensitivity also might indicate that this service is more resistant since it was not reduced every simulation of interaction strength tested. The analysis of the paths (Appendix Table III.5) showed that the node that jeopardizes habitat provisioning the most is isopod, which can also be observed from the positive input on this node (Figure III.5). However, although there was a decrease of the total biomass of *F. vesiculosus* and bivalves, the biomass of seagrass did not significantly change after 3HW and was enough to maintain the capacity of habitat provisioning of the system. In addition, the absence of an effect on habitat provisioning to heatwaves might be the lack of a positive feedback from the service to the primary producers, which explains the reason this service responded differently compared to climate regulation.

Dee et al. (2017) attempted for the importance of representing the ecosystem services within a network to avoid undesirable responses of management actions. The use of network analysis is able to detect the propagation of the effects of a disturbance (indirect effects and feedbacks) to the ecosystems, which could improve management decisions in face of climate change. This study on the operationalization of ecosystem services by coupling them with ecological interactions revealed that the predictions on the services must take into consideration how climate change propagates in the network. Furthermore, the operationalization of ecosystem services should consider experimental ecology research for improving the reliability of the outcomes for constructing future scenarios.

Conclusions

For maintaining human well-being, we have to cope with the effects of climate change. Thus, it is pivotal to understand the ecological interactions responsible for the delivery of ecosystem services. Our work operationalized ecological networks to identify the changes in ecosystem services caused by heatwaves. This study showed that sequential heatwaves generated inputs in the network that were able to jeopardize some ecosystem services even though the peak of temperatures did not exceed the lethal thresholds for all the species. The increase of heatwaves frequency is matter of concern for the provisioning of ecosystem services as shown by the devastating effects they produced in some regions (Arias-Ortiz et al. 2018). This work was a contribution to reach a step further for including ecological experimental studies in the context of ecosystem services for bridging this ecological knowledge with environmental management and to decrease uncertainties for decision-making.

General discussion

Health of ecosystems – Functioning based on feeding interactions

This thesis addressed the health of coastal ecosystem by focusing on energy flow expressed as carbon flows in single species, ecological interaction (i.e. grazing) and complex food web. The goal was to provide a holistic ecosystem analysis of the effects of climate change. In the first chapter, the thermal performance curves of the single-species' physiological responses controlled the carbon balance and the grazing activity mediated the carbon budget in the simplified food web. The second chapter showed that tracing carbon flow along the food web is able to indicate stress on the system caused by heatwaves. The exposition of the ecosystem to heatwaves resulted in the decrease of energy entering the system and changes on the intensity of the food web interactions. Finally, in the third chapter the qualitative network analysis showed that three sequential heatwaves impacted water purification and climate regulation services while habitat provisioning was not affected. In this thesis, I studied the mechanisms controlling the provisioning of ecosystem services by investigating responses from single-species up to whole-ecosystem level.

Single species analysis and implications on the trophic interactions

The single-species approach is useful for understanding how the interspecific variability responds to disturbances driven by temperature changes (Straub et al. 2019). Each species presents particular thermal performances curves – TPC (Wahl et al. 2019) – as detected in the Chapter I for the macroalgae *Fucus vesiculosus* and its main mesograzer *Idotea balthica*. Moreover, it was demonstrated that each physiological trait responded differently to temperature either in TPC shape or optimal temperature. The physiological responses were used to determine the feeding interaction between macroalgae and grazer for quantifying the carbon fixated that was stored by *F. vesiculosus*. The carbon stored was explained by temperature from 5 to 20 °C and at 25 °C making the system bottom up controlled (Figure B.1). The mesograzer controlled the carbon budget between 20 and 25 °C, thus the system became top-down controlled (Figure B.1). Mertens et al. (2015) detected the increase followed by a decline of interaction strength between grazer and macroalgae, which corroborates the findings of Chapter I. The authors found that the thermal tolerance of the primary producer was peaking at higher temperature than the thermal tolerance of the grazer. In Chapter I, a similar pattern was found, i.e. photosynthesis activity of *F. vesiculosus* did not peak in the experimental temperatures, increasing linearly until 25 °C, while the consumption of *I. balthica* peaked at 22 °C. Grazing activity is important for keeping the balance of ecosystems, for instance Alsterberg et al. (2013) found that the presence of grazers buffered the direct and indirect effects of warming and acidification in marine ecosystems. Therefore, it is necessary to take in consideration modifications in herbivory due to temperature changes in studies that investigate the marine ecosystem response to global climate change.

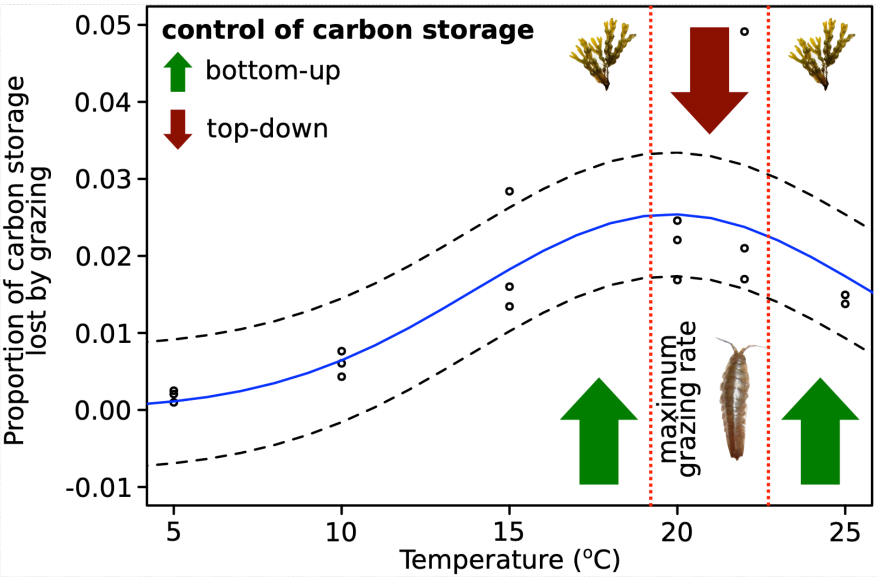


Figure B.1 – Carbon storage proportion lost by grazing based on the results of Chapter I. The green arrows correspond to bottom-up control and the red arrow corresponds to top-down control.

Food web and ecological network analysis

The report about the Baltic Sea from HELCOM (2010) acknowledged that the assessment of the marine ecosystems' health could benefit from exploring the food web analysis indicators. Indeed, the Chapter II indicated that climate change might be able to harm the health of a benthic ecosystem exposed to heatwaves.

The outcomes of the ENA in Chapter II demonstrated that one heatwave caused (1) an increase in the intercompartmental connectance and (2) decrease in the food web connectance. These results indicate that the connectance of the compartments to outside the ecosystems intensified, while internally the connectance between the living compartments decreased. One heatwave event did not strongly impact the ecosystem and it could be interpreted as early sign of the stress. However, it should not be discarded that the effects of the heatwave could be more evident after some weeks or months (Takolander et al. 2017, Edwards 2004).

Three sequential heatwaves (1) decreased the size of the ecosystem and (2) rearranged the energy flows that became more efficient and organized. The size (i.e. activity or amount of energy flow) of the ecosystem decreased due to the lower energy input through photosynthesis mainly from *F. vesiculosus* and filamentous algae, which culminated in less energy available to circulate inside the system. Other studies found that the occurrence of heatwaves is able to jeopardize benthic macrophytes (Straub et al. 2019) and, in some cases the damage is so intense that they are not able to recover causing decline of primary productivity (Nowicki et al. 2017). The increase of efficiency and organization of energy flows were indicated mainly by overhead and residual diversity (Figure II.3). The uneven distribution of the energy flows made some links more relevant. High diversity or even distribution of energy flows in ecosystems protects the environment against disturbance (Odum 1969), i.e. the disruption on energy flow caused by any disturbance might cancel whole pathways of energy transfer. Hence, the indicators resulting from the three heatwaves treatment can be interpreted as loss of resilience of the ecosystem (i.e. the ecosystem became more vulnerable to disturbances). The conclusion is that the marine ecosystem did not go through learning process after the sequential heatwaves experienced during spring and early summer. Climate change indeed is able to modify not only the structure of food webs but also energy flows (O'Gorman et al. 2019). Therefore, marine ecosystems may go through even more severe changes of ecosystem functioning since heatwaves events are predicted to become longer and more intense (Oliver et al. 2019).

