Mechanistic insights to the effective pathways of global and local climate change in a Baltic Sea seaweed – epiphyte – mesograzer system

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To my parents

Contents

Summary

Anthropogenic greenhouse gas emissions have been driving global climate change and they will continue to do so over the course of the 21st century even if stringent emission mitigations were bindingly specified at the current Paris Climate Change Conference. Due to the oceans' functioning as a key sink and storage for atmospheric heat and CO_2, fundamental changes in the marine environment in terms of warming and increased CO_2 concentrations have taken place and will be increasing in the future. Most of the marine biosphere and especially coastal marine systems have suffered from high anthropogenic pressure per se and it is possible that the novel burden of very rapidly proceeding global climate change triggers shifts to alternative regimes and functioning in marine ecosystems. In consideration of the goods and services they provide to humankind, but also with respect to the value of marine life in its own right, there is a need to understand if and how proceeding global climate change drives ecological change in marine systems and to bring forward systematic management and conservation planning.

The persistence and functioning of an ecosystem is determined by the entity of dynamic maintaining processes between the interacting biotic and abiotic components. Ecological climate change research has therefore been challenged by a high context-dependency of ecosystem responses, which means (a) that experimental testing of single species responses to single factor manipulations provides a low explanatory power for future responses on the community or ecosystem level and (b) that the responses found may be system specific. For improvement of the predictive power of ecological climate change research, experimental approaches are (logistically) challenged to account for as much realism as possible, including multiple species, trophic levels, interacting and realistically manipulated environmental factors, and seasonal effects. Furthermore, focusing on ecological process understanding may increase the ability to relate findings to other systems.

In light of this background, my thesis aims to contribute to the mechanistic understanding of global climate change effects on a common coastal marine seaweed (*Fucus vesiculosus,* Phaeophyceae) system of the Baltic Sea by taking into account several aspects of realism such as the cumulative effects of multiple stressors, global and local factors, direct and indirect effects as well as the seasonality of effects. In joint efforts with co-workers, I conducted a series of benthic mesocosm experiments, each of which using the same experimental seaweed – epiphyte – mesograzer system while addressing different (ecological) questions related to climate change. All experiments lasted for ten to twelve weeks and comprised factor manipulations according to climate change projections for the Baltic Sea region (BACC 2008).

In the first chapter of this thesis, I present the results of four benthic mesocosm studies that were conducted over the course of one year between April 2013 and April 2014. The main focus in these experiments is placed on whether the main and interactive effects of elevated seawater temperature and CO_2 concentrations directly and/ or indirectly affect the Baltic Sea *F. vesiculosus* system and whether these potential effects vary with season. The experiments show that seawater warming has stronger and more persistent effects on the tested seaweed system than increased CO_2 concentrations. The effect sign and size as well as the consequences for food-web structure, however, vary with season. The results suggest that in summer and winter temperature effects on epiphytes and the foundation species are primarily indirectly driven by altered top-down control. In summer, seawater warming disrupts grazing control and thereby facilitates overgrowth and outcompeting of *F. vesiculosus* by epiphytes. In winter, seawater warming increases grazing pressure on *F. vesiculosus*.

In the second chapter of this thesis, I present the results of one benthic mesocosm study that was conducted in summer 2014. The main focus is placed on the interactive effects of one global (combined elevated seawater temperature and CO_2 concentrations) and one local (moderate nutrient enrichment) factor on the *F. vesiculosus* system. In the experiment seawater warming in combination with nutrient enrichment has additive negative effects on the seaweed system. Temperature-induced disruption of top-down grazing and nutrient-induced higher growth of epiphytes accelerate the overgrowth and outcompeting of the foundation species *F. vesiculosus* by epiphytes.

In the third chapter of this thesis, I present the results of one benthic mesocosm study that was conducted in spring 2015. The main focus is placed on disentangling the relative importance of the direct and indirect effective pathways of warming on mesograzers and microalgae of the *F. vesiculosus* system. The same experimental set-up was used, while temperature and grazer presence were manipulated this time. The results show that seawater warming has direct positive effects on both, grazers and microalgae, in spring. Moreover, under the present resource-replete conditions in spring, temperature-enhanced grazing does not compensate for temperature-enhanced microalgal growth and biomass production. In context of the previous studies, this outcome underlines that the effective pathways (here direct bottom-up and indirect top-down) of an abiotic factor (here seawater warming) and the resulting effects on food web processes and functioning of the system vary in sign and size in dependence on the trophic state of the system and in dependence on season.

Overall, my studies provide important mechanistic clues about the underlying direct and indirect effective pathways of environmental change in a coastal marine seaweed system. To the best of my knowledge, it is one of the first studies which assess the seasonal variability of the same environmental factors on the same marine system over the course of one year. The detected context-dependency of global climate change effects within one ecosystem clearly shows that our understanding of the basic underlying ecosystem processes and patterns forms a prerequisite for testing, predicting and managing future ecological change in marine systems. Given that grazing forms a crucial ecological force in many coastal vegetated systems, the identified underlying mechanisms of change (top-down and bottom-up control) may allow reference to other similarly structured coastal systems. Importantly my findings point out, that ecological impacts of global climate change may be underestimated if local perturbation is disregarded and, thus, underline the chance and responsibility of local ecosystem management. With the 2 °C global warming goal potentially not being met, efforts to reduce local perturbation may mediate otherwise amplified pressure on ecosystems and, thus, may allow (some) marine ecosystems to resist phase shifts and to keep functioning under proceeding global climate change.

Zusammenfassung

Anthropogene Treibhausgasemissionen haben zu globalen Klimaveränderungen auf der Erde geführt und werden den Klimawandel im Verlauf des 21. Jahrhunderts vorantreiben, selbst wenn die derzeitige UN-Klimakonferenz in Paris eine stringente Reduktion der Emissionen verbindlich beschließen würde. Da die Weltmeere als wichtiger Speicher von atmosphärischer Energie und CO_2 fungieren, hat die anthropogene Klimaveränderung bereits zu einer Erwärmung und Versauerung des Oberflächenwassers der Meere geführt, die sich in Zukunft weiter verstärken werden. Da insbesondere küstennahe marine Ökosysteme bereits stark durch menschliche Eingriffe beeinträchtig sind, ist es möglich, dass die zusätzlichen schnellen und starken Veränderungen im marinen Lebensraum zu Ökosystemwechseln (*Regime-shifts*) oder veränderten Ökosystemfunktionen führen. Mit Hinblick auf die sozioökonomisch bedeutsamen Ökosystemleistungen, die marine Systeme dem Menschen bieten, aber auch in Anbetracht der Daseinsberechtigung marinen Lebens aus sich heraus, ist es von großer Bedeutung, ökologische Veränderungen in marinen Systemen in Folge des voranschreitenden globalen Klimawandels zu verstehen und geeignete Schutzmaßnahmen zu entwickeln.

Die Stabilität und Funktionsfähigkeit eines Ökosystems wird durch die Gesamtheit der systemerhaltenden Prozesse zwischen den biotischen und abiotischen Komponenten eines Systems bestimmt. Diese Kontextgebundenheit stellt wissenschaftliche Untersuchungen zu ökologischen Folgen des Klimawandels vor eine große Herausforderung, da (a) experimentelles Testen einzelner Klimafaktoren auf einzelne Arten wenig Aussagekraft über zukünftige Auswirkungen des Klimawandels auf ganze Lebensgemeinschaften oder Ökosysteme hat und (b) die identifizierten Effekte möglicherweise systemspezifisch und nicht übertragbar sind. Um die Vorhersagekraft der ökologischen Klimaforschung zu stärken, sind experimentelle Ansätze gefordert, die ganzheitlich die Effekte von realistisch manipulierten, möglicherweise zusammenwirkenden Klimafaktoren auf mehrere Arten und über trophische Ebenen hinweg in verschiedenen Jahreszeiten testen. Abgesehen von ihrer logistischen Herausforderung geben derartige Ansätze wichtige Einblicke in die sich verändernden Ökosystemprozesse, was eine Übertragbarkeit der Ergebnisse auf andere Systeme erhöhen kann.

Vor diesem Hintergrund strebt meine Thesis an, zum mechanistischen Verständnis von Effekten des Klimawandels auf ein weitverbreitetes küstennahes Seetang System (*Fucus vesiculosus*, Phaeophyceae) der Ostsee beizutragen. Unter Berücksichtigung

möglicher kumulativer Effekte mehrerer Faktoren, Effekten von globalen und lokalen Faktoren, direkten und indirekten Wirkungspfaden sowie der Jahreszeitenabhängigkeit von Effekten im System, habe ich in Zusammenarbeit mit Kollegen eine Reihe von benthischen Mesokosmen Experimenten durchgeführt. Alle Experimente beinhalteten das gleiche Seetang – Epiphyten – Mesoherbivoren System, während unterschiedliche ökologische Fragestellungen zum Klimawandel getestet wurden. Die Experimente umfassten jeweils eine Laufzeit von 10 – 12 Wochen und es wurden Faktormanipulationen gemäß den Vorhersagen von Klimaveränderungen in der Ostsee vorgenommen (BACC 2008).

Im ersten Kapitel meiner Thesis stelle ich die Ergebnisse aus vier benthischen Mesokosmen Experimenten vor, die über den Zeitraum eines Jahres zwischen April 2013 und April 2014 durchgeführt wurden. Ein Schwerpunkt dieser Studien liegt im Testen von Haupt- und wechselwirkenden Effekten von Erwärmung und erhöhter CO_2 Konzentration auf das Seetang System. Ein weiterer Schwerpunkt liegt im Erkenntnisgewinn über eine mögliche saisonale Variabilität der Effekte sowie über die direkten und indirekten Wirkungspfade im System. Die Ergebnisse zeigen, dass Erwärmung im Vergleich zu erhöhten CO_2 Konzentrationen einen deutlich stärkeren und anhaltenderen Effekt auf das getestete Seetang System hat, wobei die Wirkungsrichtung und -stärke des Temperatureffekts zwischen den Jahreszeiten variiert. Des Weiteren deuten die Ergebnisse darauf hin, dass die Temperatureffekte auf die Epiphyten und die Schlüsselart *F. vesiculosus* im Sommer und Winter primär indirekt durch eine veränderte *Top-down* Kontrolle getrieben sind. Im Sommer löst Erwärmung eine Störung des Weidedrucks durch die Mesoherbivoren des Systems aus, was ein Überwuchern und Auskonkurrieren der Schlüsselart *F. vesiculosus* durch Epiphyten fördert. Im Winter löst Erwärmung einen erhöhten Weidedruck durch die Mesoherbivoren auf die Schlüsselart *F. vesiculosus* aus.

Im zweiten Kapitel stelle ich die Ergebnisse aus einem benthischen Mesokosmen Experiment aus dem Sommer 2014 vor. Der Schwerpunkt der Studie liegt im Testen möglicher Wechselwirkungen von einem globalen (zusammenwirkende Erwärmung und erhöhte CO_2 Konzentration) und einem lokalen (moderate Nährstoffanreicherung) Faktor auf das *F. vesiculosus* System. Die Studie zeigt, dass Erwärmung in Kombination mit erhöhtem Nährstoffeintrag im Sommer additiv negative Effekte auf das Seetang System haben kann. Eine temperaturbedingte Störung des Weidedrucks und ein nährstoffbedingtes erhöhtes Wachstum der Epiphyten beschleunigen das Überwuchern und Auskonkurrieren der Schlüsselart *F. vesiculosus* durch Epiphyten.

Im dritten Kapitel der Thesis stelle ich die Ergebnisse aus einem benthischen Mesokosmen Experiment aus dem Frühjahr 2015 vor. Die Studie konzentriert sich auf die relative Wichtigkeit von direkten und indirekten Wirkungspfaden der Erwärmung im

F. vesiculosus System. Hierfür wurden die Faktoren Erwärmung und Anwesenheit von Mesoherbivoren manipuliert. Die Ergebnisse zeigen, dass sich Erwärmung im Frühjahr direkt positiv sowohl auf die Mesoherbivoren als auch auf die Mikroalgen des Systems auswirkt. Des Weiteren zeigen sie, dass ein temperaturgetriebenes schnelleres Mikroalgenwachstum unter der bestehenden Ressourcensättigung im System im Frühjahr nicht von einem temperaturgetriebenen stärkeren Weidedruck ausgeglichen werden kann. Im Kontext der vorausgegangenen Studien unterstreichen diese Ergebnisse, dass die Wirkungspfade (hier direkt *Bottom-up* und *Top-down*) eines Umweltfaktors (hier Erwärmung) und die daraus resultierenden (indirekten) Effekte auf Nahrungsnetzprozesse und Ökosystemfunktionen in Abhängigkeit von der Jahreszeit und dem Nährstoffhaushalt im System variieren.

Insgesamt liefert meine Studie wichtige mechanistische Informationen über die zugrundeliegenden direkten und indirekten Wirkungspfade von Umweltveränderung in einem küstennahen Seetang System. Nach meinem Kenntnisstand ist dies eine der ersten Studien, die die saisonale Variabilität des gleichen Umweltfaktors am gleichen System in vier aufeinanderfolgenden Jahreszeiten untersucht. Die hohe Kontextgebundenheit der Effekte im experimentellen System zeigt, dass ein Verständnis der grundlegenden Ökosystemprozesse und jahreszeitlichen Muster eine Voraussetzung für das Testen, Vorhersagen und Management von ökologischen Veränderungen in marinen Systemen ist. Da der Weidedruck durch Mesoherbivore eine essentielle strukturierende Kraft in vielen küstennahen Makroalgen und Seegras Systemen darstellt, erlaubt die hier gewonnene Erkenntnis über sich durch Erwärmung verändernde Mechanismen (*Top-down* und *Bottom-up* Kontrolle) möglicherweise Bezugnahme auf andere ähnlich strukturierte küstennahe Systeme. Wesentlich ist die Erkenntnis, dass ökologische Auswirkungen durch den globalen Klimawandel unterschätzt werden könnten, wenn bestehende lokale Belastungen von Ökosystemen nicht berücksichtigt werden. Dieses Ergebnis unterstreicht die Chance und Verantwortung von lokalem Ökosystemmanagement. Sollte das Ziel einer maximalen globalen Erwärmung unter 2 °C verpasst werden, könnten Maßnahmen zur Reduzierung lokaler Umweltbelastung eine Milderung der andernfalls sich wechselwirkend verstärkenden Faktoren bedeuten. Hierdurch könnten grundlegende Veränderungen im System (*Regime-shifts*) möglicherweise verhindert und die Ökosystemfunktionen im Zuge des globalen Klimawandels aufrechterhalten werden.

Introduction

Global Climate Change

Ever since the beginning of the industrial era, economic wealth was linked to the use of fossil energy and, thus, to the emission of greenhouse gasses to the atmosphere. Connections between atmospheric CO_2 and the planet's surface temperature were already drawn in the 19th century (e.g. Arrhenius 1896; Chamberlin 1899); it took, however, until the mid-20th century that anthropogenic greenhouse gas emissions and climate change were linked and first concerns about continuously rising emissions and potential future effects on the climate system were stressed (Callender 1949; Revelle and Suess 1957). The beginning of the atmospheric CO_2 monitoring in the 1950s can be seen as a corner stone for anthropogenic climate change research as it gave evidence to the speed and magnitude of rising atmospheric CO_2 concentrations unprecedented for millennia in the earth's natural history (Figure I).

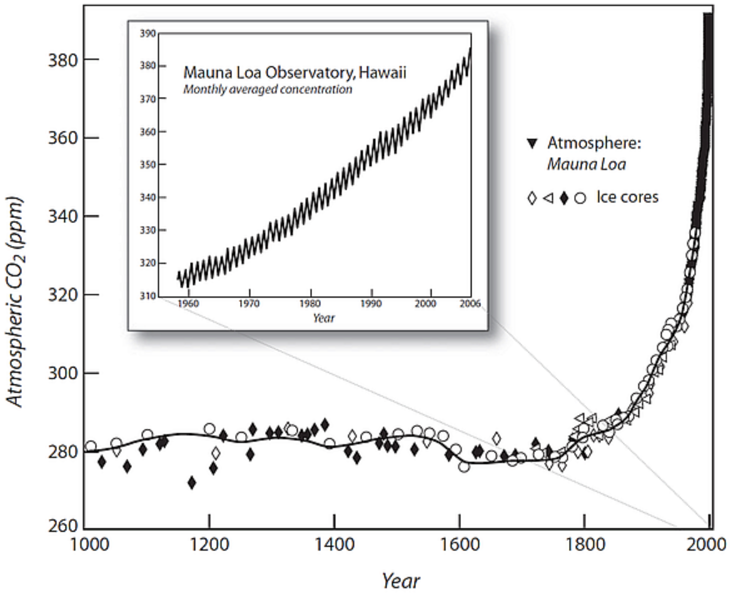


Figure I. Development of the atmospheric CO_2 concentration inferred from direct atmospheric measurement and ice core analysis. The inner graphic shows the direct atmospheric CO_2 observation from Mauna Loa, Hawai'i since the 1950s. CO_2 data are publicly available from http://www.cmdl.noaa.gov. Source: Doney and Schimel 2007.

Over the course of another half century, a new branch of global warming science developed providing increasing evidence that anthropogenic greenhouse gases (of which CO_2 is the most relevant regarding the amount emitted and its longevity) form the most likely driver of the earth's documented warming. Today, process understanding and computer-based models allow the assessment of the earth's potential climate development under future anthropogenic emission scenarios (IPCC 1990 – IPCC 2014). However, ecological process understanding and data availability for the model-based assessment of ecological change, tipping points, the resilience of ecosystems or the potential loss of ecosystem functions and services that humans utterly depend on, are incomplete.

In the most recent (5th) assessment report of the Intergovernmental Panel on Climate Change (IPCC 2014) the model-based representative concentration pathways (RCP) consider a range from unconstrained high (RCP 8.5) and intermediate emissions (RCP 4.5 and RCP 6.0) to a rigid emission mitigation (RCP 2.6). It is emphasized that the global surface temperature will continue to rise under all scenarios over the course of the 21st century (Figure II) with extreme events such as heat waves or strong precipitation being likely to occur more often or to last longer (IPCC 2012; Collins et al. 2013).

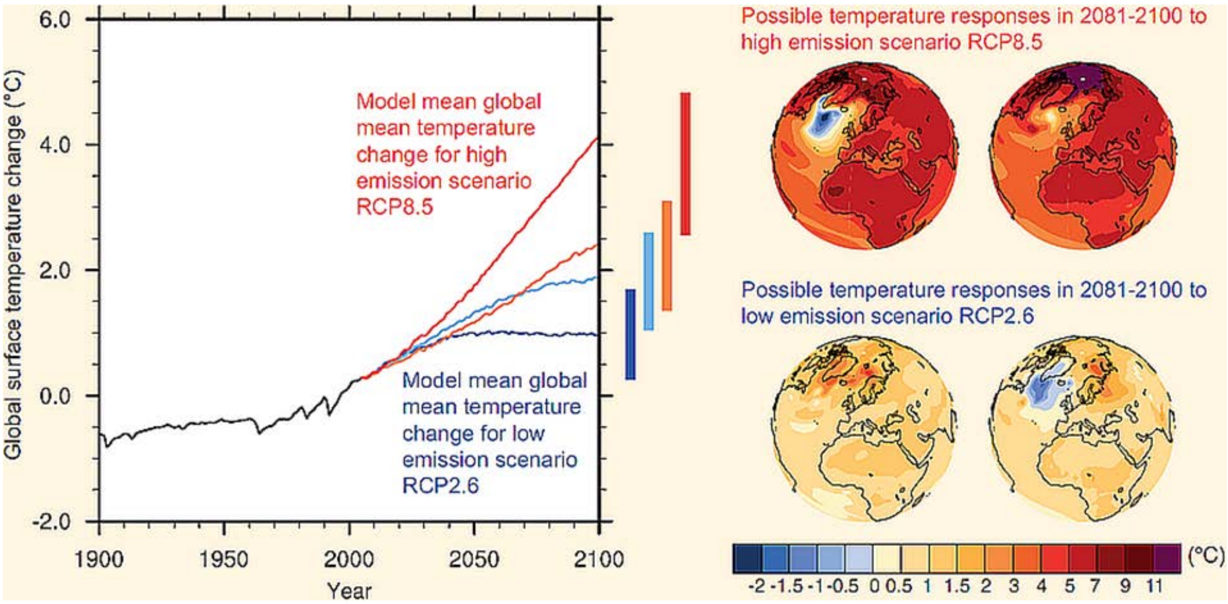


Figure II. Left: Model-based projections of the possible global mean temperature change for four Representative Concentration Pathway (RCP) scenarios. RCP2.6 (dark blue), RCP4.5 (light blue), RCP6.0 (orange) and RCP8.5 (red). The vertical bars represent the likely ranges for global temperature change until 2100. The ranges apply to the differences in two 20-year means, 2081-2100 compared to 1986-2005. Right: Illustrative map of the surface temperature change under RCP2.6 and RCP8.5 until 2100. Source: Collins et al. 2013.

It is also emphasized, however, that the magnitude of proceeding climate change can be influenced by today's emission policies, i.e. exceeding +2 °C relative to pre-industrial levels without emission constraints (RCP 6.0 and RCP 8.5) or staying below +2 °C relative to 1850 – 1900 levels through a substantial reduction of emissions (RCP 2.6) (Collins et al. 2013). The latter scenario is strongly recommended by the United Nations Framework Convention on Climate Change (UNFCCC) postulating that the growth of atmospheric greenhouse gases must be limited to "a level that would prevent dangerous anthropogenic interference with the climate system" (1992, Article 2). Between 1870 and 2011 the cumulative anthropogenic CO_2 emissions to the atmosphere comprised approximately 2040 (±310) $GtCO_2$ with highest emissions in human history occurring between 2000 and 2010 (IPCC 2014). Model estimates

(RCP 2.6) suggest that keeping global warming below +2 °C relative to pre-industrial times obliges cumulative CO_2 emissions from all anthropogenic sources to stay below 3650 $GtCO_2$ (IPCC 2014). The latest IPCC report as an executive summary of the available scientific information makes clear that the largest challenge by now is not to understand physical climate change, but to implement necessary measures to control it.

Global change in the marine environment

The oceans function as a key sink and storage of atmospheric CO_2 and heat, which on a global scale has resulted in two fundamental changes in the marine environment. Oceanic uptake of about 30% of the CO_2 emitted since the beginning of industrial times has increased the concentrations of total dissolved inorganic carbon (DIC) and hydrogen ions (H^+) in ocean surface waters. This change in concentration lowered the pH by 0.1 (ocean acidification) and altered the seawater carbonate chemistry by shifting the relative proportions of the DIC species carbon dioxide (CO_2), bicarbonate (HCO_3) and carbonate (CO_3^{2-}) towards higher CO_2, biocarbonate and hydrogen ion concentrations (Doney et al. 2009; Hoegh-Guldberg and Bruno 2010). Moreover, climate warming induced ocean surface warming by about 0.6 °C over the past 100 years (Hoegh-Guldberg and Bruno 2010). Even if emissions were considerably reduced today, ocean acidification and warming were still to continue due to the long time scale (hundreds of years to millennia) at which the oceans' surface and atmosphere equilibrate and as a result of the oceans' large thermal inertia (Archer and Brokvin 2008; Solomon et al. 2009; Collins et al. 2013).

The oceans cover about 70% of the Earth's surface and they are estimated to provide about US$ 20 trillion worth of ecosystem goods (e.g. materials and food) and services (e.g. nutrient cycling and recreation) per year (Costanza et al. 1997). Ecological transformation in consequence of the rapid and high change in the marine environment, however, may not only affect human welfare and economic development. Given that the oceans are part of the global climate system, change in ecological functioning (e.g. changes in primary producer phenology and consequent changes in carbon fixation and export of POC out of surface layers) may also feedback on global climate regulation. Considering this and also the value of marine life in its own right, it becomes obvious that the effects of proceeding global climate change on marine ecosystems and their functioning need to be understood in order to allow systematic management and conservation planning.

Challenges of ecological climate change research on marine ecosystems

The ecological balance of a community or ecosystem describes its stability (i.e. persistence and resilience) and functioning over time. It is an umbrella term that includes the entity of dynamic maintaining processes between the interacting abiotic and biotic components (Holling 1973). For instance, species composition, abundance, diversity, competitive (bottom-up control) and trophic (top-down control) interactions, but also habitat structure and environmental conditions to which the biota adapt are important determining and maintaining factors of the balanced state of a system. In order to understand if and how global climate change drives ecological change, one has to understand if and how it affects the components and processes that drive an ecosystem's stability and functioning (i.e. the ecological balance in a system).

On a global and long temporal scale temperature has been linked to species diversity with more species being present in warmer temperatures (Tittensor et al. 2010). On a smaller spatial and temporal scale, however, increasing temperature (within the thermal tolerance window of organisms) can affect food web dynamics. This has been explained by the metabolic theory of ecology (MTE) stating that biochemical reactions in general are stimulated by higher temperature, with metabolic processes of heterotrophs such as feeding, growth and reproduction being activated more strongly than photosynthetic rates of autotrophs (Brown et al. 2004; Allen et al. 2005). Increasing seawater temperature under proceeding global climate change could hence alter consumer – producer interactions and food web structure by strengthening top-down control through increased metabolic demands of consumers (Lopez-Urrutia et al. 2006; O'Connor 2009; Carr and Bruno 2013).

Elevated seawater temperatures exceeding the thermal window of organisms can impair cellular processes related to metabolism and photosynthesis (Cossins and Boweler 1987; Pörtner and Ferrell 2008). This may in particular be a threat to species already living close to their upper thermal tolerance limit today, such as in coral reef ecosystems of the (sub)tropical regions (Hoegh-Guldberg 1999; Hughes et al. 2003; Frieler et al. 2012). Related to this, geographic range shifts of species have been documented (Parmesan and Yohe 2003; Precht and Aronson 2004; Wernberg et al. 2011). Extreme events such as a summer heat wave have been found to induce malperformance and decreased abundance in temperate seagrass systems (Reusch et al. 2005).

Elevated seawater CO_2 concentrations (hereafter also referred to as [CO_2]) act as both, a stressor or a resource, for marine organisms. Numerous studies have shown that the effect sign and magnitude of ocean acidification greatly varies among taxa and life history stages (reviewed in Kroeker et al. 2013). Overall, however, changes in the carbonate chemistry in a higher CO_2 environment were found to adversely affect the growth, survival and calcification rates in calcifying taxa such as corals, calcareous algae, coccolithophores, echinoderms, mollusks and crustaceans (Kroeker et al. 2013). Particularly growth responses of echinoderms and mollusks showed highest sensitivity to [CO_2] during larval stages (Kroeker et al. 2013).

On the other hand, increased CO_2 concentrations can act as a fertilizer due to the high photosynthetic affinity of marine autotrophs to CO_2 (Koch et al. 2013). Just like in terrestrial plants, carbon dioxide capture and processing via rubisco are the fundamental processes of the Calvin cycle in aquatic autotrophs (Bowes 1985; Madsen and Sand-Jensen 1991). Accordingly, increased [CO_2] has been found to trigger higher autotrophic productivity and growth in marine plants and algae (Connell and Russell 2010; Kroeker et al.2013), and especially in those showing C3 photosynthetic characteristics (Koch et al. 2013) A high CO_2 environment may therefore competitively favor those marine autotrophs being able to rapidly sequester CO_2, and may ultimately shift ecosystems characterized by calcifying taxa towards one dominated by non-calcifying microalgae and fleshy macroalgae.

It is possible, that [CO_2] effects as the ones reported above may be less pronounced in some densely vegetated coastal marine systems. Due to distinct diurnal cycles of photosynthesis and respiration and due to upwelling events, the biota of such habitats may have been adapting to high and rapid fluctuations in [CO_2] (Thomsen et al. 2010; Saderne et al. 2013; Eklöf et al. 2015).

Past experimental findings of temperature and [CO_2] effects indicate that ecological impacts of proceeding global climate change may be highly context dependent and difficult to extrapolate on other species, communities or ecosystems. Moreover, many findings were based on single factor, single species experiments which does not reflect the reality of interacting multiple stressors and does not provide reliable information about effects on the community or ecosystem level (Harley et al. 2006; Walther 2010; Wernberg et al. 2012). For the purpose of making realistic predictions about the development of marine ecosystems under proceeding global climate change, ecological research is challenged to add more realism to experimental approaches.

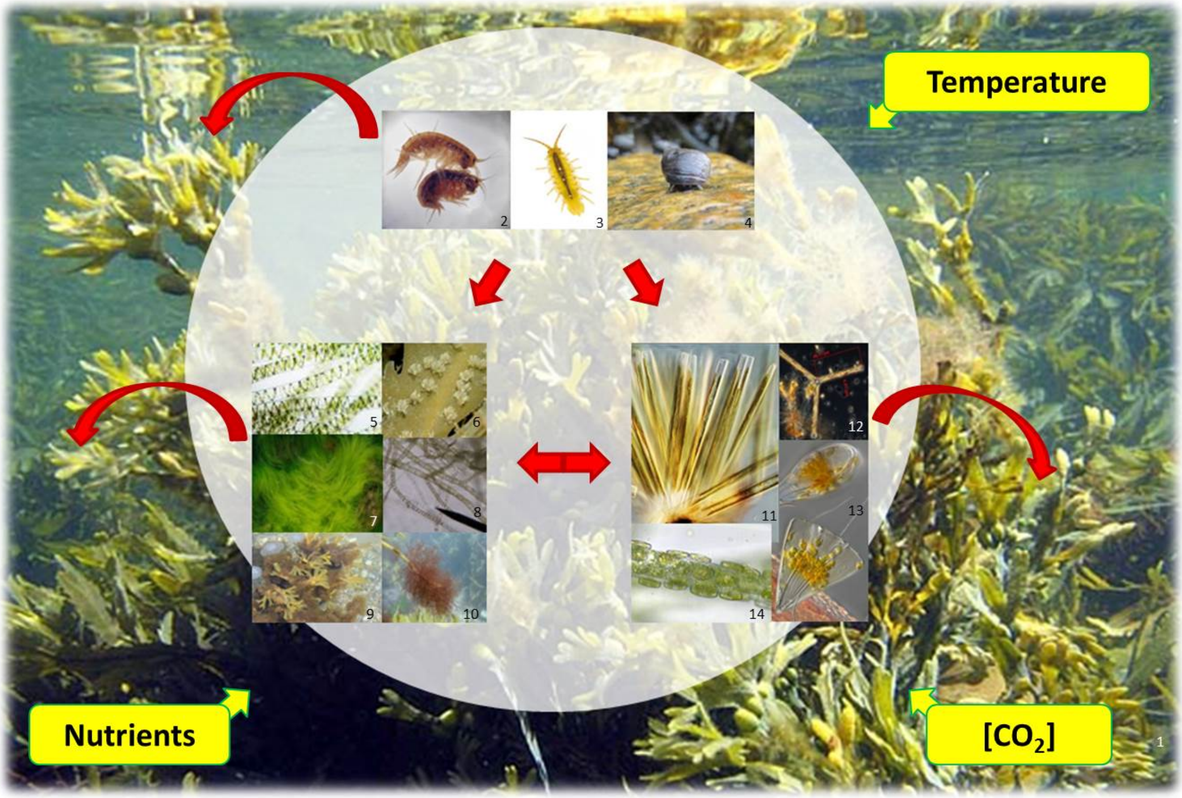
The co-occurrence of both, raised temperature and CO_2 concentrations dictates to test for their simultaneous and possibly synergistic, additive or antagonistic effects in experiments. Moreover, most parts of the world’s oceans have already been impacted by human influence (Lotze et al. 2006; Halpern 2008), which requires to consider existing local stressors (e.g. nutrient pollution, habitat change, resource exploitation, altered species composition) together with rising global climate change stressors as their cumulative effects may overstretch the capacity of marine species or entire ecosystems to acclimate or adapt.

Anthropogenic influence can trigger ecological imbalance through direct and indirect effective pathways. That means disturbance can directly affect the performance or abundance of species by exceeding their physiological tolerance ranges. Depending on the functional redundancy of the species lost, such direct effect may lead to subsequent changes on the community- or ecosystem level (i.e. overall functioning). Indirect effects of disturbance affect the sign and strength of interspecific interactions, which potentially causes change in competitive or trophic dynamics with subsequent effects on food web structure and/ or on functioning. Both effects are closely linked. Information on indirect effective pathways requires the logistically challenging assessment of near-natural communities or ecosystems (as opposed to single species approaches). But then mechanistic understanding of indirect effective pathways and their relative importance may offer valuable clues to changing ecosystem processes, which may allow reference to other communities or ecosystems rather than single species responses.

Finally, seasonal variation in the sign and size of climate change effects and their pathways has been assumed (e.g. Sommer and Lewandowska 2011) but, to my knowledge, not tested by other marine studies before. Especially in systems showing distinct seasonal patterns (e.g. in terms of species abundance or the relative importance of internal regulating mechanisms) it is possible that pronounced climate change effects identified in one season may not hold true for all seasons. Furthermore, effects in one season may manifest over time, i.e. they may carry over into the following seasons, potentially inducing re-organization in terms of composition and functioning in the system over time.

Aim of the study and thesis outline

The aim of this study was to further the mechanistic understanding of global climate change effects on a common coastal marine seaweed system of the Baltic Sea by taking into account several aspects of realism such as the cumulative effects of multiple stressors, global and local factors, direct and indirect effects as well as the seasonality of effects. For this purpose, in joint efforts with co-workers, I conducted a series of benthic mesocosm experiments, each of which using the same experimental seaweed – epiphyte – mesograzer system while addressing different (ecological) questions related to climate change.



The foundation seaweed *Fucus vesiculosus*, microepiphytes (primarily diatoms), macroepiphytes (filamentous green-, brown- and red algae) and the grazing amphipods (*Gammarus* spp.), isopods (*Idotea* spp.) and gastropods (*Littorina littorea*) form the key players on the basis of the coastal marine *F. vesiculosus* system of the southwestern Baltic Sea. Maintenance of the system is controlled by closely linked biotic interactions such as competition for resources and top-down grazing. The sources for the images used are given in the reference list.