Ecosystem services

The results of Chapter II showed the deterioration of the ecosystem functioning; thus, it was expected that some ecosystem services would be jeopardized by three sequential heatwaves. In Chapter III, instead of relying directly on ecosystem services indicators, I applied the operationalization approach for ecosystem services analysis (Dee et al. 2017). I selected a qualitative network analysis, the loop analysis, in order to detect direct, indirect effects and feedbacks (Reum et al. 2015) of the ecological interactions and ecosystem services. Loop analysis is a valuable tool for studying the impacts of disturbances in networks that involves different types of interactions, i.e. ecological, social and economic (Martone et al. 2017). The metabolic rates of the nodes were used to identify the disturbances caused by heatwaves. The metabolism of three nodes responded to the heatwaves (1) *Z. marina* responded positively, (2) isopods responded positively and (3) filamentous algae responded negatively (Figure III.2). Thus, the combination of the inputs generated 5 correct predictions out of 6; the predictions were related to the biomass of the nodes impacted or not by heatwaves. Also, the sensitivity analysis confirmed the outcomes of the analysis. The ecosystem services jeopardized were climate regulation (i.e. carbon binding, storage and sequestration) and water purification (expressed as turbidity), whilst habitat provisioning did not change. Smale et al. (2019) detected that marine heatwaves have already severely affected ecosystem service provisioning as carbon sequestration and storage, habitat provisioning and others. The conclusion is that the ecosystem services partially responded according to the functioning of the ecosystem, since not all ecosystem services were negatively impacted by the sequential heatwaves treatment. The operationalization of ecosystem services is essential to avoid misleading environmental management strategies (Dee et al. 2017). Chapter III contributed to advance this research field since it provided an exercise of how experimental ecology can be combined with modeling to provide objective analysis of the ecosystem services. The operationalization is still in its infancy and there is scope for improving the analysis of ecosystem functioning and services based on experimental dataset (Kotta et al. 2019b) for allowing more realistic evaluations and lead to efficient and adaptive management strategies.

Final considerations

In this section, there are three main considerations that I would like to expose. First, the direct conclusions I extracted from the thesis itself. The second and third considerations go beyond the thresholds of this thesis, however I think they are as valuable as the first one.

Initially, this thesis had the purpose to add a "brick on the wall" of the interface of science and society. The idea was to start from experimental ecology and find ways to translate the knowledge generated by this field into information for assisting environmental management. For achieving this goal, there was the need of connecting results of ecological experiments with modeling (Kotta et al. 2019b). Combining ecological experiments and modeling is a win-win strategy because experiments provide data about how ecosystems react to perturbations and models are able to use all the data generated to give insights on the mechanistic effects of such disturbance. Datasets from experiments can be used to validate and improve predictions and interpretations of the models. The outcomes of these models should enhance the knowledge on how ecosystems respond to the climate conditions predicted for years ahead. This approach is helpful for building different scenarios that forecast the trends the ecosystem services might follow. Finally, Neuteleers and Engelen (2015) showed that the more efficient way to get population support and demand for nature conservation is to raise awareness, which can be done by science communication. Therefore, the scenarios construction should be used to elucidate to the public in general the effects of climate change on future generations.

This thesis led me to think that ecology is more than studying the processes in nature. There is a great amount of exchange between ecology and other fields. Ecology borrowed concepts from other fields, for example economy (Leontief structure matrix by Ulanowicz (2004), modern portfolio theory by Schindler et al. (2015)). And ecology also lent concepts to other fields, for instance the ecological terms of Odum (1969) were used to explain resilience in politics and governance (Zebrowski 2013). Thus, it is not surprising that ecologists start working on other fields as well (e.g. Fath et al. 2019). Thus, the advance of ecological studies has still a lot to learn and teach to other fields. The validation of theoretical ecology using experimental approach is useful not only for ecology itself but it may be also extrapolated for other fields like sociology.

One example of how sociology could be related to ecology can be found in the book of Capra (1983). The author reports the relationship between the increase of religious or political extremisms preceding the collapse of civilizations. The same phenomenon occurs in nature; whenever an ecosystem is pushed to the extremes there are variations in parameters that precede the shift to a new stable state (Beisner et al. 2003).

A last consideration is that I gained another perception from this thesis. Ecology is not only about living and non-living interactions in nature but also societal interactions. It is necessary to make people understand that everything we experience in our daily lives is connected to ecology, e.g., economic trades, human health, poverty and wars depend on the maintenance of ecosystem functioning. We are used to a system that is economic-based; however, it is clear that this mono-dimensional approach gives rise to solutions that are not sustainable driving us to a collapse on the society as we know. Hence, it is the time for science to step forward and make use of all the knowledge that ecologists generated for moving towards social and economic equality in the world.

Future perspectives

The outcomes of the thesis raised more questions that can be explored in the future.

1) Improve the studies on the non-living compartments interactions with the living

Low trophic levels are important for the functioning of ecosystems (Lassalle et al. 2011). Ecosystems that rely intensively on detritus are considered more resilient due to the longer resident time of energy in the food web (Moore et al 2004). Detritus play important role in ecosystem dynamics due to the connections with most of the living compartments in the food web (Allesina et al. 2005). From all the experiments carried out, I realized that the composition of the detritus changed along the seasons. Although not quantified it was possible to perceive the change from decomposing fragments of macrophytes (macroalgae, seagrass leaves) during the spring to fecal material and dead organisms during summer. The detailed study of detritus could provide more information about the functioning of the ecosystem (recycling and storage of carbon, feeding interactions).

2) Coupling with other ecosystems, connectivity with larval dispersion

This thesis focused on benthic ecosystem; however, it is necessary to couple the interactions with other ecosystems (e.g. pelagic). In the Baltic Sea, the increase of temperature generates stratification that hinders the exchange of abiotic (e.g. nutrients, organic matter) and biotic (e.g. larval dispersion and feeding of pelagic fishes on benthic organisms) components between benthic and pelagic ecosystems (Griffiths et al. 2017). Climate change will disturb the ecosystems in several ways and it is pivotal to understand whether the coupling of ecosystems will have additional, synergistic or buffering effects.

3) Ecosystem services studies focusing adaptive management

Further studies are needed to demonstrate clearly how the damage to ecosystem health and, consequent, disruption of ecosystem services is affecting people directly. The studies should focus on creating different scenarios by using sensitivity analysis to exhibit the possible effects of management measures on the ecosystem services. The combination of experimental dataset, field sampling and modeling (Kotta et al. 2019b) could be used for predicting impacts of climate change on the ecosystems. Besides assisting the processes of decision-making for implementation of adaptive management focusing on services, such exercise should be used for raising awareness of the society. Stimulating the profound perception on people is a more effective manner to engage society to support the protection of the natural resources (Neuteleers and Engelen 2015).

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Appendix

Chapter I

***Appendix I.1** – Conversion of Idotea's body length to biomass (carbon content)*

To convert the body length of the *I. balthica* to biomass we collected 37 individuals of different length (from 3 to 31 mm). These individuals were collected in the Kiel fjord (54°38'N, 10°20'E) on 17th October 2016 together with the specimens used for the experiment. For each individual we obtained data regarding the length, wet, dry (48h at 80 °C) and ash free dry weight (overnight at 500 °C). Finally, we fitted regression curves for length to weight conversions. Since flows for investigating the carbon budget were expressed as grams of carbon, we first needed details concerning the dry weight. The conversion length to dry weight is based on the eqn 2 in the manuscript.

The conversion of the biomass of *I. balthica* to carbon was based on the dry weight of the grazers. The dry weight was converted into carbon using the percentage of carbon content of each *I. balthica* individual; such data were obtained from carbon content analysis.

***Appendix I.2** – Conversion of egestion to carbon*

The dry weight of fecal pellets from our experiment was converted to carbon using unpublished data provided by Dr. Lars Gutow (personal communication). We analyzed the data from Dr. Gutow to obtain the percentage of carbon content (27.66%) in dry weight of fecal pellets and applied such value for the conversion of the dry weights of our dataset.

***Appendix I.3** – Conversion of net primary production NPP and respiration rates from O_2 to carbon*

To convert NPP and respiration rates from mg $O_2 \cdot l^{-1}$ to mg C $\cdot$ day^{-1}, the following equations were applied after Wenzel and Likens (2000) and Bitton (1998):

$$NPP_C = (\Delta DO \cdot \frac{M_C}{M_{O_2}} \cdot V \cdot L) \div PQ \qquad \text{(eqn S1)}$$

$$Respiration_C = \Delta DO \cdot \frac{M_C}{M_{O_2}} \cdot V \cdot RQ \cdot D \qquad \text{(eqn S2)}$$

$$GPP_C = NPP_C + Respiration_C \qquad \text{(eqn S3)}$$

where:

NPP_C refers to NPP expressed in carbon

$Respiration_C$ indicates respiration after the conversion to carbon

GPP_C is the GPP in carbon units

ΔDO is the difference between final and initial O_2 concentrations of the incubations ($mg\ O_2 \cdot l^{-1}$).

M_C: molar mass of carbon ($12\ mg \cdot mmol^{-1}$)

M_{O2}: molar mass of O_2 ($32\ mg \cdot mmol^{-1}$)

V: volume of the incubation chamber in l

PQ is the photosynthesis quotient (1.2) (Kotta et al. 2000)

RQ is the respiration quotient (0.85) (Hawkins and Bayne, 1985)

L: represents the hours of light per day (12 hours in our experimental setup, corresponding to field conditions when *Fucus vesiculosus* and *Idotea balthica* were collected)

D: represents the 24 hours per day

The *RQ* was calculated using the maximum and minimum values described by Hawkins and Bayne (1985); such values range from 1.0 to 0.71 depending on the type of molecules that are consumed, i.e. the catabolism of carbohydrates generates higher *RQ* values compared to the catabolism of lipids and proteins.