Generally, marine seaweeds and seagrasses form the ecological foundation of many marine ecosystems in the coastal zone. They hold key functions by providing substrate, food and shelter to an associated highly diverse community of other marine macro- and microalgae, invertebrates and fish (Mann 1973; Duarte and Chiscano 1999). Marine seaweed stands and seagrass meadows rank among the most productive ecosystems on this planet and they provide ecosystem goods and services that humans depend on and economically benefit from (e.g. raw materials, food, nutrient cycling, sediment stabilization) (Costanza et al. 1997). The fact that both, seaweeds and seagrasses, most often occur in monospecific stands makes the associated ecosystems vulnerable to disturbance as the consequent malfunctioning of the foundation species may not be compensated.

In this thesis, the study system comprised the seaweed *Fucus vesiculosus* (Phaeophyceae) including its associated microepiphytes (primarily diatoms), macroepiphytes (filamentous green-, brown- and red algae) and mesograzers (gastropods, isopods, amphipods). As also known for other coastal vegetated systems, functioning of the applied *F. vesiculosus* system is maintained by closely linked biotic interactions such as competition between the substrate species and epiphytes or consumption of epiphytes and *F. vesiculosus* by mesograzers (Worm 2000; Wallentinus 1984; Worm et al. 2002; Korpinen et al. 2007). It can be assumed that effects of global climate change (either beneficial or harmful) on some of the system's components induce ecological imbalance through altered competitive or trophic interactions. Given that *F. vesiculosus* is the dominant canopy-forming brown algal system in the southwestern Baltic Sea and that it has already been affected by local anthropogenic pressures (e.g. nutrient pollution and overfishing) (Eriksson et al. 2009; HELCOM 2013), further deteriorating effects under proceeding climate change may jeopardize key functions and services provided by the foundation species and its associated diverse and productive biota in Baltic Sea coastal waters.

The experiments were conducted in outdoor mesocosms (Kiel Outdoor Benthocosms, see photographs below), each of which lasting for ten to twelve weeks. The experimental facility allows the testing of near-natural biological systems in a near-natural environment. More precisely, it exposes experimental systems to ambient light and weather conditions year round and a flow-through system, connecting the experimental tanks to the adjacent Kiel Fjord, keeps the ambient experimental conditions close to the actual ambient environmental condition of the Kiel Fjord, including its fluctuations. The technological advance of the facility allows manipulating multiple factors and its size (1.4 m^3 per experimental unit) allows establishing experimental systems comprising multiple species across trophic levels (Wahl et al. 2015).

The thesis comprises three chapters, each of which presenting and discussing the results of one or several benthic mesocosm experiments. The following gives a short overview of the motivation, key questions, and findings in each of the chapters.

The Kiel Outdoor Benthocosm facility.

Chapter I

This chapter comprises a series of four seasonal benthic mesocosm experiments that were conducted over the course of one year. My aim was to investigate whether the main and interactive effects of elevated seawater temperature (ambient and Δ+4-6 °C) and [CO_2] (ambient and Δ+600 ppm) directly and/ or indirectly affect the Baltic Sea *F. vesiculosus* system. Additionally I aimed for testing the seasonality of effects. Based on the assumption that CO_2 can be a limiting resource for marine autotrophs, I asked (i) if raised [CO_2] in the grazed system fertilizes algal biomass accrual in favor of the competitively superior opportunistic epiphytes. Based on metabolic theory concepts, I asked (ii) if temperature-intensified grazing reduces the biomass of epiphytes and/ or *F. vesiculosus*. In logical consequence of the two former effects, I asked (iii) if the [CO_2]-induced increase of algal biomass and the temperature-intensified grazing pressure cancel each other out, resulting in no net effect of both co-occurring factors on the system. Finally, I asked (iv) if the effects of increased seawater temperature and [CO_2] vary seasonally according to natural growth and reproduction periods. Specifically, I assumed to find stronger fertilizing effects of [CO_2] on autotrophs during their growing season in spring and summer and to find stronger effects of temperature-intensified grazing outside the growing season of algae in winter. I assumed to find adverse temperature effects during summer if thermal tolerance limits of *F. vesiculosus* or the associated mesograzers were exceeded.

The experiments showed that seawater warming has stronger and more persistent effects on the Baltic Sea *F. vesiculosus* - epiphyte - mesograzer system than increased [CO_2]. They revealed that elevated seawater temperature (Δ+4-6 °C) primarily affects the grazer component of the system (direct effect), thereby alters top-down grazing with subsequent (indirect) temperature effects on epiphytes and the foundation species *F. vesiculosus*. The effect sign and size of warming as well as the consequences for food-web structure, however, varied with season. Strongest effects were detected in summer and winter, where warming disrupted grazing control and thereby facilitated the overgrowth and outcompeting of *F. vesiculosus* (summer) or increased grazing pressure on *F. vesiculosus* (winter).

Chapter II

This chapter comprises one benthic mesocosm study focusing on the interacting effects of combined global (temperature and CO_2) and local (nutrient enrichment) stressors on the *F. vesiculosus* system. The study was based on the previous findings and on the prediction that global change not only enhances annual mean seawater temperatures and [CO_2], but also increases the nutrient influx to the marine environment of the Baltic Sea (BACC 2008, 2015). I used the same experimental set-up while treatments of temperature (ambient and Δ+5 °C) and CO_2 (ambient and Δ+600ppm) were combined in one greenhouse treatment and factorially crossed with nutrient enrichment (ambient and moderately elevated) this time. The experiment was conducted in summer and based on the previous findings, I hypothesized that (i) elevated seawater temperature leads to increased epiphyte biomass and outcompeting of the foundation species *F. vesiculosus* due to adverse effects on mesograzers and consequent weakened top-down control. I expected that (ii) moderate nutrient enrichment under ambient temperature and [CO_2] conditions particularly benefits the biomass accrual of epiphytes, because they are competitively superior to the slow-growing seaweed *F. vesiculosus*. In logical consequence of the former hypotheses, I expected to (iii) find additive negative effects of the combined factors (i.e. greenhouse conditions and moderate nutrient enrichment) on the *F. vesiculosus* system.

The experiment confirmed the findings of the previous studies by showing the same adverse temperature effects on the grazer component in summer. Moreover, it showed that combined seawater warming and moderate nutrient enrichment cause additive negative effects on the *F. vesiculosus* system via temperature-induced disruption of top-down regulation and nutrient-induced higher growth of epiphytes. Both factors in combination accelerated the overgrowth and outcompeting of the foundation seaweed by epiphytes.

Chapter III

The results of the studies in Chapter I and II clearly suggested that the effects of warming on epiphytes and the foundation species *F. vesiculosus* were primarily indirectly driven by altered top-down control. However, the direct and indirect effects of temperature could not be quantitatively partitioned at this point. According to the metabolic theory of ecology (MTE) both, heterotrophic metabolism and photosynthesis are stimulated by temperature (Brown et al. 2004; Allen et al. 2005) and it is therefore possible that both, the release from grazing pressure and the temperature-induced higher growth of the competitively superior epiphytes, led to overgrowth of the foundation seaweed. In order to further disentangle the effective pathways of warming, I conducted a follow-up study in spring using the same experimental system while manipulating temperature (ambient and Δ+5 °C) and grazer presence (present and absent) in a factorial design. Based on MTE predictions, I expected that (i) seawater warming in spring accelerates metabolism associated processes (i.e. feeding, growth, reproduction) of the mesograzers and that this effect is reflected in increased total grazer abundance and total grazer biomass. Based on the findings in my previous experiments, I hypothesized that (ii) warming has species specific effects on the mesograzer abundance and per capita biomass. Focusing only on the microalgal component of the epiphytic group in this experiment, I hypothesized that (iii) microalgal total biomass is reduced by grazers and that warming intensifies top-down grazing in spring, which indirectly leads to a greater reduction of microalgal biomass. On the basis of MTE, I lastly hypothesized that (iv) warming directly increases microalgal growth and total biomass accrual under the given resource replete conditions in spring. I expected this direct temperature effect on microalgal biomass to be stronger in the absence of grazers (i.e. to be offset by their presence).

In the experiment, seawater warming had direct positive effects on both, grazers and microalgae. Under the given resource-replete conditions in spring, however, temperature-enhanced microalgal growth rates and biomass production were not counterbalanced by temperature-enhanced grazing. In context of the previous findings this outcome underlines that the effective pathways (here direct bottom-up and indirect top-down) of an abiotic factor (here seawater warming) and the resulting effects on food web processes and functioning of the system vary in sign and size in dependence on the trophic state of the system and in dependence on season.

Chapter I

Temperature effects on seaweed-sustaining top-down control vary with season

Abstract

Rising seawater temperature and CO_2 concentrations (ocean acidification) represent two of the most influential factors impacting marine ecosystems in the face of global climate change. In ecological climate change research full-factorial experiments across seasons in multi-species, cross-trophic level set-ups are essential as they permit a more realistic estimation about direct and indirect effects and the relative importance of both major environmental stressors on ecosystems. In benthic mesocosm experiments we tested the responses of coastal Baltic Sea *Fucus vesiculosus* systems to elevated seawater temperature and CO_2 concentrations across four seasons of one year. While increasing [CO_2] levels only had minor effects, warming had strong and persistent effects on grazers, and the resulting effects on the *Fucus* system were found to be season dependent. In late summer a temperature-driven collapse of grazers caused a cascading effect from the consumers to the foundation species, resulting in overgrowth of *Fucus* thalli by epiphytes. In fall/ winter, outside the growing season of epiphytes, intensified grazing under warming resulted in a significant reduction of *F. vesiculosus* biomass. Thus, we were able to confirm the prediction that future increasing water temperatures influence marine food-web processes by altering top-down control, but we were also able to show that specific consequences of this for food-web structure depend on season. Since *F. vesiculosus* is the dominant habitat-forming brown algal system in the Baltic Sea, its potential decline under global warming implies the loss of key functions and services such as provision of nutrient storage, substrate, food, shelter and nursery grounds for a diverse community of marine invertebrates and fish in Baltic Sea coastal waters.

Introduction

Rising seawater temperature and CO_2 concentrations (ocean acidification) represent two of the most influential factors impacting marine ecosystems in the face of global climate change (IPCC 2014). To date, extensive research has provided valuable information about each stressor's effect on marine organisms. However, factorial manipulations assessing the impacts of both interactively operating stressors are still scarce. It is understood that moderate ocean warming more strongly affects heterotrophic organisms as compared to autotrophic ones by means of accelerating metabolism-associated processes such as feeding, growth and reproduction with possible subsequent indirect effects on primary production by increased top-down control in ecosystems (Brown et al. 2004; O'Connor et al. 2009; Kraufvelin et al. 2012). At the same time, raised seawater CO_2 concentrations (hereafter referred to as $[CO_2]$) can be a resource for macrophytes, non-calcifying single-celled algae (Kroeker et al. 2013) and turfs (Connell and Russell 2010). Furthermore, increased $[CO_2]$ was found to positively affect micro- and filamentous macroalgae under warming and in the absence of grazers (Eklöf et al. 2012; Alsterberg et al. 2013) and to have no effect on seagrass-associated macrofauna species (Eklöf et al. 2015). These findings suggest that proceeding ocean acidification could enhance bottom-up control and competition by means of fertilizing primary production of some algal groups. In combination with warming it could lead to (trophic) re-structuring of marine ecosystems. However, counteracting direct and indirect effects like increased primary production and consumption in a grazed system could just as well result in no net effects regarding the system's functioning and maintenance. In order to forecast and manage the effects of global change forcing on marine ecosystems it is therefore crucial to elucidate the direct and indirect effects of both co-occurring stressors in multi-species, cross-trophic level settings. Moreover, we expect temperature and $[CO_2]$ effect sign and size to vary between seasons, i.e. according to natural growth and reproduction periods of the marine biota. Therefore, we claim that seasonality of effects needs to be considered in experimental work.

We set out to experimentally test the direct and indirect effects of increased seawater temperature and $[CO_2]$ on a coastal marine seaweed (*Fucus vesiculosus*) system across four seasonal phases of one year. Generally, seaweed stands and seagrass meadows rank among the most productive ecosystems in coastal marine zones of the North Atlantic, the North Sea as well as the Baltic Sea (Mann 1973; Duarte and Chiscano 1999). Both systems are characterized by a sensitive interdependency between the substrate species and its associated biota. In the rocky (sub)littoral zone of the Baltic Sea, the macrophyte *F. vesiculosus* represents the dominant belt-forming brown algal system. The seaweed holds key functions as a primary producer (approximately 160 g C m^{-2} $year^{-1}$ in moderately wave exposed habitats) (Raffaelli and Hawkins 1999), foundation species (e.g. Kautsky et al. 1992; Wikström and Kautsky 2007), nutrient sink and storage (Pedersen and Borum 1996) as well as a nursery and feeding ground for fish (e.g. gadoid species) (Phil et al. 1994; Borg et al. 1997; Persson et al. 2012; HELCOM 2013). As also seen for seagrass meadows, *Fucus* belt functioning is maintained by fine-tuned biotic interactions such as competition for resources, consumption and beneficial co-occurrence. That is, *F. vesiculosus* competes with its epiphytes which comprise opportunistic filamentous macro- and single-celled microalgae. A high epiphyte load can impede the macrophyte's ecosystem functioning through shading, obstruction of nutrient uptake and - eventually - exclusion from primary substrate (Wallentinus 1984; Sand-Jensen and Borum 1991; Worm and Sommer 2000). Dominance of epiphytes and competitive exclusion of *F. vesiculosus* are significantly counteracted by grazing (e.g. Hillebrand 2009; Poore et al. 2012). In *Fucus* stands of the southwestern Baltic Sea, the gastropod *Littorina littorea* and the crustaceans *Gammarus* spp. and *Idotea* spp. constitute the most abundant mesograzers. All of them are generalized herbivores with complementary feeding preferences. More precisely, *L. littorea* primarily feeds on microepiphytic biofilm (diatoms) (Steneck and Watling 1982; Sommer 2000) whereas the amphipod *Gammarus* spp. and the isopod I*dotea* spp. feed on filamentous macroepiphytes but also on filamentous microalgae (Sommer 2000; Worm et al. 2000; Goecker and Kåll 2003). All three grazers also feed on the structurally more complex *F. vesiculosus*, depending on the density of grazers and the availability of epiphytes (Engkvist et al. 2000; Goecker and Kåll 2003; Kotta et al. 2006). Despite competition *F. vesiculosus* therefore also benefits from epiphytic growth as the former is less fed upon if epiphytes are abundant ('protective coating') (Karez et al. 2000).

In a fine-tuned and interdependent system alike, change of environmental conditions (with beneficial or harmful effects on some of the associated organisms) may induce a change of biotic interactions with subsequent indirect effects on the entire ecosystem. Using benthic mesocosms (hereafter referred to as benthocosms) we exposed a complex *F. vesiculosus* system to full-factorially manipulated seawater temperature and [CO_2] as predicted for the Baltic Sea region for the year 2100 (BACC 2008, 2015; Schernewski et al. 2010). Our main objective was to investigate if the regulating and maintaining mechanisms between *F. vesiculosus* and its associated epiphytes and mesograzers change in response to proceeding climate change across different seasons of one year. Specifically we asked (i) if [CO_2] fertilizes algal biomass in a grazed system. Given that carbon can be a limiting resource for marine autotrophs, we assumed that, despite grazing, excess carbon availability enhances the biomass accumulation of competitively superior algal species that can rapidly sequester CO_2. We asked (ii) if temperature-intensified grazing results in reduced epiphyte biomass. Based on predictions related to metabolic theory and tests of them in experimental or meta-analytical work (Brown et al. 2004; Hillebrand et al. 2009b; O'Connor et al. 2009), we expected a shifted balance from autotrophic production to heterotrophic consumption under warming. Furthermore, we asked (iii) if effects of concurrently raised seawater temperature and [CO_2] cancel each other out. We assumed that [CO_2]-induced increase of algal biomass is counteracted by temperature-intensified grazing in the mesograzer – epiphyte – *Fucus* system. Finally, we asked (iv) if the effects of increased seawater temperature and [CO_2] vary seasonally according to natural growth and reproduction periods. We expected to find a stronger fertilizing effect of [CO_2] on algal biomass during the growing season between spring and late summer. At the same time, we presumed that seawater warming during the summer months could exceed the thermal tolerance limits of the foundation species *F. vesiculosus* and its associated grazers. In winter we expected seawater warming to enhance the mesograzers' (feeding) activity.

Methods

Experimental set-up

In order to test for a seasonal variation of treatment effects on the system, all four experiments were conducted consecutively within one year. The first experiment started out in April 2013 and ran until June 2013 (hereafter referred to as early summer experiment), the second one lasted from July until September 2013 (late summer experiment), the third one ran from October till December 2013 (fall/ winter experiment) and the fourth experiment started out in January 2014 and continued until April 2014 (winter/ spring experiment). Each experiment lasted for 10-12 weeks (see Figure Appendix I-A for start and end dates). All four experiments were conducted in the Kiel Outdoor Benthocosms, a permanent experimental facility installed outdoors on a jetty in the Kiel Fjord, Germany. A detailed technical description of the Kiel Benthocosms, their installation, programming and monitoring can be found in Wahl et al. (2015). In short, the Kiel Benthocosms comprise of 12 tanks, each holding a water volume of 1.4 m3. The experimental units are exposed to ambient light and weather conditions year-round. They are equipped with gas-tight, transparent covers and can be controlled for environmental factors such as seawater [CO_2], temperature, and nutrient concentrations. In our study the experimental units were supplied with non-filtered seawater taken from the Kiel Fjord, in close vicinity to the experimental platform and from 1 m depth. The water body was exchanged once per day via a flow-through system, which kept the ambient experimental conditions very close to the actual ambient conditions of the Kiel Fjord, including its environmental fluctuations (see below). For seawater [CO_2] manipulations pure CO_2 was given into the headspace of each experimental unit. A wave generator regularly induced water motion and thereby promoted diffusion of CO_2 from the headspace into the water column. Temperature was controlled via heat exchangers and internal heating elements (Titan 2000, Aqua Medic, Bissendorf, Germany and Schego Titan, 600 Watt, Schemel and Goetz, Offenbach/ Main, Germany). Key variables such as pH, temperature, oxygen and salinity were continuously logged (Sensors: Profilux 3ex, GHL Advanced Technology, Kaiserslautern, Germany). Given the size and technological advance, the experimental facility allows the testing of near natural scenarios, not only in terms of multiple environmental stressors that can be manipulated simultaneously, but also with regard to the biota being assessed (i.e. entire systems, including multiple species, functional groups and trophic levels).