***Appendix I.4** – I. balthica density in the field*

The density of grazers in the field according to temperature (Table SI.1) was estimated based on the data from Anders and Möller (1980). The authors carried out annual samplings and quantified the density of grazers per biomass of *Fucus vesiculosus*. We extracted the biomass of *I. balthica* and the water temperature of the field and modelled the effect of temperature on the biomass of *I. balthica* with a linear regression ($R^2 = 0.753$; $F_{1,7} = 21.34$; p-value = 0.002).

$$y = 0.40x - 1.05 \qquad \text{eqn S4}$$

where:

y is the biomass of *I. balthica* per kg dw of *F. vesiculosus*

x refers to temperature (°C)

Appendix Table I.1 – Predictions of *I. balthica* biomass per kg of dry weight *F. vesiculosus.* The columns lower and upper report the limits corresponding to 95% confidence interval

Temperature (°C)	***I. balthica* (g DW)**	**lower**	**upper**
5	0.9553	-0.6803	2.5910
10	2.9580	1.6070	4.3090
15	4.9607	3.2066	6.7149
20	6.9635	4.4276	9.4993
22	7.7645	4.8731	10.6560
25	8.9662	5.5185	12.4138

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Chapter II

***Appendix II.1** – Literature review on feeding preferences*

We screened the literature available to determine the feeding preferences of each species found in the tanks of KOB at the end of the experiment. This information was used for carrying out stable isotopes analysis and aggregating the species into compartments.

Appendix Table II.1 – Information about the consumer species collected in the experimental ecosystems

Species	Taxa	Feeding behavior	Target species	Habitat	References
Gammarus sp.	Amphipoda	Omnivore	Micro and macroalgae, detritus, zooplankton and occasionally cannibalism	Benthic (free swimming)	Anderson et al. (2009)
Corophium sp.	Amphipoda	Suspension-feeder	Benthic and pelagic microalgae, detritus and bacteria	Burrower (7-15 cm depth in the sediment)	Gerdol & Hughes (1994)
Microdeutopus gryllotalpa	Amphipoda	Deposit-feeder	Microalgae	Burrower (1-2 cm depth in the sediment)	DeWitt & Levinton (1985); Köhn & Gosselck (1989)
Mytilus edulis	Bivalve	Suspension-feeder	Seston	Sessile (attached to hard bottom, macrophytes or sediment)	Jagnow & Gosselck (1987)
Cardium sp.	Bivalve	Suspension-feeder	Seston	Sediment infauna	Jagnow & Gosselck (1987)
Corbula gibba	Bivalve	Suspension-feeder	Seston	Sediment infauna	Jagnow & Gosselck (1987)
Limecola balthica	Bivalve	Suspension and deposit-feeder	Benthic and pelagic microalgae, detritus	Sediment infauna (1-190 m depth)	Beukema et al. (1985); Lin & Hine (1994); Brey (1991)
Mya truncata	Bivalve	Suspension-feeder	Seston	Sediment infauna (up to 10 m depth)	Winter (1969)
Kurtiella bidentata	Bivalve	Suspension-feeder	Benthic and pelagic	Sediment infauna	Josefson (1998)

			microalgae, detritus		
Littorina littorea	Gastropod	Herbivore	Micro and macroalgae	Benthic (creeper)	Jagnow & Gosselck (1987)
Hydrobia sp.	Gastropod	Herbivoreand detritivore	Micro and macroalgae and detritus	Benthic (creeper)	Aberle et al. (2009); Jagnow & Gosselck (1987)
Idotea baltica	Isopod	Omnivore	Micro and macroalgae, detritus and occasionally cannibalism	Benthic (crawler / free swimming)	Leidenberger et al. (2012)
Jaera albifrons	Isopod	Herbivore and detritivore	Microalgae and detritus	Benthic (crawler)	Jones (1972)
Ampharete sp	Polychaeta	Deposit-feeder	Microalgae and detritus	Benthic infauna (burrower)	Fauchald & Jumars (1979); Bick & Gosselck (1985)
Arenicola marina	Polychaeta	Deposit-feeder	Microalgae, detritus and bacteria	Benthic infauna (burrower)	
Marenzelleria viridis	Polychaeta	Deposit-feeder	Microalgae, detritus and bacteria	Benthic infauna (burrower)	Kotta & Olafson (2003)
Polydora cornuta	Polychaeta	Suspension-feeder	Microalgae, detritus and bacteria	Benthic infauna (burrower)	Dauer et al. (1981); Takata et al. (2011)
Pygospio elegans	Polychaeta	Deposit-feeder	Microalgae, detritus and bacteria	Benthic infauna (burrower)	Brey (1991); Bick & Gosselck (1985)
Eteone longa	Polychaeta	Carnivore	Spionids (e.g. Polydora and Pygospio) and occasionally cannibalism	Benthic epifauna	Zajac (1995); Schubert & Reise (1986); Bick & Gosselck (1985)
Harmothoe imbricata	Polychaeta	Omnivore	Microalgae, small crustaceans (e.g. *Corophium* sp), other polychaete (e.g. Nereis sp), juvenile of bivalves and gastropods	Benthic epifauna (within algae rhizoids)	Plyuscheva et al. (2010); Watson, et al. (2000)
*Nereis sp**	Polychaeta	Omnivore	Microalgae, zooplankton,	Benthic in- (burrower) or	Bick & Gosselck (1985)

			meiofauna, carrion and other macrofauna.	epifauna (within macrophytes and hard bottoms)	
Scoloplos armiger	Polychaeta	Omnivore	Detritus, macrofauna and occasionally cannibalism	Benthic in- and epifauna	Schubert & Reise (1986), Kruse 2002
Phyllodoce mucosa	Polychaeta	Scavenger	Decomposing animals	Benthic infauna	Hernández-Guevara (2004)

Appendix II.2 *– PB, CB and EB ratios*

Appendix Table II.2 – The productivity, consumption and egestion per biomass ratios (PB, CB and EB, respectively) collected from the literature and calculated taking into consideration the Q10 specific for the temperature at the end of the experiment (de la Vega et al. 2018)

Taxon	**PB (20 °C)**	**CB (20 °C)**	**EB (20 °C)**	**References**
zooplankton	0.2829	0.8745	3.8819	de la Vega et al. 2019
Hydrobia ulvae	0.0127	0.0713	0.0530	de la Vega et al. 2019
Littorina littorea	0.0023	0.0233	0.0140	de la Vega et al. 2019
Arenicola marina	0.0158	0.1216	0.0899	de la Vega et al. 2019
Scoloplos intertidalis	0.0021	0.0556	0.0392	de la Vega et al. 2019
Nereis diversicolor	0.0039	0.0595	0.0410	de la Vega et al. 2019
Pygospio elegans	0.0107	0.0536	0.0150	de la Vega et al. 2019
Corophium sp.	0.0105	0.0733	0.0131	de la Vega et al. 2019
Gammarus sp.	0.0157	0.1074	0.0236	de la Vega et al. 2019
Idotea balthica	0.0280	0.0460	0.0011	Ito et al. 2019a
Mytilus edullis	0.0026	0.0182	0.0026	de la Vega et al. 2019
Mya arenaria	0.0082	0.0303	0.0082	de la Vega et al. 2019
Limecola baltica	0.0103	0.1637	0.0741	de la Vega et al. 2019
Cerastoderma sp.	0.0050	0.0253	0.0182	de la Vega et al. 2019
Phyllodocidae	0.0064	0.0772	0.0086	de la Vega et al. 2019
small polychaeta	0.0107	0.0772	0.0171	de la Vega et al. 2019
Marenzelleria sp.	0.0080	0.0777	0.0348	Zettler 1997
Microdeutopus grillotalpa	0.0320	0.0733	0.0131	Drake and Arias 1995
free living bacteria	16.670	33.3321	0.1586	de la Vega et al. 2019
sediment bacteria	0.3644	0.9603	0.1543	de la Vega et al. 2019

Appendix II.3 *– Conversion of net primary production (NPP) and respiration rates from* O_2 *to carbon*

To convert NPP and respiration rates from mg $O_2 \cdot l^{-1}$ to mg C $\cdot$ day^{-1}, the equations applied were based on Wenzel and Likens (2000) and Bitton (1998):

$$NPP_C = (\Delta DO \cdot \frac{M_C}{M_{O_2}} \cdot V \cdot L) \div PQ \qquad \text{(eqn S1)}$$

$$Respiration_C = \Delta DO \cdot \frac{M_C}{M_{O_2}} \cdot V \cdot RQ \cdot D \qquad \text{(eqn S2)}$$

$$GPP_C = NPP_C + Respiration_C \qquad \text{(eqn S3)}$$

where:

NPP_C refers to NPP expressed in carbon

$Respiration_C$ indicates respiration after the conversion to carbon

GPP_C is the GPP in carbon units

ΔDO is the difference between final and initial O_2 concentrations of the incubations (mg $O_2 \cdot l^{-1}$).

M_C: molar mass of carbon (12 mg $\cdot$ mmol^{-1})

M_{O2}: molar mass of O_2 (32 mg $\cdot$ mmol^{-1})

V: volume of the incubation chamber in l

PQ is the photosynthesis quotient (1.2) (Kotta et al. 2000)

RQ is the respiration quotient (0.85) (Hawkins and Bayne, 1985)

L: represents the hours of light per day

D: represents the hours of dark per day

The RQ was calculated using the maximum and minimum values described by Hawkins and Bayne (1985); such values range from 1.0 to 0.71 depending on the type of molecules that are consumed, i.e. the catabolism of carbohydrates generates higher RQ values compared to the catabolism of lipids and proteins.

Appendix II.4 *– Conversion from length to biomass (carbon content)*

Since flows for investigating the food web were expressed as grams of carbon, we first needed details concerning the dry weight. To convert the body length of the organisms to biomass we measured the length and dry weight (dried for at least 48h at 80 °C). We fitted linear regressions for length to weight conversions. The conversion length to dry weight is based on the Table S1.

Appendix Table II.3 – Linear model results of the body length (l) in mm and dry weight (m) in mg relationship. The linear models follow the equation $\log(l) = a + b \cdot \log(m)$. The parameters a and b refer to the terms presented below.

Species	Model	Term	Estimate	Std. Error	t-value	p-value
Idotea balthica	$R^2 = 0.87$; $F_{1,42} = 287.90$;	a	-1.77	0.17	-10.40	< 0.001
	p-value < 0.001	b	2.51	0.15	16.97	< 0.001
Gammarus sp.	$R^2 = 0.92$; $F_{1,69} = 754.10$;	a	-1.69	0.09	-17.77	< 0.001
	p-value < 0.001	b	2.60	0.09	27.46	< 0.001
Littorina littorea	$R^2 = 0.89$; $F_{1,9} = 70.66$;	a	0.19	0.37	0.51	0.625
	p-value < 0.001	b	2.34	0.28	8.41	< 0.001
Polychaeta	$R^2 = 0.54$; $F_{1,9} = 10.48$;	a	38.80	37.13	1.04	0.323
	p-value = 0.010	b	0.88	0.27	3.24	0.10

The conversion of the biomass to carbon was based on the dry weight of the organisms. The dry weight was converted into carbon using the percentage of carbon content for the organisms from each treatment; such data were obtained from carbon content analysis (Table S3).

Appendix Table II.4 – Stable isotopes analysis and relative carbon content to dry weight (mean ± SD)

Species	Treatment	$\delta^{15}N$	$\delta^{13}C$	Carbon content (%)
Fucus vesiculosus[1]	0HW	7.08 ± 0.51	-13.99 ± 1.10	32.06
	1HW	7.22 ± 0.78	-14.52 ± 2.42	34.18
	3HW	7.11 ± 1.94	-14.39 ± 1.95	28.19
Zostera marina[1]	0HW	6.62 ± 0.64	-14.25 ± 5.92	37.98
	1HW	7.17 ± 0.36	-11.11 ± 1.15	36.72
	3HW	5.93 ± 0.43	-14.70 ± 6.96	32.64
Filamentous algae[1]	0HW	6.79 ± 0.33	-25.21 ± 0.91	42.03
	1HW	6.45 ± 0.59	-24.50 ± 1.38	38.94
	3HW	7.83 ± 1.03	-21.91 ± 2.34	35.34
Zooplankton[2, 3]	0HW	7.23 ± 1.72	-22.32 ± 1.38	11.50 (C per individual)
	1HW	7.07 ± 1.73	-22.35 ± 1.45	
	3HW	7.57 ± 1.23	-22.96 ± 1.70	
Bivalves[1]	0HW	8.65 ± 0.53	-18.65 ± 0.65	42.94
	1HW	8.06 ± 0.33	-18.64 ± 0.92	42.50
	3HW	6.42 ± 0.37	-18.46 ± 0.38	37.24
Amphipod-deposit[1, 3]	0HW	7.52 ± 1.70	-20.34 ± 0.24	36.83
	1HW	7.52 ± 1.70	-20.34 ± 0.24	31.19
	3HW	7.52 ± 1.70	-20.34 ± 0.24	33.40
Amphipod-omnivore[1]	0HW	8.48 ± 0.41	-17.46 ± 0.94	35.94

	1HW	8.66 ± 0.31	-18.35 ± 2.30	31.19
	3HW	8.70 ± 0.57	-17.35 ± 0.72	32.91
Isopod[1]	0HW	8.89 ± 0.64	-14.56 ± 1.03	30.27
	1HW	8.95 ± 0.42	-14.59 ± 1.46	30.10
	3HW	8.58 ± 0.81	-13.96 ± 0.93	33.16
Gastropod[1]	0HW	8.08 ± 0.23	-17.36 ± 1.92	37.89
	1HW	8.01 ± 0.05	-18.59 ± 0.31	27.89
	3HW	9.12 ± 0.52	-17.56 ± 0.84	47.66
Polychaeta-deposit[1, 3]	0HW	10.93 ± 0.71	-19.31 ± 1.76	40.88
	1HW	10.93 ± 0.71	-19.31 ± 1.76	29.95
	3HW	10.93 ± 0.71	-19.31 ± 1.76	30.54
Polychaeta-omnivore[1]	0HW	9.84 ± 1.03	-18.75 ± 2.07	40.47
	1HW	10.42 ± 0.44	-17.93 ± 0.78	29.95
	3HW	9.84 ± 0.82	-17.21 ± 0.53	30.54
Seston[1, 3]	0HW	5.16 ± 2.23	-20.40 ± 1.54	6.92
	1HW	5.16 ± 2.23	-20.40 ± 1.54	6.87
	3HW	4.96 ± 0.88	-22.58 ± 1.78	7.18

[1] the data was measured for this experiment; [2] the carbon content data was obtained from Rumohr et al. 1987; [3] the stable isotope data was obtained from Mittermayr et al. 2014

Appendix Table II.5 – Matrix of interaction – 0HW treatment, the energy flow is represented from the row to the columns where PP: phytoplankton, MPB: microphytobenthos, ZM: *Zostera marina*, FV: *Fucus vesiculosus*, FA: filamentous algae, ZP: zooplankton, BF: bivalve-filter, AD: amphipod-detritivore, AO: amphipod-omnivore, IO: isopod-omnivore, GH: gastropod-herbivore, PD: polychaeta-detritivore, PO: polychaeta-omnivore, Sdet: sediment detritus, Wdet: water column detritus, DOC: dissolved organic carbon, Z: imports of energy to the system, E: exports of energy from the system, R: losses of energy from the system (respiration)

	PP	MPB	ZM	FV	FA	ZO	BF	AD	AO	IO	GH	PD	PO	Sdet	Wdet	DOC	Z	E	R
PP	0	0	0	0	0	19.58	10.37	0	0	0	0	0.37	0.80	168.16	25.49	8.63	249.87	0	16.47
MPB	0	0	0	0	0	1.53	1.09	8.37	8.90	0.27	38.65	2.75	0.79	0	47.18	71.83	218.31	0	36.95
ZM	0	0	0	0	0	0	0	0	3.23	0.68	9.78	0	0	60.53	0	6.31	393.81	91.85	221.42
FV	0	0	0	0	0	0	0	0	4.74	3.81	13.45	0	0	0	0	8.61	373.13	12.23	330.29
FA	0	0	0	0	0	0	0	0	5.08	3.19	29.96	0	0	2.25	0	15.95	750.34	416.82	277.08
ZO	0	0	0	0	0	0	0	0	1.87	0.53	0	0	0.92	46.35	10.28	0	0	0	20.33
BF	0	0	0	0	0	0	0	0	0	0	0	0	0	3.72	0	0	0	0	10.90
AD	0	0	0	0	0	0	0	0	0	0	0	0	0	2.76	0	0	0	0	6.11
AO	0	0	0	0	0	0	0	0	1.54	0	0	0	0	8.26	0	0	0	0	25.59
IO	0	0	0	0	0	0	0	0	0	2.39	0	0	0	1.65	0	0	0	0	7.13
GH	0	0	0	0	0	0	0	0	0	0	0	0	0	112.37	0	0	0	0	22.97
PD	0	0	0	0	0	0	0	0	0	0	0	0	1.29	13.37	0	0	0	0	16.47
PO	0	0	0	0	0	0	0	0	0	0	0	0	2.32	31.63	0	0	0	0	12.06
Sdet	0	0	0	0	0	0	1.23	0.50	10.02	0.30	43.51	27.94	39.04	10.63	10.11	0	0	341.38	41.40
Wdet	0	0	0	0	0	59.17	1.92	0	0	0	0	0.07	0.85	2.62	2.64	0	0	0	77.99
DOC	0	0	0	0	0	0	0	0	0	0	0	0	0	61.77	49.55	0	0	0	0