Here, twenty thalli of the macrophyte *F. vesiculosus* including its associated flora and fauna such as microepiphytes (diatoms) and macroepiphytes (mainly of the genus *Cladophora, Elachista, Ulva, Pilayella, Ceramium*), the bacterial biofilm as well as mesograzers were established in each experimental unit. For all experiments, collections of the *F. vesiculosus* systems were made at the same site in the Kiel Fjord (Bülk), southwestern Baltic Sea, Germany. All thalli were kept attached to their natural rock substratum. After they had been collected, the macrophytes and their epibiota were immediately placed into water-filled buckets and transported to the experimental site. *Fucus* thalli were sorted into three size classes (≤15cm, ≤30cm, ≥30cm) for an approximate even size distribution in all experimental tanks. They were identified by numbered tags and defaunated by shortly (20–30 s) being submerged in freshwater (Holmlund et al. 1990). In the benthocosms, the rock substrata of each *Fucus* thallus was placed into a small plastic dish (Ø = 14 cm, h = 4 cm) in order to keep the evenly distributed thalli from being swept away by the water current. The plastic dishes were fixed on a concrete grating by cable ties. The concrete grating was hooked in all experimental units at a water depth of 0.40 m. The three most important mesograzers caught with the collected *Fucus* thalli – *Littorina littorea*, *Idotea* spp. and *Gammarus* spp. – were sorted, counted and evenly distributed into the experimental units. The initial amount of grazers given into the system varied between experiments according to the natural variability of their abundance across seasons (see Table Appendix I-B).

Treatments

In order to test for single and interactive effects, we full-factorially crossed two temperature and [CO_2] levels (ambient vs. elevated), creating a total of four treatment combinations. The ambient treatment (A) reflected the Kiel Fjord in-situ condition. The elevated treatment described a delta value of $\Delta T = +4\text{-}6$ °C (+T and +C+T) and/ or $\Delta pCO_2 = +600$ ppm (+C, +C+T) as compared to the ambient temperature and [CO_2] level. Both manipulations were chosen according to Baltic Sea climate change predictions for the year

2100 (BACC 2008, 2015; Schernewski et al. 2010). The nominal condition of the ambient and elevated treatments did not describe a fixed value, but followed diurnal and seasonal fluctuation (Wahl et al. 2015). Each treatment combination was replicated three times.

Sampling and response variables

For reasons of clarity and space this manuscript focuses on the final sampling of each of the four seasonal experiments. Biomass of *F. vesiculosus* was expressed as fresh weight [g FW] after the removal of epiphytes and a defined drying procedure (i.e. gently shaking the thallus 5 times). Two *Fucus* individuals per experimental unit growing solitarily on similar sized rocks and having shown similar starting sizes and weights were used for biomass measurements. Microepiphyte biomass was expressed as carbon content [pg C]. For the analysis one randomly chosen apical branch (1.5-2 mg DW) of two randomly chosen *Fucus* thalli per experimental unit was carefully removed and taken to the laboratory for further analysis. The epiphytic material of each *Fucus* sample was scraped and rinsed off with a razor blade and a defined volume of sterile filtered seawater (200-250 ml, 0.2 µm), respectively. The removed epiphytic material of both *Fucus* thalli per experimental unit was pooled. The sample was homogenized and about 100 ml were fixed with Lugol's iodine for microscopic identification and counting (Utermöhl 1958). Microepiphyte biomass was then estimated from cell biovolume (Hillebrand et al. 1999) converted to carbon content (Menden-Deuer and Lessard 2000). Macroepiphyte biomass was expressed as dry weight [g DW]. For the analysis, all macroepiphytes were collected from the *Fucus* thalli that also had been sampled for microepiphyte biomass analysis. During final sampling all mesograzers were removed from the experimental tanks. They were identified, sorted and counted. A subsample of 15-20 individuals per grazer group per experimental unit was taken for the analysis of total grazer biomass, expressed as ash free dry weight [g AFDW without shell] and per capita biomass per grazer species [mg AFDW without shell].

Samples for determining seawater total alkalinity (TA) and dissolved inorganic carbon (DIC) were taken directly from the experimental units at a definite time (9.00-11.00 a.m.) one day prior to the sampling. Samples for DIC were taken with a peristaltic pump. They were filtered through sterile syringe filters (0.2 µm, RC25, Minisart, Sartorius, Göttingen, Germany) into headspace crimp vials (10 ml), sealed with butyl rubber septa and stored at 4° C until further analysis with a gas chromatographic system (SRI-8610, Torrance, CA, USA) (Hansen et al. 2013). Samples for total alkalinity were filtered (Whatmann GF/F, Ø 47mm) and quantified with a Titrino plus 848 (Metrohm, Filderstadt, Germany). TA, DIC, salinity and temperature data were used to calculate the partial pressure of CO_2 (pCO_2) with the CO2SYS program for Excel (Pierrot et al. 2006). Data of the manipulated seawater temperature and pCO_2 are reported in Figure Appendix I-A.

Statistical Analysis

Prior to the analysis, data were tested for normal distribution and homogeneity of variances and were transformed if necessary. A full factorial analysis of variance (ANOVA) was then applied to test the effects of [CO_2], temperature and the interaction of both on the biomass of *F. vesiculosus*, of micro- and macroepiphytes and on the total abundance and total biomass of the three most important grazers. Taking into account that the analysis of a pooled grazer data set might obliterate grazer species specific sensitivities to a treatment, single grazer species responses in terms of their total abundance and per capita biomass were analyzed using MANOVA. To estimate the relative importance of each of the contributing factors, effect sizes were calculated as omega squared (ω^2 = SS treatment – df treatment * MS error) / SS total + MS error) (Hughes and Stachowicz 2009). In order to identify indirect pathways of treatment effects via trophic connections in the consumer – producer system, Pearson's correlations were computed among significantly affected response variables (Boyce et al. 2015).

Results

Under ambient conditions (A) the experimental *F. vesiculosus* systems reflected seasonal (growth) patterns that can naturally be observed in the southwestern Baltic Sea. Biomass of *F. vesiculosus* was highest in early and late summer under ambient conditions (Figure 1a, b), whereas it was lowest in winter/ spring (Figure 1d). Biomass of microepiphytes was highest in early summer and winter/ spring under ambient conditions (Figure 1e, h) and it was lowest in fall/ winter and in late summer (Figure 1g, f). Biomass of filamentous macroepiphytes was highest in late summer in the ambient treatment (Figure 1j) and lowest in fall/ winter (Figure 1k). Total grazer abundance under ambient conditions was one order of magnitude higher in late summer as compared to any other season (Figure 1n). In early summer, fall/ winter and winter/ spring, grazers showed relatively similar lower abundances (Figure 1m, o, p). Throughout all seasons total grazer biomass reflected the pattern observed for the total grazer abundance, i.e. an in- or decrease of total abundance was accompanied by an in- or decrease of total biomass, respectively (Figure 1m-p).

Treatment effects of temperature and [CO_2] showed a high seasonal variability. Generally, seawater warming (+T, +C+T) had significantly stronger and more persistent effects on the *Fucus* systems than increased [CO_2] (see Table Appendix I-D to I-G for treatment effect sizes ω^2). Effects of [CO_2] (+C, +C+T) were weak and inconsistent in that they occurred only in late summer and fall/ winter (Table Appendix I-D; Table Appendix I-E; see Appendix I-C for a more detailed description of the effects of [CO_2]).

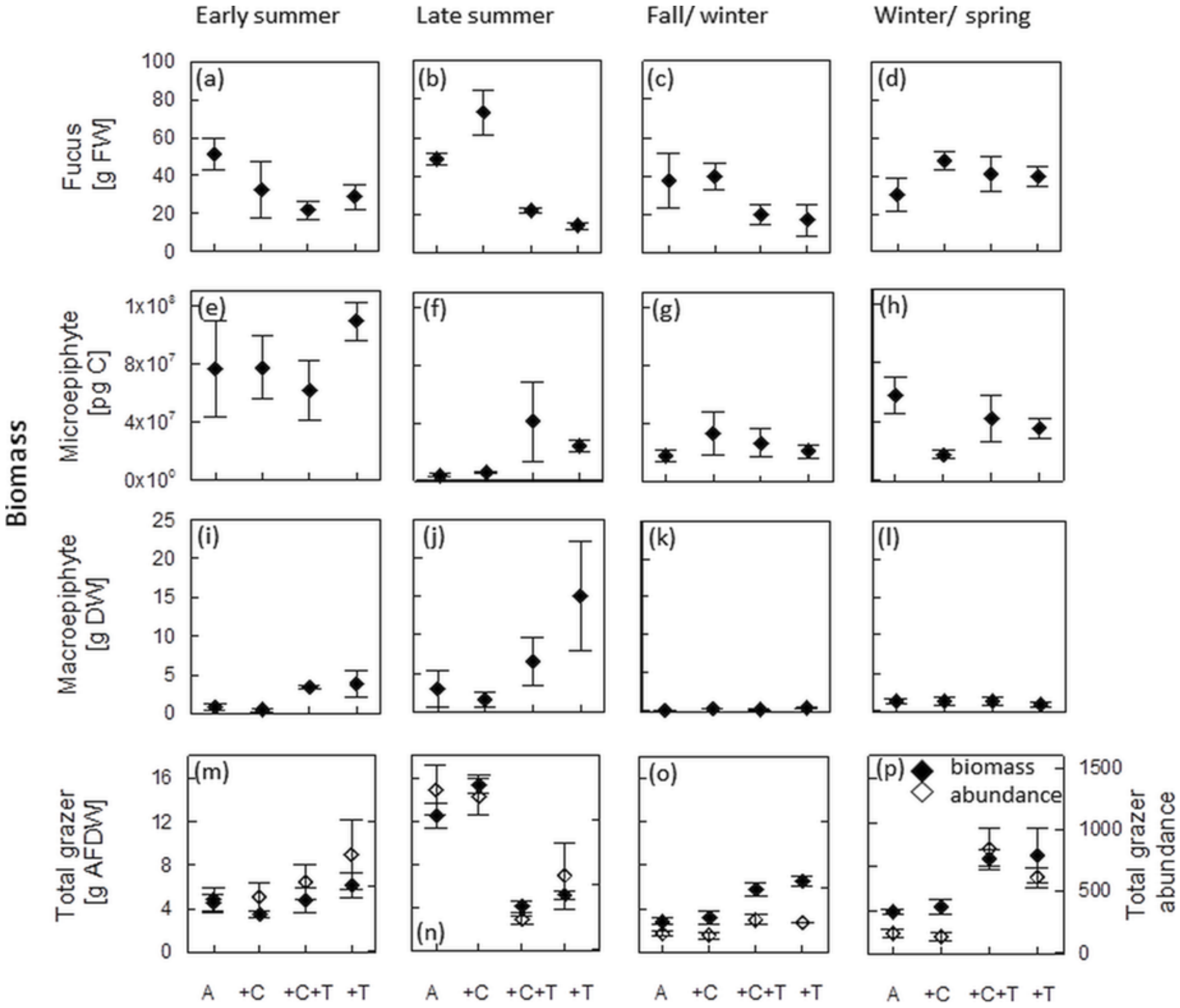


Figure 1. Display (mean ± SE) of the final biomass of (a-d) *Fucus vesiculosus* [g FW], (e-h) microepiphytes [pg C], (i-l) macroepiphytes [g DW] and (m-p) the final total grazer biomass (filled diamonds) [g AFDW without shell] and total grazer abundance (open diamonds). Responses are shown for all seawater [CO_2] and temperature treatment combinations (n = 12) across all four seasons of experimental runtime (early summer, late summer, fall/ winter, winter/ spring). Treatment combinations are shown as A: ambient; +C: high [CO_2]/ ambient temperature; +C+T: high [CO_2]/ high temperature; +T: ambient [CO_2]/ high temperature.

Throughout all seasons, grazers (though not all mesograzer species to the same extent) were affected by elevated temperature. However, a propagation of the temperature effect from mesograzers to epiphytes and/ or to the foundation species via altered consumption depended on season and grazer species identity. Only in late summer warming led to a cascading effect impacting the entire mesograzer – epiphyte – seaweed system. More specifically, in late summer, total grazer abundance and biomass collapsed under warming (Figure 1n; Table Appendix I-D), whereas the biomass of microepiphytes and filamentous macroepiphytes showed a steep increase by one order of magnitude and threefold, respectively (Figure 1f, j; Table Appendix I-D). In parallel, the biomass of *F. vesiculosus* declined by up to 70 % (Figure 1b; Table Appendix I-D). Total grazer abundance and/ or biomass correlated negatively with the biomass of micro- and macroepiphytes (Figure 3a-d) and positively with the biomass of *F. vesiculosus* (Figure 3e-f; Table Appendix I-H). Moreover, biomass of *F. vesiculosus* correlated negatively with the biomass of micro- and macroepiphytes (Figure 3g, h; Table Appendix I-H). This relation suggests that warming indirectly benefited epiphyte biomass accumulation and disadvantaged *Fucus* biomass via reduced grazing. Analysis of grazer species specific responses to warming showed that the loss of grazing in late summer was primarily driven by a decline of the crustaceans *Idotea* spp. and *Gammarus* spp. (Figure 2f, j; Table Appendix I-D). *Littorina littorea*, the third mesograzer species included in the experiments, showed hardly any response to any of the treatment combinations in any season. Only in late summer the gastropod’s per capita biomass significantly decreased, indicating a reduction of its physiological fitness under warming even though its abundance had not yet changed (Figure 2b; Table Appendix I-D). Species specifically, the abundance of *Idotea* spp. and *Gammarus* spp. correlated negatively with microepiphyte biomass (Table Appendix I-H). The per capita biomass of *Idotea* spp. and *L. littorea* correlated positively with the biomass of *F. vesiculosus* (Table Appendix I-H).

In fall/ winter, seawater warming increased the total abundance and total biomass of the mesograzers (Figure 1o). The effect was driven by the responses of *Idotea* spp. and *Gammarus* spp. (Figure 2g, k; Table Appendix I-E). Particularly the per capita biomass of *Idotea* spp. increased with elevated seawater temperature (Figure 2g), indicating enhanced individual growth instead of recruitment. Moreover, warming decreased the biomass of *F. vesiculosus* (Figure 1c; Table Appendix I-E), whereas it had no effect on either epiphytic group (Figure 1g, k; Table Appendix I-E). Biomass of *F. vesiculosus* negatively correlated with the per capita biomass of *Idotea* spp. (Table Appendix I-H), suggesting that the larger individuals of *Idotea* in warm treatments fed directly on *F. vesiculosus* (Figure 1g, k) in fall/ winter. .