Appendix Table II.6 – Matrix of interaction – 1HW treatment, the energy flow is represented from the row to the columns where PP: phytoplankton, MPB: microphytobenthos, ZM: *Zostera marina*, FV: *Fucus vesiculosus*, FA: filamentous algae, ZP: zooplankton, BF: bivalve-filter, AD: amphipod-detritivore, AO: amphipod-omnivore, IO: isopod-omnivore, GH: gastropod-herbivore, PD: polychaeta-detritivore, PO: polychaeta-omnivore, Sdet: sediment detritus, Wdet: water column detritus, DOC: dissolved organic carbon, Z: imports of energy to the system, E: exports of energy from the system, R: losses of energy from the system (respiration)

	PP	MPB	ZM	FV	FA	ZO	BF	AD	AO	IO	GH	PD	PO	Sdet	Wdet	DOC	Z	E	R
PP	0	0	0	0	0	19.51	4.47	0	0	0	0	0.26	0.31	161.80	26.69	8.66	237.52	0	15.81
MPB	0	0	0	0	0	1.47	0.45	10.95	12.21	0.03	62.12	1.89	0.30	0	22.40	69.35	215.26	0	34.09
ZM	0	0	0	0	0	0	0	0	3.92	0.09	17.62	0	0	110.51	0	7.84	475.19	66.51	268.70
FV	0	0	0	0	0	0	0	0	6.44	0.33	16.74	0	0	0	0	10.44	374.79	34.34	306.50
FA	0	0	0	0	0	0	0	0	7.80	0.39	53.53	0	0	12.26	0	11.68	520.39	150.59	284.12
ZO	0	0	0	0	0	0	0	0	3.97	0.06	0	0	1.02	41.32	9.97	0	0	0	18.08
BF	0	0	0	0	0	0	0	0	0	0	0	0	0	2.17	0	0	0	0	4.03
AD	0	0	0	0	0	0	0	0	0	0	0	0	0	3.49	0	0	0	0	8.14
AO	0	0	0	0	0	0	0	0	2.87	0	0	0	0	11.85	0	0	0	0	36.62
IO	0	0	0	0	0	0	0	0	0	0.22	0	0	0	0.18	0	0	0	0	0.76
GH	0	0	0	0	0	0	0	0	0	0	0	0	0	187.83	0	0	0	0	34.10
PD	0	0	0	0	0	0	0	0	0	0	0	0	1.48	9.31	0	0	0	0	11.12
PO	0	0	0	0	0	0	0	0	0	0	0	0	3.51	22.12	0	0	0	0	8.41
Sdet	0	0	0	0	0	0	0.52	0.68	14.13	0.04	71.91	19.71	27.12	10.11	13.20	0	0	434.09	39.29
Wdet	0	0	0	0	0	53.45	0.75	0	0	0	0	0.045	0.30	0.21	2.51	0	0	0	67.84
DOC	0	0	0	0	0	0	0	0	0	0	0	0	0	57.65	50.32	0	0	0	0

Appendix Table II.7 – Matrix of interaction – 3HW treatment, the energy flow is represented from the row to the columns where PP: phytoplankton, MPB: microphytobenthos, ZM: *Zostera marina*, FV: *Fucus vesiculosus*, FA: filamentous algae, ZP: zooplankton, BF: bivalve-filter, AD: amphipod-detritivore, AO: amphipod-omnivore, IO: isopod-omnivore, GH: gastropod-herbivore, PD: polychaeta-detritivore, PO: polychaeta-omnivore, Sdet: sediment detritus, Wdet: water column detritus, DOC: dissolved organic carbon, Z: imports of energy to the system, E: exports of energy from the system, R: losses of energy from the system (respiration)

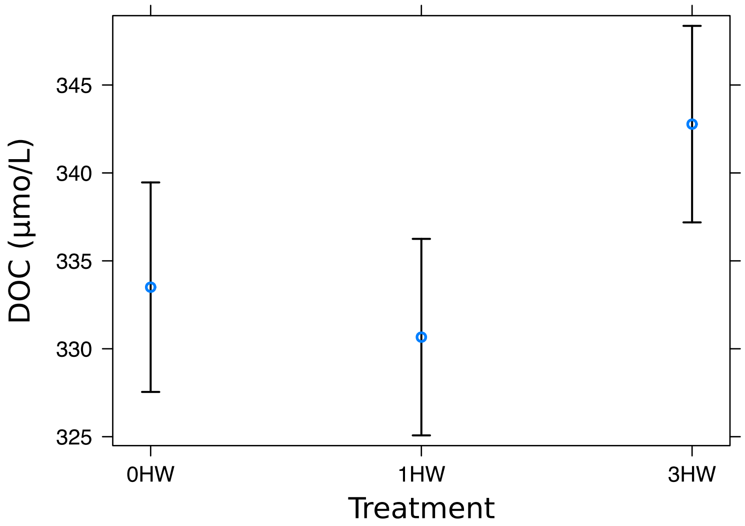
	PP	MPB	ZM	FV	FA	ZO	BF	AD	AO	IO	GH	PD	PO	Sdet	Wdet	DOC	Z	E	R
PP	0	0	0	0	0	20.07	4.36	0	0	0	0	0.22	0.80	169.70	25.38	9.13	246.17	0	16.50
MPB	0	0	0	0	0	1.61	0.47	7.05	7.09	0.41	29.83	1.69	0.82	0	48.23	78.07	213.28	0	38.01
ZM	0	0	0	0	0	0	0	0	1.43	1.01	5.13	0	0	166.62	0	6.86	421.59	49.79	190.76
FV	0	0	0	0	0	0	0	0	5.98	5.07	13.30	0	0	0	0	8.19	377.44	3.09	341.80
FA	0	0	0	0	0	0	0	0	3.60	3.74	27.20	0	0	1.55	0	4.20	205.21	0.01	164.91
ZO	0	0	0	0	0	0	0	0	4.69	0.64	0	0	0.99	46.30	10.13	0	0	0	20.16
BF	0	0	0	0	0	0	0	0	0	0	0	0	0	2.23	0	0	0	0	3.92
AD	0	0	0	0	0	0	0	0	0	0	0	0	0	2.69	0	0	0	0	4.76
AO	0	0	0	0	0	0	0	0	1.21	0	0	0	0	7.45	0	0	0	0	22.91
IO	0	0	0	0	0	0	0	0	0	3.72	0	0	0	2.13	0	0	0	0	9.17
GH	0	0	0	0	0	0	0	0	0	0	0	0	0	86.57	0	0	0	0	20.74
PD	0	0	0	0	0	0	0	0	0	0	0	0	0.97	7.88	0	0	0	0	9.40
PO	0	0	0	0	0	0	0	0	0	0	0	0	2.68	30.31	0	0	0	0	11.47
Sdet	0	0	0	0	0	0	0.50	0.40	7.56	0.44	31.85	16.30	37.33	10.45	11.25	0	0	437.07	40.39
Wdet	0	0	0	0	0	61.22	0.81	0	0	0	0	0.04	0.86	0.24	2.65	0	0	0	78.84
DOC	0	0	0	0	0	0	0	0	0	0	0	0	0	59.43	47.02	0	0	0	0

Appendix Table II.8 – Description and interpretation of the indices obtained from the ecological network analysis (Ulanowicz 2001, 2004; Scotti et al. 2009; de la Vega et al. 2018). The notation used in this table considers a network of *N* nodes, where flow from compartment $i = 0$ refers to the imports from outside the system (i.e. photosynthesis or carbon entering the system through non-living compartments); flows among compartments $i, j = 1, 2, 3, \ldots, N$ refers to exchanges between compartments; flows to compartments j = N+1 and j = N+2 indicates outflows that leave the ecosystem either as usable or non-usable energy (i.e. exports and respiration/dissipation, respectively)

Indices	Equation	Definition	Interpretation
The total system throughput (TST)	$TST = inputs + internal\ flows + respiration\ flows + exports$	It corresponds to the total amount of carbon flowing in the system showing growth and development of the system (Ulanowicz 2004)	It determines the size and activity of the ecosystem. The larger and more active the ecosystem, the higher the TST
Average mutual information (AMI)	$AMI = \sum_{i=0}^{N+2}\sum_{j=0}^{N+2}\left(\frac{T_{ij}}{TST}\right)\log_2\left(\frac{T_{ij}\cdot TST}{T_{i.}\cdot T_{.j}}\right)$	It shows the configuration of the flows of carbon through the system, demonstrating whether the compartments are more specialized (Ulanowicz 2004)	It refers to the efficiency of the system to spread energy and therefore, it is related to stability. The higher the AMI, the higher the efficiency of energy exchange
Flow diversity (FD)	$FD = -\sum_{i=o}^{N+2}\sum_{j=0}^{N+2}\frac{T_{ij}}{TST}\cdot\log_2\left(\frac{T_{ij}}{TST}\right)$	Based on Shannon-Weaver diversity index. It takes into consideration the number and diversity of flows embedded in the TST	The higher the flow diversity the more evenly distributed the energy flow of the ecological interactions
Development capacity (DC)	$DC = TST \cdot FC$ or $DC = A + \phi$	It is the upper limit of development of an ecosystem. This index is the result of the flows diversity and ecosystem activity	The higher the index the higher the scope for growth
Ascendency (A)	$A = TST \cdot AMI = \sum_{i=0}^{N+2}\sum_{j=0}^{N+2} T_{ij}\log_2\left(\frac{T_{ij}\cdot TST}{T_{i.}\cdot T_{.j}}\right)$	It corresponds to the developed part of the system, i.e. the organized	The higher the value the higher the ‘maturity’ of the ecosystem