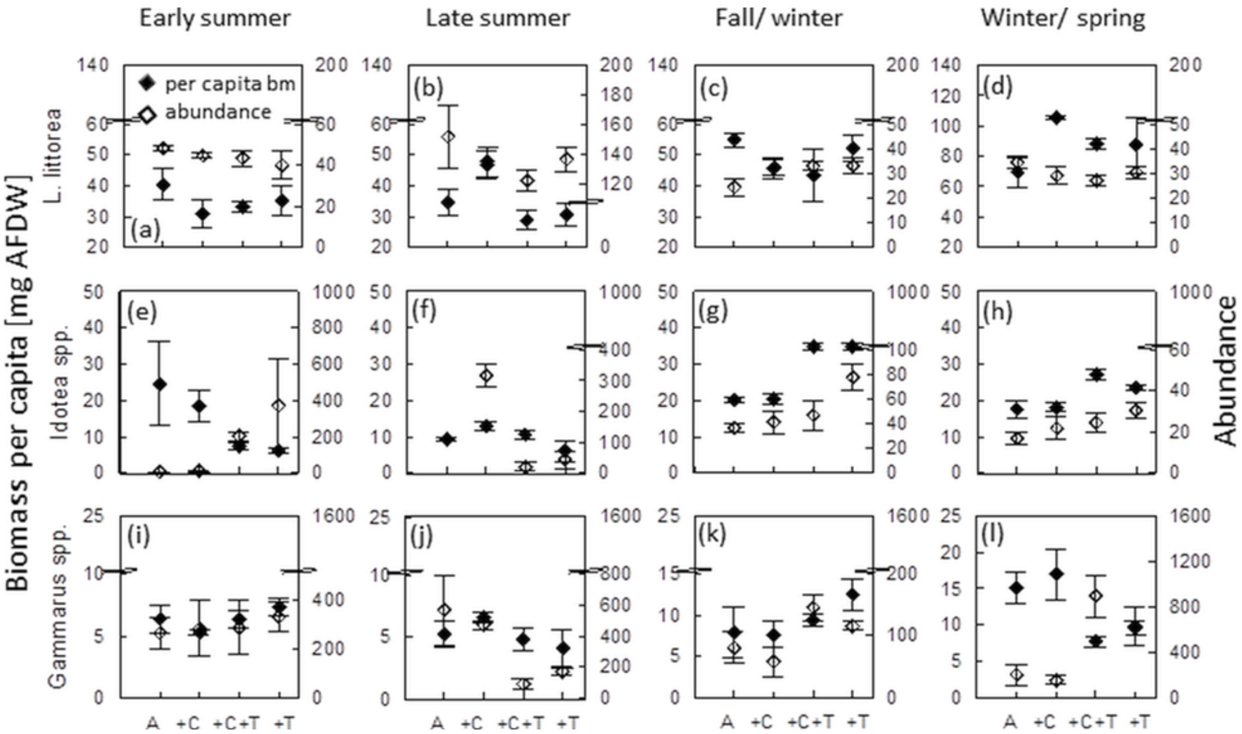


Figure 2 Display (mean ± SE) of the per capita biomass (filled diamonds) [mg AFDW without shell] and grazer species specific abundance (open diamonds) for all seawater [CO_2] and temperature treatment combinations (n = 12) encoded as A: ambient; +C: high [CO_2]/ ambient temperature; +C+T: high [CO_2]/ high temperature; +T: ambient [CO_2]/ high temperature. Shown are the responses for (a-d) *L. littorea*, (e-h) *Idotea* spp., (i-l) *Gammarus* spp. across all seasons (early summer, late summer, fall/ winter, winter/ spring).

In winter/ spring, elevated temperature positively affected mesograzer total abundance and total biomass (Figure 1p; Table Appendix I-F). This time, however, the effect was primarily driven by *Gammarus* spp., which showed a steep increase in abundance and a significant decrease in its per capita biomass under warming (Figure 2l; Table Appendix I-F). The latter indicates enhanced gammarid recruitment instead of individual growth. The per capita biomass of the second crustacean grazer *Idotea* spp. increased in warm treatments, whereas its abundance did not significantly change (Figure 2h; Table Appendix I-F). Seawater warming did not affect the biomass of either epiphytic group or *F. vesiculosus* (Figure 1d, h, l; Table Appendix I-F) in winter/ spring. Temperature-induced changes of the abundance or the per capita biomass of any grazer species did not correlate with the biomass of epiphytes or *Fucus* ($n = 12$; $r \leq 0.124$; $p \geq 0.69$).

In early summer, seawater warming did not have a significant effect on total grazer abundance and total grazer biomass (Figure 1m; Table Appendix I-G). Species specifically, warming increased the abundance of *Idotea* spp., but decreased its per capita biomass (Figure 2e; Table Appendix I-G), indicating its enhanced recruitment under warm conditions in early summer. Moreover, warming increased the biomass of macroepiphytes, whereas it had no effect on the biomass of microepiphytes and *F. vesiculosus* (Figure 1a, e, i; Table Appendix I-G). Macroepiphyte biomass positively correlated with *Idotea* spp. abundance (Table Appendix I-H), suggesting that the increased abundance of small *Idotea* specimens under warming did not intensify the grazing pressure on macroepiphytes.

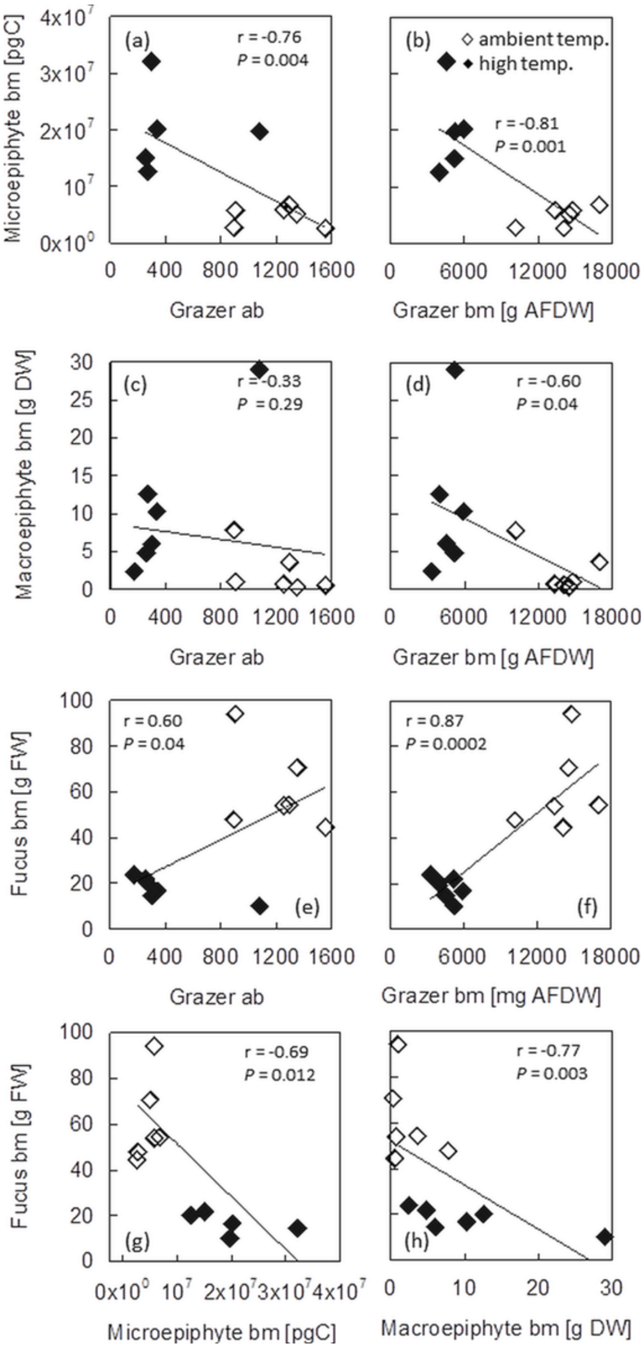


Figure 3 Pearson's correlations between the biomass (bm) of (a-b) microepiphytes, (c-d) macroepiphytes and (e-h) *F. vesiculosus* to grazer abundance (ab), grazer biomass (bm), micro- and macroepiphyte biomass (bm) in ambient (open diamonds) and high (filled diamonds) temperature treatments. Sample size (n) for each analysis was twelve. Shown are the results for late summer, during which the effects of seawater warming cascaded through all levels of the mesograzer – epiphyte – foundation species system.

Discussion

Our experimental results suggest that warming has much stronger effects on coastal food-webs than elevated [CO_2]. In the investigated grazed system (i) [CO_2] did not enhance the biomass production of primary producers. The experimental benthic community comprised of two trophic levels, of which (ii) consumers (mesograzers) were directly affected by warming whereas primary producers (epiphytes and *F. vesiculosus*) were primarily indirectly affected via temperature-induced changes of top-down control. Concurrently raised seawater temperature and [CO_2] (iii) did not reveal antagonistic effects on the system. The effects of warming on the food-web structure (iv) depended on the season and mesograzer species identity. This outcome highlights two challenges for ongoing ecological climate change research: first, the relevance of considering seasonal variation of climate change impacts on natural systems; second, the importance of identifying changes of ecosystem processes (between species and trophic levels), that may influence the buffering capacity of an ecosystem with regard to proceeding global climate change.

Under ambient conditions, the experimental *Fucus* systems described a fine-tuned balance between primary production and grazing, not only in the highly productive spring and summer months but also outside the growing season, in fall and winter. Seawater warming by 4-6° C disrupted this balance in late summer and fall/ winter by impairing top-down control on epiphytes and by intensifying grazing on *Fucus*, respectively. More specifically, in late summer, warming resulted in a cascading effect from the mesograzers to the epiphytes to the foundation seaweed *F. vesiculosus*. At this time, temperatures in warm treatments rose above 28° C, (most likely) causing thermal stress related mortality to both crustacean mesograzer species (*Idotea* spp., *Gammarus* spp.) (Leidenberger et al. 2012). In consequence, epiphytes overgrew large parts of the *Fucus* thalli. This outcome relates to a recent study showing that the effects of environmental stressors are mediated by mesograzers (Alsterberg et al. 2013). The reduction of *Fucus* biomass by up to 70 % under warming in late summer cannot, however, be solely explained by the identified indirect (grazing) effect. Most likely, the drop in biomass was also due to direct heat stress impeding *F. vesiculosus*' photosynthetic activity and growth (Graiff et al. 2015). In fall/ winter prolonged higher seawater temperatures (above 10° C) in warm treatments led to larger specimens of *Idotea* spp. (i.e. increased per capita biomass) and to reduced biomass of *F. vesiculosus*. Previous studies have shown that adult specimens of *Idotea* readily feed on the structurally more complex macrophyte in dependence on the availability of epiphytes and grazer density, whereas juveniles predominantly feed on filamentous epiphytes (e.g. Little and Kitching 1996; Engkvist et al. 2000; Leidenberger et al. 2012). Our results suggest that enlarged

Idotea specimens in warm treatments fed more on *Fucus* when epiphytes were less abundant outside the growing season in winter. This interpretation is also supported by a considerable amount of bite marks observed on *Fucus* thalli in warm treatments.

Conforming to our expectations, warming differentially affected consumer and resource species. In line with concepts of metabolic theory and tests of them in experimental and meta-analytical studies (e.g. Brown et al. 2004; Hillebrand et al. 2009; O'Connor et al. 2009), herbivore metabolism (i.e. processes such as consumption, growth and reproduction) were found to be more sensitive to temperature than algal primary production (biomass accumulation). Grazer abundance and biomass were directly affected by warming throughout all seasons, whereas the results clearly suggest that autotrophic biomass was indirectly affected by warming via temperature-induced changes of top-down control. We can, thus, confirm the prediction that future increases in water temperatures influence marine food-web processes by altering top-down regulation. However, the results also show that effects of this on food web structure depend on the season and grazer species identity. A similar suggestion was made in two studies on plankton, which showed that warming altered top-down control and thereby changed the dynamics of the entire system (Sommer and Lewandowska 2011; Lewandowska et al. 2014). Both studies concluded that effects of seawater warming on phytoplankton and herbivores may also depend on season.

We are aware that the chosen correlative approach can only suggest indirect pathways and that it does not allow conclusions to be drawn about the relative strengths of direct and indirect effects. In fact, structural equation modeling (SEM) (Grace 2006) would have been a more appropriate statistical tool for such analysis. However, the sample size derived from this experimental design was rather small and would have rendered a SEM analysis not robust. Nevertheless, the calculated correlation matrices provide a good estimate for the indirect temperature - consumer - producer pathways (Boyce et al. 2015), and they are substantiated by the fact that temperature effects on autotrophic biomass occurred only when consumers were significantly affected by temperature as well. In fact, the direction and size of the effect of elevated temperature on the foundation seaweed or its associated micro- and macroepiphytes seemed to depend on the direction and size of the effect of elevated temperature on grazers, which clearly varied with season.

Based on previous studies that observed increased biomass production in aquatic autotrophic communities under elevated seawater [CO_2] (e.g. Connell and Russell 2010; Johnson et al. 2013; Kroeker et al. 2013), we hypothesized that enhanced primary production would be seen in the tested benthic system, which, however, was not the case. Eklöf et al. (2015) suggest that the naturally high diurnal fluctuation of [CO_2] in coastal marine vegetation may explain its adaptation and lack of response to (realistic) experimental [CO_2] treatments. In addition to diurnal changes, the marine biota of the Kiel Fjord undergoes regular wind-driven upwelling events that bring deep and CO_2-enriched water masses to the surface. Seawater CO_2 conditions of 2300 ppm and consequent changes of pH by up to 0.7 units occur naturally in the Kiel Fjord (Thomsen et al. 2010). The experimental systems in the benthocosms followed natural fluctuations (diurnal cycles and upwelling), which resulted in temporary maximum values of about 2500–2800 ppm in the high [CO_2] treatments (see Figure Appendix I-A). It is possible that the established autotrophic communities were DIC saturated or that they rapidly used up some of the excess carbon until other resources (e.g. other inorganic nutrients, space, and light) became limiting, and that the systems were otherwise unaffected by the manipulated changes in seawater [CO_2].

Based on the evidence we presented in this work, we expect the most critical effects of seawater warming on the Baltic Sea *Fucus* system to occur in late summer and fall/ winter. In both of these seasons, negative effects of temperature resulted in a significant decline in *F. vesiculosus*, the key species of the investigated coastal system. The experimental high temperature treatment of ΔT = +4-6° C above ambient aligns with predictions made for the Baltic Sea region until 2100 (BACC 2008; 2015; Schernewski et al. 2010). However, Baltic Sea surface water temperatures above 25° C and consequent harmful effects on seagrass communities have already been observed during a summer heat wave in 2003 (Reusch et al. 2005). Given that climatic extremes are predicted to increase in the face of global climate change (IPCC 2014), our experiments were conducted under plausible (future) environmental scenarios. Even though we cannot pinpoint a threshold value for a heat stress related breakdown of top-down regulation, our results imply that a cascading effect of seawater warming in summer may be able to trigger a shift of the coastal *F. vesiculosus* system toward one dominated by epiphytic ephemeral (in particular filamentous) algae. Winter warming had a reverse effect on mesograzers, again with negative effects on the foundation species *F. vesiculosus*. A reduced standing stock of *Fucus* due to intensified grazing under winter warming may imply a reduced fitness at the beginning of the following growing season and a greater risk of competitive exclusion by fast-growing epiphytes. We cannot account for such carry-over effects, because in this study the experimental *Fucus* systems were renewed at the onset of each experiment.

Generally, the Baltic Sea has been under high anthropogenic pressure ever since human population density, agriculture, and industry increased along the coastline of this semi-enclosed sea (Lotze et al. 2006). Since then, eutrophication has been one of the most severe environmental problems especially for coastal ecosystems (e.g. Elmgren 1989; Jansson and Dahlberg 1999; HELCOM 2014). In the past, nutrient pollution primarily elevated the production of fast-growing ephemeral algal species and phytoplankton, which in turn detrimentally affected coastal key vegetation such as seagrass meadows and perennial

Fucus belts (Torn et al. 2006; HELCOM 2013). Under future global climate change, nutrient influxes to Baltic Sea coastal areas are predicted to increase due to proceeding industrial agriculture and changed precipitation patterns (BACC 2008, 2015). Such local environmental threats are likely to combine with emerging climate change stressors to potentially cause amplified stress to marine systems. Given that warming alone resulted in impairment of the foundation species *Fucus* in our study, it seems likely that future eutrophication and warming will produce additive deteriorating effects on Baltic Sea *Fucus* communities by accelerating epiphytic overgrowth (Werner et al. in review). Since *F. vesiculosus* is the dominant habitat-forming brown algal system in the Baltic Sea, its decline jeopardizes key functions and services such as nutrient storage and provision of substrate, food, and shelter for a diverse community of marine invertebrates and fish.

Acknowledgments

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Chapter II

Even moderate nutrient enrichment negatively adds up to global climate change effects on a habitat-forming seaweed system

Abstract

Coastal marine ecosystems have been under high anthropogenic pressure and it can be assumed that prevalent local perturbation interacts with rising global stressors under proceeding climate change. Understanding their effective pathways and cumulative effects is of high relevance, not only with regard to future risk assessment but also for current ecosystem management. In benthic mesocosms, we factorially tested the direct and indirect effects of one global (combined elevated seawater temperature and CO_2 concentration) and one local (nutrient enrichment) stressor on a common coastal Baltic seaweed system (*F. vesiculosus*). Both treatments in combination had additive negative impacts on the seaweed – epiphyte – mesograzer system by altering its regulatory mechanisms. That is, warming decreased the biomass of two mesograzer species (weakened top-down control), whereas moderate nutrient enrichment increased epiphyte biomass (intensified bottom-up control), which ultimately resulted in a significant biomass reduction of the foundation seaweed. Our results suggest that climate change impacts might be underestimated if local pressures are disregarded. It further gives implication for local ecological management as the mitigation of local perturbation may limit climate change impacts on marine ecosystems.

Introduction

Coastal marine ecosystems face cumulative anthropogenic pressure composed of globally determined stressors, such as rising seawater temperature and carbon dioxide concentrations, and locally determined stressors, such as nutrient enrichment, increased sedimentation and overharvesting of natural resources. Recent experimental and meta-analytical studies showed that two and more environmental stressors in combination can exert additive, antagonistic or synergistic effects on single species or species assemblages (Crain et al. 2008; Russell et al. 2009; Strain et al. 2014). The direction and size of effects, however, showed to be highly dependent on context, i.e. on the factors combined and the species or species assemblages investigated. Thus, with regard to future risk assessment and the development of conservation strategies, it will be increasingly relevant to integrate local stressors in climate change research and to understand the underlying mechanisms (i.e. direct and indirect pathways) by which multiple stressors interactively drive ecosystem change.