A/DC		A/DC is the proportion of growth and development compared to the most efficient configuration	The increase of such index shows that the energy flows became more organized.
Overhead on imports (O_i)		This index is related to the disorder of the flows involved in the import of energy	This value demonstrates how much the system depends on diverse flows related to import of energy
Overhead on exports (O_e)		It demonstrated how disorganized are the energy flows that are exported from the ecosystem	The higher this value, the more diverse the flows of the medium that are transported to another system
Dissipative overhead (O_d)		The disorder of flows of energy that is lost from the system in form of respiration	The lower this value the less flows involved in the loss of the medium through respiration
Redundancy (O_r)		The quantity of parallel flows	The increase of this index indicates the increase in the amount of 'backup' flows that can be used as alternative in case some pathways are interrupted
Total overhead (O_t)	$O = O_I + O_E + O_D + O_R = -\sum_{i=0}^{N+2}\sum_{j=0}^{N+2} T_{ij}\log_2\left(\frac{T_{ij}^2}{T_{i.}\cdot T_{.j}}\right)$	Overhead is the opposite of A. It measures the level of disorder of the ecosystem. It reveals the quantity of redundancy for energy circulation	The higher the index the higher the level of disorganization of the energy flow and higher the resilience
Residual diversity (H_c)	$H_C = O \div TST = -k\sum_{i=0}^{N+2}\sum_{j=0}^{N+2} \frac{T_{ij}}{TST}\log_2\left(\frac{T_{ij}^2}{T_{i.}\cdot T_{.j}}\right)$	The residual diversity is related to specialization of the flows	The decrease of H_c means that the flows are less diverse and more specialized. It makes the system more efficient in exchanging energy however it lowers the stability due to the high specialization of the nodes

Internal capacity (DC_i)		The upper limit of development of the ecosystem without considering external inputs and outputs	
Internal ascendency (A_i)		It is the organized part of the system in relation to internal capacity	
Overall connectance (CC_o)		Proportion of realized links, i.e. number of connections a node establishes in an ecosystem (link density)	The less connectance, the less resilience due to loss of complexity of the interactions
Intercompartmental connectance (CC_i)		Connectivity of living and non-living compartments	The increase of the connectivity is related to the increase in number of connections between the compartments
Food web connectance (CC_{fw})		Connectivity of the living compartments	
Finn-cycling index (FCI)	$FCI = \frac{1}{TST}\sum_{i=1}^{N} T_{.i}\left(\frac{s_{ii}-1}{s_{ii}}\right)$	Fraction of TST that is being recycled	The increase of the value might mean that the ecosystem is recycling more energy, thus it should be more ‘mature’. However, this index must be analyzed in parallel to the structure of the cycles since its increase can also be related to short length cycles, which represents a sign of stress



Appendix II.5 – Dissolved organic carbon (DOC) concentration in the different treatments (mean, 95% CI). The DOC was significantly higher at 3HW than 0HW (p-value = 0.040) and than 1HW (p-value = 0.003) but not significantly different between 0HW and 1HW (p-value = 0.738)

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Chapter III

Appendix Table III.1 – The consumption per biomass (CB) ratios collected from the literature and calculated taking into consideration the Q10 specific for our experimental temperature (de la Vega et al. 2018)

Taxon	**CB (20 °C)**	**References**
Hydrobia ulvae	0.0713	Baird et al. 2019
Littorina littorea	0.0233	Baird et al. 2019
Gammarus sp.	0.1074	Baird et al. 2019
Idotea balthica	0.0460	Ito et al. 2019a
Mytilus edulis	0.0182	Baird et al. 2019
Mya arenaria	0.0303	Baird et al. 2019
Limecola baltica	0.1637	Baird et al. 2019
Cerastoderma sp.	0.0253	Baird et al. 2019

Appendix Table III.2 – Information collected for constructing the matrix of interactions

From	**To**	**Effect**	**Description**
Habitat provisioning	Isopod	+	Habitat provisioning increases the biomass of invertebrates (Wikström and Kautsky 2007)
Habitat provisioning	Amphipod	+	Habitat provisioning increases the biomass of invertebrates (Wikström and Kautsky 2007)
Habitat provisioning	Bivalve	+	Habitat provisioning increases the biomass of invertebrates (Wikström and Kautsky 2007)
Fucus vesiculosus	Habitat provisioning	+	*Fucus vesiculosus* is responsible for providing habitat for several species (Wikström and Kautsky 2007)
Zostera marina	Habitat provisioning	+	*Zostera marina* support a wide range of species above and below ground (Möller et al. 1985)
Bivalve	Habitat provisioning	+	Bivalves provide 3D structure which other species use as shelter (Norling and Kautsky 2008)
Fucus vesiculosus	Climate regulation	+	Carbon storage (Queirós et al. 2019)
Zostera marina	Climate regulation	+	Carbon storage, carbon trap and primary production (Röhr et al. 2018)
Filamentous algae	Climate regulation	+	Carbon storage and primary production (Trevathan-Tackett et al. 2015)
Phytoplankton	Turbidity	+	High phytoplankton biomass increases turbidity
Climate regulation	*Zostera marina*	+	Seagrass are sensitive to climate change, e.g. heatwaves have already caused massive mortality of seagrasses (Reusch et al. 2005). Thus, the regulation of climate could be beneficial for this species
Climate regulation	*Fucus vesiculosus*	+	Our results showed that 3HW decreased the biomass of filamentous algae, thus the macroalgae would benefit from climate regulation

Climate regulation	Filamentous algae	+	Our results showed that 3HW decreased the biomass of filamentous algae, thus the macroalgae would benefit from climate regulation
Climate regulation	Amphipod	+	Amphipods responded negatively to 3HW in comparison to 0HW, thus the climate regulation would benefit amphipods population
Climate regulation	Bivalve	+	Sessile organisms are affected by climate change (Wernberg et al. 2012) and bivalves become more vulnerable to high frequency of heatwaves (Seuront et al. 2019).
Turbidity	*Zostera marina*	-	Turbidity jeopardizes photosynthesis
Turbidity	*Fucus vesiculosus*	-	Turbidity jeopardizes photosynthesis
Isopod	*Fucus vesiculosus*	-	Feeding interaction
Amphipod	*Fucus vesiculosus*	-	Feeding interaction
Isopod	Filamentous algae	-	Feeding interaction
Amphipod	Filamentous algae	-	Feeding interaction
Gastropod	Filamentous algae	-	Feeding interaction
Isopod	*Zostera marina*	-	Feeding interaction
Bivalve	Phytoplankton	-	Feeding interaction
Fucus vesiculosus	Isopod	+	Feeding interaction
Fucus vesiculosus	Amphipod	+	Feeding interaction
Filamentous algae	Isopod	+	Feeding interaction
Filamentous algae	Amphipod	+	Feeding interaction
Filamentous algae	Gastropod	+	Feeding interaction
Zostera marina	Isopod	+	Feeding interaction
Phytoplankton	Bivalve	+	Feeding interaction

Appendix Table III.3 – Path analysis of all nodes to turbidity, path nodes present all the nodes involved in the pathway to turbidity, path sign is positive for increase of turbidity (which implies the decrease of water purification service) and negative for decrease of turbidity (enhancement of water purification service). Where PP: phytoplankton, FV: *Fucus vesiculosus*, ZM: *Zostera marina*, FA: filamentous algae, AO: amphipods, IO: isopods, BF: bivalves, Tb: turbidity

From – To	**Path nodes**	**Path sign**
PP – Tb	PP, Tb	+1
FV – Tb	FV, hp, AO, FA, cr, BF, PP, Tb	+1
	FV, hp, AO, FA, IO, ZM, cr, BF, PP, Tb	-1
	FV, hp, IO, ZM, cr, BF, PP, Tb	+1
	FV, hp, IO, FA, cr, BF, PP, Tb	+1
	FV, hp, BF, PP, Tb	-1
	FV, cr, ZM, hp, BF, PP, Tb	-1
	FV, cr, FA, IO, ZM, hp, BF, PP, Tb	+1
	FV, cr, AO, FA, IO, ZM, hp, BF, PP, Tb	-1
	FV, cr, BF, PP, Tb	-1
	FV, IO, ZM, hp, AO, FA, cr, BF, PP, Tb	-1
	FV, IO, ZM, hp, BF, PP, Tb	+1
	FV, IO, ZM, cr, BF, PP, Tb	+1
	FV, IO, FA, cr, ZM, hp, BF, PP, Tb	+1