We used benthic mesocosms (hereafter referred to as benthocosms) and experimentally tested the effects of combined elevated seawater temperature and carbon dioxide concentration (hereafter referred to as [CO_2]) and moderate nutrient enrichment on the Baltic Sea *Fucus vesiculosus* system (hereafter referred to as *Fucus* system), including the associated epiphytes and mesograzers. The selected model system plays a fundamental role in structuring the rocky coastal marine habitat of the Baltic Sea. Being the most dominant large scale habitat-forming brown algae, *F. vesiculosus* holds key functions by providing substrate, food and shelter to a diverse community of epiphytic single-celled micro- and filamentous macroalgae and the associated crustacean and gastropod mesograzers. The entire system delivers ecosystem services such as nutrient cycling and storage and provision of habitat and nursery grounds for fish (Pedersen and Borum 1996; Phil et al. 1994; Borg et al. 1997; Persson et al. 2012; HELCOM 2013). Functioning of the *Fucus* system is maintained by fine-tuned biotic interactions such as competition (bottom-up regulation), consumption (top-down control) and beneficial co-occurrence. More precisely, the foundation seaweed competes with micro- and filamentous macroepiphytes for space, light and nutrients. A high epiphytic load can impede the functioning of the seaweed through shading, obstruction of nutrient uptake and exclusion from the primary substrate (Sand-Jensen and Borum 1991; Duarte 1995; Raffaelli et al. 1998). Competitive exclusion of the foundation seaweed by epiphytes is controlled by top-down grazing of *Idotea* spp. (isopod), *Gammarus* spp. (amphipod) and *Littorina littorea* (gastropod) (e.g. Lubchenco 1978; Råberg and Kautsky 2007; Hillebrand 2009). All three herbivores show complementary feeding preferences for epiphytes, but they may also feed on the structurally more complex *F. vesiculosus*, depending on the density of grazers and the availability of epiphytes

(Jormalainen et al. 2001; Engkvist et al. 2000; Goecker and Kåll 2003; Kotta et al. 2006). Despite competition the foundation seaweed, thus, also benefits from epiphytic growth as the former is less fed upon if epiphytes are abundant ('protective coating') (Karez et al. 2000).

In previous seasonal benthocosm studies we manipulated seawater temperature and [CO_2] according to future global change predictions for the Baltic Sea region (BACC 2008, 2015; Gräwe et al. 2013) and showed that elevated seawater temperature alone can impair the functioning of the *Fucus* system by altering top-down control in late summer and fall/winter (Werner et al. early view). In this follow-up study we seek to give further mechanistic insights about potential interactive direct and indirect effects of these co-occurring global change forces and a prevalent local stressor (nutrient enrichment) on the Baltic Sea *Fucus* system.

The Baltic Sea has been under high anthropogenic pressure per se. In fact, well before the discourse emerged about potential climate change impacts, eutrophication driven by human activities such as industrial agriculture, fossil fuel combustion, wastewater discharges and shipping was recognized as one of its oldest and most severe environmental problems (Elmgren 1989; Cederwall and Elmgren 1990; Lotze et al. 2006; HELCOM 2014). Generally nutrient enrichment was attributed to cause shifts in the submerged aquatic vegetation by favoring the growth of opportunistic micro- and macroalgae which alter the turbidity, the light and oxygen regime and ultimately supersede the perennial habitat-forming vegetation (e.g. Eriksson et al. 1998 and references therein; HELCOM 2009). Related to this, the decline of *F. vesiculosus* in the rocky littoral zone and its withdrawal from habitats deeper than 3 m since the 1980s has been linked to the eutrophication status of the Baltic Sea (Torn et al. 2006; Rohde et al. 2008; HELCOM 2009). Based on this and our previous experimental findings during late summer, we hypothesized that (i) elevated seawater temperature negatively impacts mesograzers and thus reduces top-down control. In consequence, warming leads to increased epiphyte biomass and outcompeting of *F. vesiculosus* (Werner et al. early view). We expected that (ii) nutrient enrichment under ambient temperature and [CO_2] conditions particularly benefits the biomass accumulation of epiphytes as they are competitively superior to the slow-growing seaweed *F. vesiculosus*. We hypothesized that (iii) combined high temperature and high [CO_2] together with nutrient enrichment act additively negative on the *Fucus* system in such that temperature-induced disruption of top-down control and nutrient-induced elevated growth of epiphytes accelerate the overgrowth and outcompeting of the foundation seaweed by epiphytes.

Methods

Experimental design

The experiment was conducted in the Kiel Outdoor Benthocosms, a permanent experimental facility situated outdoors on a jetty in the Kiel Fjord, Germany. The benthocosms comprised of twelve experimental tanks each holding a water volume of 1.4 m^3. All tanks were equipped with gas-tight transparent covers and filled with non-filtered seawater taken from the Kiel Fjord in close vicinity to the experimental platform and from 1 m depth. The water body was exchanged once per day via a flow-through system, which kept the ambient experimental conditions close to the actual ambient conditions of the Kiel Fjord, including its environmental fluctuations. One wave generator per experimental unit induced water motion and thereby promoted diffusion of the introduced CO_2 from the headspace into the water column.

Temperature and [CO_2] were combined in one treatment (hereafter referred to as greenhouse treatment or Gh) and full factorially crossed with nutrient concentration (N) as a second factor. This approach was justifiable since the single and interactive effects of temperature and [CO_2] on complex *Fucus* systems in the same experimental set-up had already been tested and the effects of [CO_2] had shown to be negligible (Werner et al., early view). Nonetheless both global stressors were combined as they have been rising concurrently and most likely interact with prevalent local stressors in nature. A full three-factorial design was not realizable given the limited amount of experimental tanks (12) and our demand of minimal three replicates per treatment. The applied design resulted in a total of four treatment combinations. The ambient treatment (-Gh-N) reflected the Kiel Fjord in situ condition, including its natural fluctuation of temperature, [CO_2] and nutrient concentrations. The combined elevated temperature and [CO_2] treatment (+Gh-N) described a delta value of $\Delta T = +5$ °C and $\Delta pCO_2 = +600$ ppm relative to the ambient conditions (see Figure Appendix II-A), following climate change predictions for the Baltic Sea region (HELCOM 2007; BACC 2008, 2015; Gräwe et al. 2013). The nutrient enrichment treatment (-Gh+N) comprised ambient temperature and [CO_2] conditions and a moderately raised (i.e. doubled) nutrient concentration according to the natural mean concentrations of nitrate, phosphate and silicate in the Kiel Fjord averaged over the respective months July and August over the past seven years (see below or Table Appendix II-B). The fourth treatment combination comprised the elevated levels of all stressors (+Gh+N). Each treatment combination was replicated three times. The experiment ran for six weeks between July and August 2014.

Temperature was controlled via heat exchangers and internal heating elements (Titan 2000, Aqua Medic, Bissendorf, Germany and Schego Titan, 600 Watt, Schemel and Goetz, Offenback/ Main, Germany). [CO_2] was controlled via infrared spectroscopy (Scenty, HTK, IR Spectroscopy, Hamburg) which automatically initiated the injection of CO_2 into the greenhouse treatment tanks' headspace if low threshold levels were reached (for details see Wahl et al. 2015). Nutrient enrichment was manipulated manually and moderately in such that a daily mean concentration of 1.5 µmol L^{-1} NO_3, 1 µmol L^{-1} PO_4 and 28.8 µmol L^{-1} SiO_4 was maintained in July and of 1.9 µmol L^{-1} NO_3, 1.3 µmol L^{-1} PO_4 and 35.3 µmol L^{-1} SiO_4 in August 2014 (see also Table Appendix II-B). Temperature, pH, salinity and oxygen were continuously logged (Profilux sensors 3ex, GHL Advanced Technology, Kaiserslautern, Germany). Other key variables such as total alkalinity and dissolved inorganic carbon were sampled and analyzed once per week (see below). Detailed technical information about the experimental facility, the installation and monitoring can be found in Wahl et al. (2015).

Prior to the application of treatments, twenty plants of the seaweed *F. vesiculosus* including its associated flora and fauna such as micro- and macroepiphytes, the bacterial biofilm as well as mesograzers were established in each experimental unit. The *F. vesiculosus* systems were collected in the Kiel Fjord (Bülk), Western Baltic Sea, Germany (54°27'N; 10°12'E). All plants were kept attached to their natural rock substratum. After their collection, the macrophytes and their epibiota were immediately placed into water-filled buckets and transported to the experimental site. Prior to their distribution to the experimental units, the *Fucus* thalli were sorted into three size classes (≤15cm, ≤30cm, ≥30cm), identified by numbered tags and defaunated by shortly (20-30s) being submerged in freshwater (Holmlund et al. 1990). In the experimental tanks the *Fucus* thalli were evenly distributed at a water depth of 0.40 m. The three most important mesograzers caught with the collected *Fucus* thalli (*Idotea* spp., *Gammarus* spp. *Littorina littorea*) were sorted and counted. Prior to their even distribution into the experimental units, a random subsample of 15 to 20 individuals per grazer species was taken for the analysis of initial biomass (expressed as mg ash free dry weight without shell, hereafter mg AFDW without shell). Table Appendix II-C shows the total and species specific amount of grazers added to the tanks.

Sampling and response variables

Biomass of *F. vesiculosus* was expressed as fresh weight [g FW] after the removal of epiphytes and a defined drying procedure (i.e. gently shaking the plant 5 times). Per experimental unit, two individuals of *F. vesiculosus* growing solitarily on similar sized rocks and having shown similar starting sizes and weights were used for biomass measurements. Microepiphyte biomass was expressed as Chlorophyll a [µg L^{-1}] content. Due to the high patchiness of epiphytes on the *Fucus* thalli, unglazed ceramic tiles (5x5cm) were placed between the *F. vesiculosus* plants for the analysis of the succession of microepiphyte biomass. Three randomly chosen tiles were sampled. The epiphytic material was scraped and rinsed off with a razor blade and a defined volume of sterile filtered seawater (200-250 ml, 0.2 µm), respectively. The removed epiphytic material was pooled and homogenized per experimental unit. About 5-15 ml of the diluted sample was filtered on pre-combusted Whatman GF/F filters and stored at -20° C until further analysis. Macroepiphyte biomass was expressed as dry weight [g DW]. All macroepiphytes were directly collected from the Fucus thalli on the final sampling day of the experiment. All mesograzers were removed from the experimental tanks during final sampling. They were identified, sorted and counted. A subsample of 15-20 individuals per grazer group and experimental unit was taken for the analysis of the final grazer biomass [mg AFDW without shell].

Samples for seawater total alkalinity (TA) and dissolved inorganic carbon (DIC) were taken directly from the experimental units once per week at a fixed time (09:00-11:00 a.m.). Samples for DIC were taken with a peristaltic pump. They were filtered through sterile syringe filters (0.2 µm, RC25, Minisart, Sartorius, Göttingen, Germany) into headspace crimp vials (10 ml), sealed with butyl rubber septa and stored at 4° C until further analysis with a gas chromatographic system (SRI-8610, Torrance, CA, USA) (Hansen et al. 2013). Samples for total alkalinity were filtered (Whatmann GF/F, Ø 47 mm) and quantified with a Titrino plus 848 (Metrohm, Filderstadt, Germany). Data of TA, DIC, salinity and temperature were used to calculate the partial pressure of CO_2 (pCO_2) with the CO2SYS program for Excel (Pierrot et al. 2006). Data of the seawater temperature and pCO2 treatment are reported in Figure Appendix II-A.

Statistical analyses

Prior to the analysis, data were tested for normal distribution and homogeneity of variances and were transformed if necessary. A full factorial analysis of variance (ANOVA) was then applied to test the effects of the greenhouse treatment (Gh) and nutrient enrichment (N) and their interaction on the biomass of *F. vesiculosus*, of micro- and macroepiphytes and on the biomass of the three most important grazers. Taking grazer species specific sensitivities to the treatment combinations into account, single grazer species responses regarding their biomass were analyzed using MANOVA. For the purpose of estimating the relative importance of each of the contributing factors, effect sizes were calculated as omega squared (ω^2 = SS treatment – df treatment * MS error) / SS total + MS error) (Hughes and Stachowicz 2009). In order to identify indirect pathways of treatment effects (especially with regard to altered trophic interactions), Pearson’s correlations were calculated among significantly affected response variables. Statistical analyses were conducted using Statistica 6.1 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

The biomass of *F. vesiculosus* decreased by 50% in the greenhouse as compared to the ambient treatment (Table Appendix II-D; Figure 1a). It was not significantly affected by nutrient enrichment under ambient temperature and [CO_2] (Table Appendix II-D; Figure 1a). Under combined greenhouse and nutrient enrichment conditions, however, biomass of *F. vesiculosus* decreased by 80% (Table Appendix II-D; Figure 1a).

The biomass of microepiphytes increased in each single treatment (greenhouse or nutrient enrichment) by the same order of magnitude (Table Appendix II-D; Figure 1b). Under combined greenhouse and nutrient enrichment conditions, the biomass of microepiphytes doubled as compared to the single treatments, suggesting an additive positive effect of the combined stressors (Table Appendix II-D; Figure 1b). The biomass of macroepiphytes showed the same increasing trend in the greenhouse and the combined greenhouse and nutrient enrichment treatment. However, the effects were statistically non-significant (Table Appendix II-D; Figure 1c).

Whereas the greenhouse treatment had no effect on total grazer biomass (Table Appendix II-D), it showed grazer species specific effects. That is, the biomasses of *Idotea* spp. and *Gammarus* spp. were significantly reduced under greenhouse conditions regardless of the eutrophication status of the respective treatment (Table Appendix II-D; Figure 1d, e). In contrast to this, the biomass of *L. littorea* remained unaffected by any of the treatment combinations (Table Appendix II-D; Figure 1f).

The biomass of *F. vesiculosus* correlated negatively with the biomass of micro- and macroepiphytes, indicating the competitive relationship between the foundation species and the associated epiphytes (Table Appendix II-E; Figure 2a, b). In contrast to this, the biomass of *F. vesiculosus* correlated positively with the biomass of the mesograzers *Idotea* spp. and *Gammarus* spp., indicating the balancing effect of top-down control (Table Appendix II-E; Figure 2c-d). Supporting this, the biomass of micro- and macroepiphytes correlated negatively with the biomass of *Idotea* spp. and *Gammarus* spp., respectively (Table Appendix II-E; Figure 2e-f). These relations indicate that the greenhouse conditions indirectly disadvantaged *F. vesiculosus* biomass and benefited epiphyte biomass accumulation by disrupting the balancing effect of top-down control. The negative correlation between *F. vesiculosus* and microepiphytes was driven by nutrient enrichment in the greenhouse treatment (Figure 2a, filled squares).

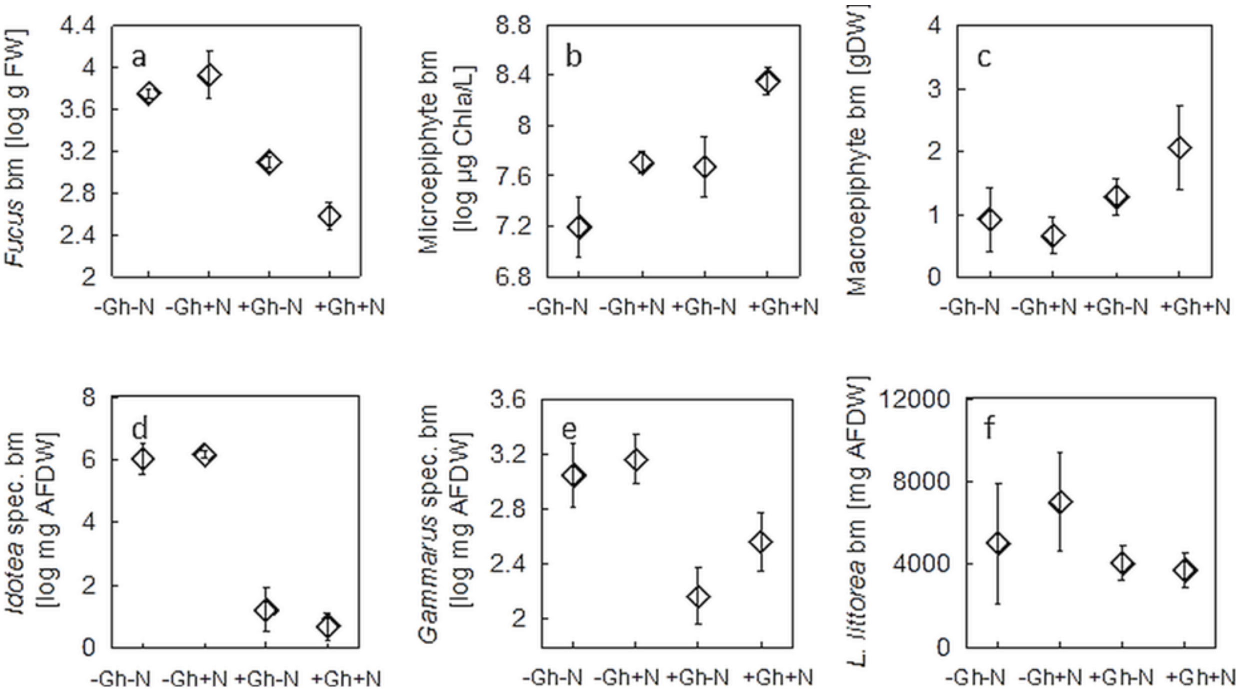

Figure 1 Display (mean ± SE) of the final biomass (bm) of (a) *Fucus vesiculosus* [log g FW], (b) microepiphytes [log µg Chla L^{-1}], (c) macroepiphytes [g DW], (d) *Idotea* spp. [log mg AFDW], (e) *Gammarus* spp. [log mg AFDW] and (f) *L. littorea* [mg AFDW]. Responses are shown for all greenhouse (i.e. seawater temperature and [CO_2] combined in Gh) and nutrient enrichment (N) treatment combinations. Treatments are shown as -Gh-N: ambient; -Gh+N: ambient temperature/ [CO_2] and nutrient enrichment; +Gh-N: high temperature/ [CO_2] and ambient nutrient concentrations; +Gh+N: high temperature/ [CO_2] and nutrient enrichment. Sample size (n) was twelve.