	FV, IO, FA, cr, BF, PP, Tb	+1
ZM – Tb	ZM, hp, AO, FA, cr, BF, PP, Tb	+1
	ZM, hp, AO, FA, IO, FV, cr, BF, PP, Tb	-1
	ZM, hp, IO, FV, cr, BF, PP, Tb	+1
	ZM, hp, IO, FA, cr, BF, PP, Tb	+1
	ZM, hp, BF, PP, Tb	-1
	ZM, cr, FV, hp, BF, PP, Tb	-1
	ZM, cr, FA, IO, FV, hp, BF, PP, Tb	+1
	ZM, cr, AO, FA, IO, FV, hp, BF, PP, Tb	-1
	ZM, cr, BF, PP, Tb	-1
	ZM, IO, FV, hp, AO, FA, cr, BF, PP, Tb	-1
	ZM, IO, FV, hp, BF, PP, Tb	+1
	ZM, IO, FV, cr, BF, PP, Tb	+1
	ZM, IO, FA, cr, FV, hp, BF, PP, Tb	+1
	ZM, IO, FA, cr, BF, PP, Tb	+1
FA – Tb	FA, cr, ZM, hp, BF, PP, Tb	-1
	FA, cr, ZM, IO, FV, hp, BF, PP, Tb	+1
	FA, cr, FV, hp, BF, PP, Tb	-1
	FA, cr, FV, IO, ZM, hp, BF, PP, Tb	+1
	FA, cr, BF, PP, Tb	-1
	FA, IO, ZM, hp, BF, PP, Tb	+1
	FA, IO, ZM, cr, FV, hp, BF, PP, Tb	+1
	FA, IO, ZM, cr, BF, PP, Tb	+1
	FA, IO, FV, hp, BF, PP, Tb	+1
	FA, IO, FV, cr, ZM, hp, BF, PP, Tb	+1
	FA, IO, FV, cr, BF, PP, Tb	+1
AO – Tb	AO, FA, cr, ZM, hp, BF, PP, Tb	+1
	AO, FA, cr, ZM, IO, FV, hp, BF, PP, Tb	-1
	AO, FA, cr, FV, hp, BF, PP, Tb	+1
	AO, FA, cr, FV, IO, ZM, hp, BF, PP, Tb	-1
	AO, FA, cr, BF, PP, Tb	+1
	AO, FA, IO, ZM, hp, BF, PP, Tb	-1
	AO, FA, IO, ZM, cr, FV, hp, BF, PP, Tb	-1
	AO, FA, IO, ZM, cr, BF, PP, Tb	-1
	AO, FA, IO, FV, hp, BF, PP, Tb	-1
	AO, FA, IO, FV, cr, ZM, hp, BF, PP, Tb	-1
	AO, FA, IO, FV, cr, BF, PP, Tb	-1
IO – Tb	IO, ZM, hp, AO, FA, cr, BF, PP, Tb	-1
	IO, ZM, hp, BF, PP, Tb	+1
	IO, ZM, cr, FV, hp, BF, PP, Tb	+1
	IO, ZM, cr, BF, PP, Tb	+1
	IO, FV, hp, AO, FA, cr, BF, PP, Tb	-1
	IO, FV, hp, BF, PP, Tb	+1
	IO, FV, cr, ZM, hp, BF, PP, Tb	+1
	IO, FV, cr, BF, PP, Tb	+1
	IO, FA, cr, ZM, hp, BF, PP, Tb	+1
	IO, FA, cr, FV, hp, BF, PP, Tb	+1
	IO, FA, cr, BF, PP, Tb	+1

BF – Tb	BF, PP, Tb	-1

Appendix Table III.4 – Path analysis of all nodes to climate regulation, path nodes present all the nodes involved in the pathway to climate regulation service, path sign is positive for increase of climate regulation and negative for decrease of the provisioning of the service. Where PP: phytoplankton, FV: *Fucus vesiculosus*, ZM: *Zostera marina*, FA: filamentous algae, AO: amphipods, IO: isopods, BF: bivalves, cr: climate regulation

From – to	**Path nodes**	**Path sign**
PP – cr	PP, Tb, ZM, hp, AO, FA, cr	+1
	PP, Tb, ZM, hp, AO, FA, IO, FV, cr	-1
	PP, Tb, ZM, hp, IO, FV, cr	+1
	PP, Tb, ZM, hp, IO, FA, cr	+1
	PP, Tb, ZM, cr	-1
	PP, Tb, ZM, IO, FV, hp, AO, FA, cr	-1
	PP, Tb, ZM, IO, FV, cr	+1
	PP, Tb, ZM, IO, FA, cr	+1
	PP, Tb, FV, hp, AO, FA, cr	+1
	PP, Tb, FV, hp, AO, FA, IO, ZM, cr	-1
	PP, Tb, FV, hp, IO, ZM, cr	+1
	PP, Tb, FV, hp, IO, FA, cr	+1
	PP, Tb, FV, cr	-1
	PP, Tb, FV, IO, ZM, hp, AO, FA, cr	-1
	PP, Tb, FV, IO, ZM, cr	+1
	PP, Tb, FV, IO, FA, cr	+1
	PP, BF, hp, AO, FA, cr	-1
	PP, BF, hp, AO, FA, IO, ZM, cr	+1
	PP, BF, hp, AO, FA, IO, FV, cr	+1
	PP, BF, hp, IO, ZM, cr	-1
	PP, BF, hp, IO, FV, cr	-1
	PP, BF, hp, IO, FA, cr	-1
FV – cr	FV, hp, AO, FA, cr	-1
	FV, hp, AO, FA, IO, ZM, cr	+1
	FV, hp, IO, ZM, cr	-1
	FV, hp, IO, FA, cr	-1
	FV, hp, BF, PP, Tb, ZM, cr	+1
	FV, hp, BF, PP, Tb, ZM, IO, FA, cr	-1
	FV, cr	+1
	FV, IO, ZM, hp, AO, FA, cr	+1
	FV, IO, ZM, cr	-1
	FV, IO, FA, cr	-1
ZM – cr	ZM, hp, AO, FA, cr	-1
	ZM, hp, AO, FA, IO, FV, cr	+1
	ZM, hp, IO, FV, cr	-1
	ZM, hp, IO, FA, cr	-1
	ZM, hp, BF, PP, Tb, FV, cr	+1
	ZM, hp, BF, PP, Tb, FV, IO, FA, cr	-1
	ZM, cr	+1

	ZM, IO, FV, hp, AO, FA, cr	+1
	ZM, IO, FV, cr	-1
	ZM, IO, FA, cr	-1
FA – cr	FA, cr	+1
	FA, IO, ZM, hp, BF, PP, Tb, FV, cr	-1
	FA, IO, ZM, cr	-1
	FA, IO, FV, hp, BF, PP, Tb, ZM, cr	-1
	FA, IO, FV, cr	-1
AO – cr	AO, FA, cr	-1
	AO, FA, IO, ZM, hp, BF, PP, Tb, FV, cr	+1
	AO, FA, IO, ZM, cr	+1
	AO, FA, IO, FV, hp, BF, PP, Tb, ZM, cr	+1
	AO, FA, IO, FV, cr	+1
IO – cr	IO, ZM, hp, AO, FA, cr	+1
	IO, ZM, hp, BF, PP, Tb, FV, cr	-1
	IO, ZM, cr	-1
	IO, FV, hp, AO, FA, cr	+1
	IO, FV, hp, BF, PP, Tb, ZM, cr	-1
	IO, FV, cr	-1
	IO, FA, cr	-1
BF – cr	BF, hp, AO, FA, cr	-1
	BF, hp, AO, FA, IO, ZM, cr	+1
	BF, hp, AO, FA, IO, FV, cr	+1
	BF, hp, IO, ZM, cr	-1
	BF, hp, IO, FV, cr	-1
	BF, hp, IO, FA, cr	-1
	BF, PP, Tb, ZM, hp, AO, FA, cr	-1
	BF, PP, Tb, ZM, hp, AO, FA, IO, FV, cr	+1
	BF, PP, Tb, ZM, hp, IO, FV, cr	-1
	BF, PP, Tb, ZM, hp, IO, FA, cr	-1
	BF, PP, Tb, ZM, cr	+1
	BF, PP, Tb, ZM, IO, FV, hp, AO, FA, cr	+1
	BF, PP, Tb, ZM, IO, FV, cr	-1
	BF, PP, Tb, ZM, IO, FA, cr	-1
	BF, PP, Tb, FV, hp, AO, FA, cr	-1
	BF, PP, Tb, FV, hp, AO, FA, IO, ZM, cr	+1
	BF, PP, Tb, FV, hp, IO, ZM, cr	-1
	BF, PP, Tb, FV, hp, IO, FA, cr	-1
	BF, PP, Tb, FV, cr	+1
	BF, PP, Tb, FV, IO, ZM, hp, AO, FA, cr	+1
	BF, PP, Tb, FV, IO, ZM, cr	-1
	BF, PP, Tb, FV, IO, FA, cr	-1