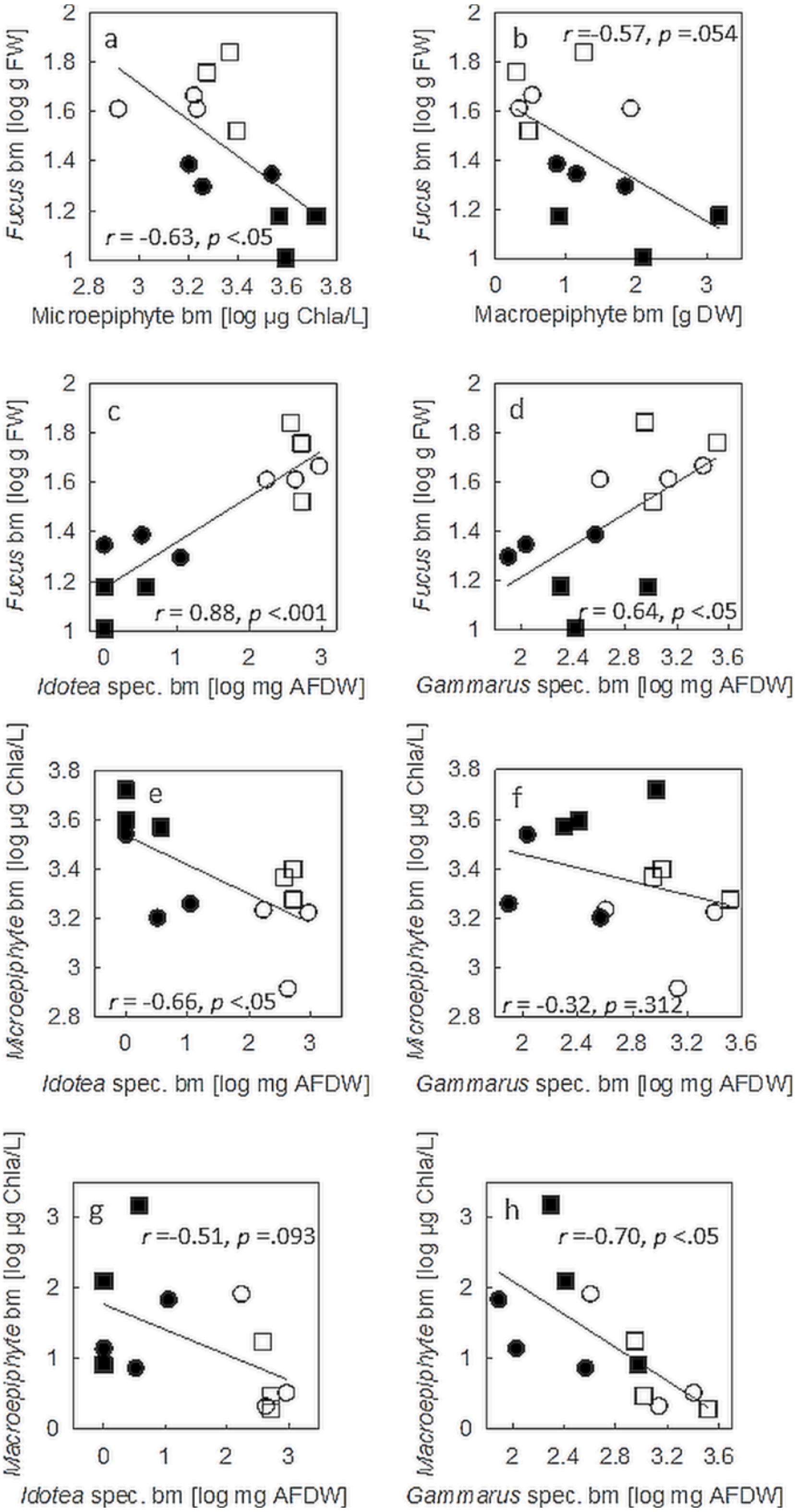

Figure 2 Pearson's correlations between the biomasses (bm) of *Fucus vesiculosus*, microepiphytes, macroepiphytes, *Idotea* spp. and *Gammarus* spp. in the treatments ambient (open circles), ambient temperature/ CO_2 and nutrient enrichment (open squares), high temperature/ CO_2 and ambient nutrients (filled circles) and high temperature/ CO_2 and nutrient enrichment (filled squares). Sample size (n) for each analysis was twelve.

Discussion

Our results are in line with the findings of a few recent studies indicating that local and global environmental stressors can exert interactive effects on ecosystems with an overall amplified negative outcome (Crain et al. 2008; Russell et al. 2009; Strain et al. 2014). In fact, our results clearly suggest that even moderate levels of a local stressor can accelerate future global climate change impacts. This global - local connection demonstrated here and by others gives important implications, not only to future risk assessment but also to current ecosystem management as the state of an ecosystem under proceeding global climate change may significantly depend on the control of local anthropogenic perturbations.

The results of our study explain the effective pathways of one global (warming and [CO_2] combined in the greenhouse treatment) and one local (nutrient enrichment) stressor on a common temperate coastal marine seaweed system. Conforming to metabolic theory describing a generally steeper reaction norm of heterotrophic processes to temperature (Gillooly 2001; Allen 2005), the greenhouse treatment had a stronger direct effect on the heterotroph component (mesograzers) and thereby indirectly affected the autotroph component (epiphytes and the foundation species *F. vesiculosus*) (confirming hypothesis 1). Based on our previous findings, suggesting the tested system to be well-adapted to fluctuating [CO_2], we assume that temperature but not [CO_2] was the main driver of the observed decline of top-down control in the greenhouse treatment (Werner et al., early view). Temperatures in warm treatments raised above 27 °C for several days, (most likely) causing heat stress related mortality to the crustaceans *Idotea* spp. and *Gammarus* spp. (Leidenberger et al. 2012). This grazer species specific response was not reflected in the final total grazer biomass as it was masked by the resilience of *L. littorea* and an observed fast recovery of *Gammarus* spp. (occurrence of many small individuals) when temperatures decreased again (see Figure Appendix II-A for the temperature development). Neither *L. littorea* nor the high gammarid recruitment, however, compensated for the significantly decreased top-down regulation. Instead, the direct impact of warming triggered a cascading effect in such that the release from grazing pressure led to enhanced biomass accumulation of epiphytes (overgrowth) and a subsequent die-off of the foundation species *F. vesiculosus*. The reduction of *F. vesiculosus* biomass by nearly 50% in greenhouse treatments, however, cannot solely be explained by the indirect temperature effect. Most likely direct heat stress impeding *F. vesiculosus*' photosynthetic activity and growth additionally promoted the decline of its biomass (Graiff et al. 2015). The latter is supported by the fact that microepiphyte biomass similarly increased in the nutrient enrichment treatment without having such detrimental effects on *F. vesiculosus* biomass in the absence of thermal stress (see below).

Expectedly and in line with numerous former studies on eutrophication impacts (e.g. Bonsdorff et al. 1997; Worm and Sommer 2000; Bergstrom et al. 2003; Duarte 2009;

Korpinen et al. 2010) moderate nutrient enrichment as a single factor directly benefited microepiphyte biomass (accepting hypothesis 2), but not macroepiphyte biomass. The head start of microepiphytes may be explained by the enrichment status of the system, the competitive ability of microepiphytes, and grazing. The nutrient enrichment treatment comprised a doubling of the study site's low post-bloom summer concentration of dissolved inorganic nutrients. In fact, even in the nutrient enrichment treatment the system remained N-limited containing daily mean concentrations of dissolved inorganic nitrogen and phosphorus below 2 µmol L^{-1} and 1.5 µmol L^{-1}, respectively (Table Appendix II-B). This very moderate concentration of additional resources was probably fastest exploited by single-celled microepiphytes, which are competitively superior not only to perennial macrophytes, but also to filamentous macroepiphytes (Nielsen and Sand-Jensen 1990; Sand-Jensen and Borum 1991). Apart from competition, grazing of particularly *Idotea* spp. and *Gammarus* spp. possibly antagonized macroepiphytic (over-)growth in the nutrient enrichment treatment. Conspicuously, however, microepiphyte biomass increased equally in the nutrient enrichment or greenhouse treatment, despite the respective undisturbed and disrupted top-down control in the treatments. In consistence with former studies, this implies that grazing could not entirely override the effects of even moderately raised nutrient concentrations (Hauxwell et al. 1998; Worm and Lotze 2006). Yet, *F. vesiculosus* biomass was not negatively impacted by the increased microepiphyte biomass under nutrient enrichment as compared to the greenhouse treatment. This might be explained by the relatively moderate increase of microepiphyte biomass controlled by moderately manipulated nutrient concentrations and by undisturbed grazing. However, it may also confirm the negative direct impact of warming on *F. vesiculosus* fitness (see above), which was absent in the nutrient enrichment treatment. Unfortunately, in this study we cannot disentangle the relative importance of these direct and indirect effective pathways.

Combined greenhouse and nutrient enrichment conditions showed additive direct and indirect negative effects on the *Fucus* system (accepting hypothesis 3). Temperature-induced release from grazing pressure and simultaneous elevated resource availability (nutrients) fueled the biomass accumulation of micro- and macroepiphytes by three- and twofold, respectively. The foundation seaweed *F. vesiculosus* showed the steepest biomass decline (80%) due to overgrowth and outcompeting, and potentially due to direct thermal stress. Both stressors (global and local) in combination generated amplified imbalance of the regulatory mechanisms of the *Fucus* system (i.e. bottom-up and top-down control) and thereby promoted the shift from a *Fucus* dominated system towards one dominated by single-celled and opportunistic, filamentous epiphytes. This indicates that future climate change impacts on ecosystems might be underestimated if local perturbations are disregarded.

The loss of canopy forming perennial algae such as *Fucus* or kelp has been shown to trigger changes in the associated ecosystem, including its functioning and services (Wikström and Kautsky 2007; Airoldi et al. 2008; Connell et al. 2008; Gorman and Connell 2009). As for the coastal Baltic Sea, *Fucus* represents the most important large-scale habitat-forming brown-algae. The seaweed and its associated biota provide fundamental functions (e.g. habitat structure, food, shelter) and services, which are also of economic value to humans (e.g. fisheries, recreation, nutrient cycling and storage). Its decline most likely implies a profound change of species diversity and productivity in the rocky littoral zone. A decline of *Fucus* systems and a reduction of their distribution depth could already be observed in the past in response to the eutrophication status of the Baltic Sea (e.g. Elmgren 1989; Eriksson et al. 2002). Consequent nutrient reduction measures implemented in international agreements such as the Water Framework Directive (WFD, European Parliament, 2000) or in the Baltic Sea Action Plan (BSAP, 2007) have only been partially successful so far (HELCOM 2014; BACC 2015). To date, *Fucus* systems remain absent in highly eutrophied areas such as sheltered bays and inlets to the Baltic Sea (HELCOM 2013). Future climate change projections for the Baltic Sea region suggest an increase of the annual mean seawater temperature, higher frequencies of extreme weather events such as heat waves, altered precipitation patterns and runoffs from land (Gräwe et al. 2013; HELCOM 2014; BACC 2015). In this context and in consideration of our previous work showing that seawater warming alone can have detrimental effects on the *Fucus* system, the outcome of this follow-up study strongly encourages an establishment of a good ecological status with respect to eutrophication in the Baltic Sea. With the global 2 °C warming goal potentially not being met, efforts to mitigate local perturbations (such as nutrient enrichment) may limit amplified pressure and, thus, may allow (some) marine ecosystems to resist phase shifts under proceeding global climate change.

Acknowledgments

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Chapter III

Warming has stronger direct than indirect effects on *Fucus vesiculosus*-associated microalgal biomass in spring

Abstract

Climate change studies on marine systems have increasingly provided evidence that indirect effects (i.e. altered species interactions) can play a key role in driving an ecosystem's overall response to proceeding global climate change. However, experimental approaches that simultaneously assess the relative importance of both, direct and indirect effects of environmental factors in multispecies settings across trophic levels are still scarce. Using benthic mesocosms, we mechanistically tested the direct and indirect (here altered top-down control) effects of elevated seawater temperature on *Fucus vesiculosus*-associated microalgae by manipulating temperature and mesograzer presence in a factorial design. In the experiment, warming directly positively affected the total biomass of both, microalgae and mesograzers. Moreover, under the present resource-replete conditions in spring direct effects of warming exerted significantly stronger influence on microalgal growth and total biomass than indirect effects through altered top-down control. In the context of previous experimental work, this outcome adds another challenging aspect to the overarching goal of understanding and predicting climate change effects on ecosystems by suggesting that the effective pathways of an environmental factor (here direct bottom-up and indirect top-down) and the resulting effects on food web processes and functioning of the system can vary in sign and size in dependence on the trophic state of the system and on season.

Introduction

Climate change studies on marine systems have increasingly provided evidence that altered species interactions (i.e. indirect effects) can play a key role in driving an ecosystem's overall response to proceeding global climate change (e.g. Schiel et al. 2004; Traill et al. 2010; Kordas et al. 2011 and references therein; Alsterberg et al. 2013). On the basis of marine food webs, top-down control (grazing) was identified as a crucial interface where direct effects of rising seawater temperature mediate or transfer into indirect effects on primary producers with regard to algal size fractionation, community composition and overall biomass production (Sommer and Lengfellner 2008; O'Connor 2009; Sommer and Lewandowska 2011; Alsterberg et al. 2013; Falkenberg et al. 2014; Brodeur et al. 2015, Werner et al. early view). This indirect pathway of temperature effects was explained by the metabolic theory of ecology (MTE), stating that (bio)chemical reactions in general are stimulated by temperature with metabolic processes of heterotrophs such as feeding, growth and reproduction being activated more strongly than photosynthetic rates of autotrophs (Brown et al. 2004; Allen et al. 2005; Lopez-Urrutia et al. 2006; O'Connor et al. 2009; Carr and Bruno 2013). Based on this, it is generally assumed that marine food webs may face a shift in balance between autotrophic production and heterotrophic consumption under proceeding global warming with potential consequences for the structure and functioning of the associated ecosystem. However, studies involving multiple species across trophic levels that clearly test the relative importance of both direct and indirect temperature effects on primary biomass are still scarce.

We set out to experimentally disentangle the direct and indirect effects of elevated seawater temperature on *Fucus vesiculosus*-associated microalgae. This group of unicellular algae (predominantly diatoms) together with filamentous macroepiphytes exerts strong structuring control in seaweed stands and seagrass meadows of coastal marine habitats. Both epiphytically growing algal groups function as important primary food source on the basis of the seagrass- or seaweed-associated food web (Underwood and Kromkamp 1999; Fredriksen et al. 2005; Lebreton et al. 2011), but then can also impede functioning of the system through overgrowth and outcompeting of the foundation macrophyte (Sand-Jensen 1977; Wallentinus 1984; Schramm and Nienhuis 1996; Worm and Sommer 2000). Dominance of fast-growing epiphytes and competitive exclusion of the foundation species are counterbalanced by the top-down control of mesograzers (Howard 1982; Neckles et al. 1993; Worm et al. 2000; Burkepile and Hay 2006; Valentine and Duffy 2006). In *F. vesiculosus* stands of the southwestern Baltic Sea, the gastropod *Littorina littorea* and the crustaceans *Idotea* spp. and *Gammarus* spp. constitute the most abundant mesograzers with complementary feeding modes and preferences (Parker et al. 1993; Sommer 1999a, b; Lotze 1998). With regard to microalgal biofilms, *L. littorea* exerts the most efficient grazing control by leaving algal-cleared feeding tracks on the substrate (Steneck and Watling 1982; Sommer 1999a, 2000).

Recent work on this common coastal Baltic Sea *F. vesiculosus* – epiphyte – mesograzer system found the ecological balance between competition and consumption to change with elevated seawater temperature (Werner et al. early view). Moreover, top-down regulation (grazing) was found to be one key driver of primary producer biomass under global change scenarios (Werner et al. early view). Warming (Δ+5 °C), however, did not generally strengthen top-down control as is commonly assumed on the basis of MTE. Whereas it intensified consumption in winter, warming exceeded the thermal tolerance limit of two (*Gammarus* spp. and *Idotea* spp.) of the three predominant mesograzer species in summer, leading to significantly weakened top-down control and to intensified overgrowth of the foundation seaweed *F. vesiculosus* by epiphytes. While the temperature effects on algal biomass seemed considerably indirectly driven by altered top-down control, the direct and indirect effective pathways could not be quantitatively partitioned at this point. According to MTE both, heterotrophic metabolism and photosynthesis are stimulated by temperature, though at different activation rates (Brown et al. 2004; Allen et al. 2005; Lopez-Urrutia et al. 2006). Under sufficient resource availability (e.g. inorganic nutrients and light) it is therefore possible that both, the release from grazing pressure and the temperature-enhanced growth of the competitively superior epiphytes led to outcompeting of the seaweed.