Appendix Table III.5 – Path analysis of all nodes to turbidity, path nodes present all the nodes involved in the pathway to habitat provision service, path sign is positive for increase of habitat provision and negative for decrease of the provisioning of the service. Where PP: phytoplankton, FV: *Fucus vesiculosus*, ZM: *Zostera marina*, FA: filamentous algae, AO: amphipods, IO: isopods, BF: bivalves, hp: habitat provision

From – to	**Path nodes**	**Path sign**
PP – hp	PP, Tb, ZM, hp	-1
	PP, Tb, ZM, cr, FV, hp	-1
	PP, Tb, ZM, cr, FA, IO, FV, hp	+1
	PP, Tb, ZM, cr, AO, FA, IO, FV, hp	-1
	PP, Tb, ZM, cr, BF, hp	-1
	PP, Tb, ZM, IO, FV, hp	+1
	PP, Tb, ZM, IO, FV, cr, BF, hp	+1
	PP, Tb, ZM, IO, FA, cr, FV, hp	+1
	PP, Tb, ZM, IO, FA, cr, BF, hp	+1
	PP, Tb, FV, hp	-1
	PP, Tb, FV, cr, ZM, hp	-1
	PP, Tb, FV, cr, FA, IO, ZM, hp	+1
	PP, Tb, FV, cr, AO, FA, IO, ZM, hp	-1
	PP, Tb, FV, cr, BF, hp	-1
	PP, Tb, FV, IO, ZM, hp	+1
	PP, Tb, FV, IO, ZM, cr, BF, hp	+1
	PP, Tb, FV, IO, FA, cr, ZM, hp	+1
	PP, Tb, FV, IO, FA, cr, BF, hp	+1
	PP, BF, hp	+1
FV – hp	FV, hp	+1
	FV, cr, ZM, hp	+1
	FV, cr, FA, IO, ZM, hp	-1
	FV, cr, AO, FA, IO, ZM, hp	+1
	FV, cr, BF, hp	+1
	FV, cr, BF, PP, Tb, ZM, hp	+1
	FV, IO, ZM, hp	-1
	FV, IO, ZM, cr, BF, hp	-1
	FV, IO, FA, cr, ZM, hp	-1
	FV, IO, FA, cr, BF, hp	-1
	FV, IO, FA, cr, BF, PP, Tb, ZM, hp	-1
ZM – hp	ZM, hp	+1
	ZM, cr, FV, hp	+1
	ZM, cr, FA, IO, FV, hp	-1
	ZM, cr, AO, FA, IO, FV, hp	+1
	ZM, cr, BF, hp	+1
	ZM, cr, BF, PP, Tb, FV, hp	+1
	ZM, IO, FV, hp	-1
	ZM, IO, FV, cr, BF, hp	-1
	ZM, IO, FA, cr, FV, hp	-1
	ZM, IO, FA, cr, BF, hp	-1
	ZM, IO, FA, cr, BF, PP, Tb, FV, hp	-1
FA – hp	FA, cr, ZM, hp	+1

	FA, cr, ZM, IO, FV, hp	-1
	FA, cr, FV, hp	+1
	FA, cr, FV, IO, ZM, hp	-1
	FA, cr, BF, hp	+1
	FA, cr, BF, PP, Tb, ZM, hp	+1
	FA, cr, BF, PP, Tb, ZM, IO, FV, hp	-1
	FA, cr, BF, PP, Tb, FV, hp	+1
	FA, cr, BF, PP, Tb, FV, IO, ZM, hp	-1
	FA, IO, ZM, hp	-1
	FA, IO, ZM, cr, FV, hp	-1
	FA, IO, ZM, cr, BF, hp	-1
	FA, IO, ZM, cr, BF, PP, Tb, FV, hp	-1
	FA, IO, FV, hp	-1
	FA, IO, FV, cr, ZM, hp	-1
	FA, IO, FV, cr, BF, hp	-1
	FA, IO, FV, cr, BF, PP, Tb, ZM, hp	-1
AO – hp	AO, FA, cr, ZM, hp	-1
	AO, FA, cr, ZM, IO, FV, hp	+1
	AO, FA, cr, FV, hp	-1
	AO, FA, cr, FV, IO, ZM, hp	+1
	AO, FA, cr, BF, hp	-1
	AO, FA, cr, BF, PP, Tb, ZM, hp	-1
	AO, FA, cr, BF, PP, Tb, ZM, IO, FV, hp	+1
	AO, FA, cr, BF, PP, Tb, FV, hp	-1
	AO, FA, cr, BF, PP, Tb, FV, IO, ZM, hp	+1
	AO, FA, IO, ZM, hp	+1
	AO, FA, IO, ZM, cr, FV, hp	+1
	AO, FA, IO, ZM, cr, BF, hp	+1
	AO, FA, IO, ZM, cr, BF, PP, Tb, FV, hp	+1
	AO, FA, IO, FV, hp	+1
	AO, FA, IO, FV, cr, ZM, hp	+1
	AO, FA, IO, FV, cr, BF, hp	+1
	AO, FA, IO, FV, cr, BF, PP, Tb, ZM, hp	+1
IO – hp	IO, ZM, hp	-1
	IO, ZM, cr, FV, hp	-1
	IO, ZM, cr, BF, hp	-1
	IO, ZM, cr, BF, PP, Tb, FV, hp	-1
	IO, FV, hp	-1
	IO, FV, cr, ZM, hp	-1
	IO, FV, cr, BF, hp	-1
	IO, FV, cr, BF, PP, Tb, ZM, hp	-1
	IO, FA, cr, ZM, hp	-1
	IO, FA, cr, FV, hp	-1
	IO, FA, cr, BF, hp	-1
	IO, FA, cr, BF, PP, Tb, ZM, hp	-1
	IO, FA, cr, BF, PP, Tb, FV, hp	-1
BF – hp	BF, hp	+1
	BF, PP, Tb, ZM, hp	+1

	BF, PP, Tb, ZM, cr, FV, hp	+1
	BF, PP, Tb, ZM, cr, FA, IO, FV, hp	-1
	BF, PP, Tb, ZM, cr, AO, FA, IO, FV, hp	+1
	BF, PP, Tb, ZM, IO, FV, hp	-1
	BF, PP, Tb, ZM, IO, FA, cr, FV, hp	-1
	BF, PP, Tb, FV, hp	+1
	BF, PP, Tb, FV, cr, ZM, hp	+1
	BF, PP, Tb, FV, cr, FA, IO, ZM, hp	-1
	BF, PP, Tb, FV, cr, AO, FA, IO, ZM, hp	+1
	BF, PP, Tb, FV, IO, ZM, hp	-1
	BF, PP, Tb, FV, IO, FA, cr, ZM, hp	-1

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Description of Author contributions

Chapter I: Effects of temperature on carbon circulation in macroalgal food webs are mediated by herbivores

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Contributions: MI and MW conceived and designed the study. MI, MS, MF, FRB and BB conducted the experiment. MI, MS, MZ, FRB and TGH analyzed the data. MI wrote the first draft of the manuscript. All authors significantly contributed to the preparation and revision of the manuscript.

Chapter II: Temperate benthic ecosystems become less productive and resilient when exposed to sequential heatwaves

Authors: Maysa Ito, Markus Franz, Yvonne Sawall, Björn Buchholz, Thomas Hansen, Philipp Neitzel, Martin Wahl, Florian Weinberger, Tobias Steinhoff, Christian Pansch, Catriona Clemmesen-Bockelmann and Marco Scotti[1]

Under preparation to be submitted

Contributions: MI and MS conceived and designed the study. MW conceived the heatwaves experiment. MI, MS, MF, YS, BB, MW, FW and CP carried out the experiment. MI, MS, TH, PN and TS sorted and analyzed the samples. MS and MI carried out the ENA analysis and the statistical analysis. MI wrote the first draft of the manuscript. All authors are significantly contributing to the preparation of the manuscript.

Chapter III: Sequential heatwaves decrease regulating and maintenance ecosystem services

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Contributions: MI and MS conceived the design of the study. MI, MS and AB analyzed the data. MI, MS, UJ and AB interpreted the data. MI wrote the first draft of the manuscript. All authors significantly contributed to the preparation and revision of the manuscript.

Declaration

I, Maysa Ito, hereby declare that the dissertation submitted, entitled “Climate change impacts on ecosystem functioning and services provided by temperate benthic ecosystem” was independently written by me and only using the sources listed. The content and design of this thesis, apart from the supervisor’s guidance, is my own work. The thesis has not been submitted either partially or wholly as a part of a doctoral degree to another examining body and is my first and only doctoral procedure. Chapter I of this thesis was published in the scientific journal “Marine Biology” in 2019. The authors' share of the manuscripts is explained in the section "Author contributions" (pages 151 and 152). This work has been prepared respecting the Rules of Good Scientific Practice of the German Research Foundation. I have not been deprived of an academic degree.

Kiel, 24.04.2020 …………………………..

Maysa Ito