In order to further disentangle the effective pathways of warming we conducted a follow-up study in spring 2015 using the same experimental seaweed – epiphyte – mesograzer system while manipulating temperature and grazer presence in a factorial design. We (i) assumed based on MTE predictions, that seawater warming accelerates metabolic processes such as feeding, growth and reproduction in heterotrophic mesograzers and that this effect is reflected in increased total grazer abundance and total grazer biomass. We (ii) expected on the basis of previous findings, that warming has species specific effects on mesograzer abundance and per capita biomass. We (iii) hypothesized that microalgal total biomass is reduced by grazers and that warming intensifies top-down control and therefore indirectly reduces algal total biomass. Lastly, we (iv) hypothesized on the basis of MTE that warming directly increases microalgal growth and total biomass accumulation under the given resource-replete conditions in spring. We expected this direct temperature effect on algal biomass to be stronger in the absence of grazers (i.e. to be offset in their presence).

Methods

Experimental design

The experiment was conducted in the Kiel Outdoor Benthocosms, a permanent experimental facility situated outdoors on a jetty in the Kiel Fjord, Germany. The benthocosms comprise of twelve experimental tanks each holding a water volume of 1.4 m^3. The experimental units are exposed to ambient light and weather conditions year-round. In this experiment, all tanks were filled with non-filtered seawater taken from the Kiel Fjord in close vicinity to the experimental platform and from 1 m depth. The water body was exchanged once per day via a flow-through system, which kept the ambient experimental conditions close to the environmental conditions of the Kiel Fjord. Temperature was controlled via heat exchangers and internal heating elements (Titan 2000, Aqua Medic, Bissendorf, Germany and Schego Titan, 600 Watt, Schemel and Goetz, Offenback/ Main, Germany). Temperature, pH, salinity and oxygen were continuously logged (Profilux sensors 3ex, GHL Advanced Technology, Kaiserslautern, Germany). A detailed technical description of the Kiel Benthocosms, their installation, programming and monitoring can be found in Wahl et al. (2015). Prior to the application of treatments the experimental *F. vesiculosus* systems were established in the benthocosms as described in Werner et al. (early view). Additionally one PVC plate (0.60 x 0.40 m) holding 24 unglazed ceramic tiles (5 x 5 cm) was installed on the wall of each experimental tank. All tiles were facing the same direction and had been pre-colonized by microalgae in the Kiel Fjord for ten days. Similar microalgal starting biomass on the tiles was ensured by testing a subsample of three randomly selected tiles for their chlorophyll a content prior to the placement of tiles into the tanks.

Treatments

Two levels of grazers (present vs. absent) and temperature (ambient vs. elevated) were full-factorially crossed, resulting in a total of four treatment combinations. For the grazer manipulation, the three most important mesograzers of the *Fucus* system (*Idotea* spp., *Gammarus* spp., *Littorina littorea*) were collected, sorted and counted. 29 individuals of *Idotea* spp., 48 *L. littorea* and 225 *Gammarus* spp. were evenly distributed to half of the experimental tanks. Temperature manipulations were chosen according to climate change predictions for the Baltic Sea region (HELCOM 2007; BACC 2008, 2015; Schernewski et al. 2010). The nominal condition of the ambient and elevated temperature treatments did not describe a fixed value, but followed diurnal and seasonal fluctuations (Wahl et al. 2015). The no-grazer treatment (-G) reflected the ambient seawater temperature conditions of the Kiel Fjord while mesograzers were excluded from the experimental communities. The grazer treatment (+G) reflected the ambient temperature of the Kiel Fjord with grazers being present. The elevated temperature no-grazer treatment (+T-G) described a delta value of

ΔT = +5 °C relative to the ambient temperature treatment (see Figure Appendix III-A) in the absence of grazers. The elevated temperature and grazer treatment (+T+G) comprised the same temperature treatment in the presence of grazers. Each treatment combination was replicated three times. The experiment ran for six weeks from March 5th to April 15th 2015.

Sampling and response variables

Microalgal total biomass was expressed as total chlorophyll a content [µg cm^{-2}] (hereafter Chla). Microalgal growth was calculated as growth rate day^{-1} using chlorophyll a measurements: $\mu = \ln(N_2)/\ln(N_1)/(t_2 - t_1)$. During sampling three randomly chosen tiles per tank were sampled. The microalgal material was scraped and rinsed off with a razor blade and a defined volume of sterile filtered seawater (75-80 ml, 0.2 µm), respectively. The removed algal material was pooled and homogenized per experimental unit. About 2 ml of the diluted sample was filtered on pre-combusted Whatman GF/F filters and stored at -20 °C until further analysis. Chlorophyll a analysis was conducted spectrophotometrically according to Jeffrey and Humphrey (1975). During harvest of the experiment all mesograzers were removed from the experimental tanks. They were identified, sorted and counted. A subsample of 15 to 20 individuals per grazer group and experimental unit was taken for the analysis of the final grazer biomass [mg AFDW without shell].

Statistical analyses

Prior to the analysis, data were tested for normal distribution and homogeneity of variances and were transformed if necessary. A full factorial analysis of variance (ANOVA) was then applied to test the main effect of grazers (G) and temperature (T) and their interaction on the total biomass and growth of microalgae. In order to disentangle the effects of grazers and temperature on algal total biomass and growth, a priori planned comparisons of treatments were conducted. More specifically, to test the effect of grazers on total biomass of microalgae according to hypothesis (3) grazer treatments against no-grazer treatments were compared in either ambient or high temperature treatments (i.e. -G vs. +G and +T-G vs. +T+G). Furthermore, to test the effect of temperature on the growth and the total biomass of microalgae according to hypothesis (4) ambient against high temperature treatments were compared in either no-grazer treatments (i.e. -G vs. +T-G) or under grazed conditions (i.e. +G vs. +T+G).

Taking grazer species specific sensitivities to temperature into account, single grazer species responses regarding their abundance and per capita biomass were analyzed using MANOVA. The statistical analyses were conducted using Statistica 6.1 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Elevated seawater temperature significantly increased the total grazer abundance and total grazer biomass (Figure 1; Table Appendix III-B). However, the effect of warming differed between grazer species. Warming significantly increased the abundance of *Gammarus* spp. and the per capita biomass of *Idotea* spp. (Figure 3a, b; Table Appendix III-B). In contrast, warming decreased the per capita biomass of *L. littorea* (Figure 3c; Table Appendix III-B).

The presence of grazers only showed a non-significant trend of a negative main effect on microalgal growth and total biomass (Figure 2; Table Appendix III-C). In contrast to this, seawater warming had a significant positive main effect on microalgal growth and total biomass (Figure 2; Table Appendix III-C).

A priori planned comparison assessing the effect of grazers on microalgal total biomass in ambient or high temperature treatments (i.e. +G vs. -G and +T+G vs. +T-G) turned out non-significant (Table Appendix III-D). Nevertheless, grazing reduced the biomass of microalgae by on average 52 µg Chla cm^{-2} in ambient, and by on average 43 µg Chla cm^{-2} in warm treatments (Figure 2).

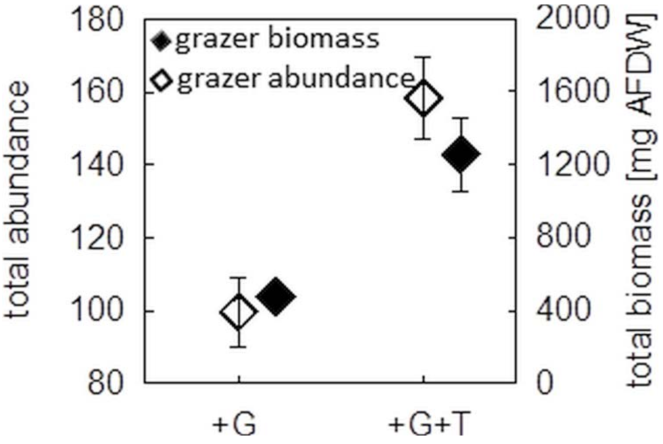

Figure 1. Display (mean ± SE) of the final total grazer abundance (open diamonds) and the final total grazer biomss [mg AFDW without shell] (filled diamonds) in ambient (+G) and high temperature (+G+T) treatments. Sample size (n) was six.

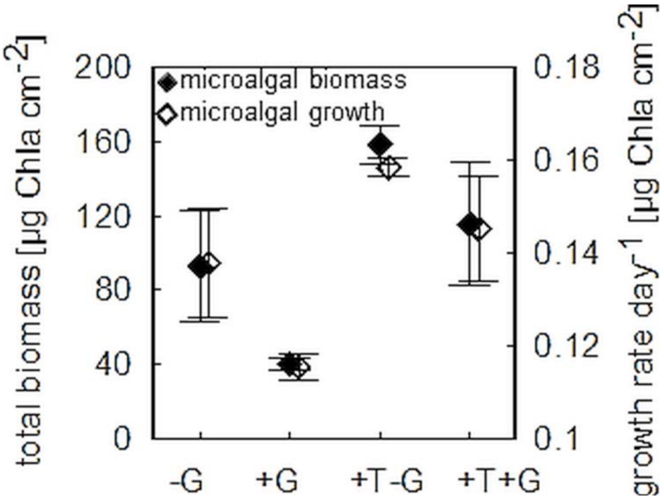

Figure 2. Display (mean ± SE) of the final total biomass and growth rate day-1 of microalgae measured as chlorophyll a [µg cm-2]. Responses are shown for all seawater temperature and grazer manipulations. Treatment combinations are shown as -G: ambient temperature/ grazer absent; +G: ambient temperature/ grazer present; +T-G: high temperature/ grazer absent; +T+G: high temperature/ grazer present. The sample size (n) was twelve.

A priori planned comparison assessing the effect of temperature on microalgal total biomass and growth in non-grazed or grazed treatments revealed a significant positive effect under grazed conditions (i.e. +G vs. +T+G). It revealed only a trend of a positive effect on microalgal total biomass, but no effect on microalgal growth in non-grazed treatments (i.e. -G vs. +T-G) (Table Appendix III-D). Microalgal total biomass in warm treatments showed a slightly steeper increase under grazed conditions (by on average 65 %) in comparison to non-grazed treatments (by on average 41 %) (Figure 2).

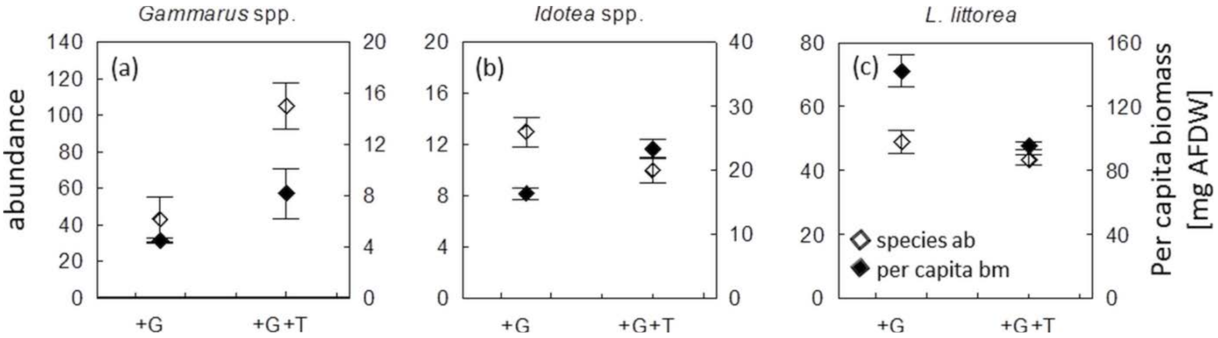

Figure 3. Display (mean ± SE) of the final grazer species specific abundance (open diamonds) and per capita biomass [mg AFDW without shell] (filled diamonds) for (a) *Gammarus* spp., (b) *Idotea* spp. and (c) *L. littorea*, in ambient (+G) and high temperature (+G+T) treatments. Sample size (n) was six.

Discussion

The results indicate that in spring direct effects of seawater warming constitute a more important determinant of microalgal growth and total biomass than indirect effects via altered top-down regulation. In fact, they suggest that in spring combined elevated temperature and grazing can facilitate microalgal biomass accrual. This outcome adds to previous findings by showing that not only the effect sign and size of an environmental factor vary with season (compare Werner et al. early view), but also the relative importance of the direct or indirect effective pathways.

In the experiment the presence of grazers only led to a non-significant reduction of microalgal total biomass and, contrary to expectations, the positive effects of warming on mesograzers did not lead to a stronger depletion of algal total biomass. Moreover, warming increased microalgal biomass by 41 % in the absence of grazers and by 57 % in their presence. This suggests that the direct positive effect of temperature on mesograzers did not translate into significantly higher grazing pressure on microalgae or, if it did, that the direct positive effect of warming on microalgal growth and total biomass exceeded the negative (indirect) effect of enhanced top-down forcing. Both effective pathways can be explained by mesograzer species specific feeding effects and by season.

The applied grazer species naturally co-occur in *F. vesiculosus* belts of the southwestern Baltic Sea. They are known to feed on epiphytes and the foundation seaweed *F. vesiculosus* with, however, differences in their feeding mode and, thus, efficiency (Parker et al. 1993; Lotze 1998; Sommer 1999a, b). More precisely, feeding of the crustaceans *Gammarus* spp. and *Idotea* spp. is described as picking and lawn-mowing, which does not fully remove epiphytic biofilms from the substrate (Lotze 1998; Sommer 1999a). In contrast, feeding by the gastropod *L. littorea* is described as bulldozer-like and more efficient in clearing microalgal biofilms (Sommer 1999a, b, 2000). Warming significantly increased the total abundance and biomass of mesograzers, which indicates enhanced feeding, growth and reproduction and conforms to MTE predictions, stating accelerated metabolism-associated processes in heterotrophs under warming (e.g. Brown et al. 2004; Allen et al. 2005). The response of grazers to warming, however, varied species specifically which can be attributed to species specific differences in life history strategies. The abundance of *Gammarus* spp., for instance, increased by nearly threefold, pointing to enhanced recruitment under warming in spring, which matches an nearly all-season reproductive pattern described for the different species of *Gammarus* in the Baltic Sea (Welton and Clarke 1980; Kolding and Fenchel 1979). In contrast to this, the per capita biomass of *Idotea* spp. doubled, indicating higher individual growth instead of recruitment in warm treatments. This response conforms with life cycle characteristics of the isopod that describe a somatic growth phase in spring prior to recruitment in early summer (Salemaa 1979; Kroer 1989). Contrasting the positive effects on the crustacean mesograzers, warming led to decreased per capita biomass of *L. littorea*, which could indicate reduced physiological fitness of the gastropod. However, *L. littorina* from the same experimental site and in the same experimental set-up (i.e. rate of warming until target temperature was reached) was found unaffected by much higher temperatures in summer (Werner et al. early view), which makes a passing of its thermal tolerance limit in this study unlikely. Additionally, heat coma reactions of the gastropod were described for higher temperatures (~30 °C) (Clarke et al. 2000). Therefore, the decline of *L. littorea*'s per capita biomass may simply be explained by the loss of on average five individuals in warm treatments over the course of the experiment. At the onset, different size classes of the gastropod were evenly distributed among the experimental units and a (statistically non-significant) loss of five large individuals may be reflected in significantly lowered overall per capita biomass of the species. The positive effects of warming on total grazer abundance and biomass suggest that top-down control increased in warm treatments. However, the grazer species specific results reveal that such a change in top-down regulation was primarily driven by the positive effect of warming on both crustacean species, of which the grazing impact was possibly not sufficient to counteract the enhanced biomass accumulation of microalgae in spring. Instead their feeding modes may have even facilitated algal growth by re-opening space without fully clearing the substrate from microalgal cells.

The experiment was conducted in spring, which in temperate regions such as the Kiel Fjord is characterized by blooming of marine autotrophs, because inorganic nutrients, light intensity, photoperiod and temperature constitute less limiting abiotic constraints. At the onset of the experiment inorganic nutrient concentrations comprised about 15 µmol L^{-1} total dissolved inorganic N (including nitrate, nitrite and ammonia), 0.5 µmol L^{-1} Phosphate and 10 µmol L^{-1} Silicate and day length was about 11 hours. Water transparency was not documented but can be assumed sufficient in coastal shallow-water *Fucus* systems in spring (compare time series data on Secchi depth in Lennartz et al. 2014). During the experimental runtime seawater manipulation by delta 5 °C resulted in a relatively constant temperature regime between 10° C and 12 °C in warm treatments. At the experimental site (Kiel Fjord) such temperature levels naturally occur later in spring or early summer, approximately at the beginning of May (monitoring data 2007-2013, Webers et al. in prep). Evidently, this earlier onset of warmer temperatures initiated higher growth, which under the present resource-replete conditions translated into higher total biomass of microalgae. Laboratory studies on temperature - microalgal growth - relationships showed that an increase of temperature closer toward the (size and species specific) optimum in non-limiting conditions can trigger higher growth rates of up to 2.5 doublings day^{-1} in diatoms (Admiraal 1976). Such increase of growth is explained by accelerated enzymatic processes related to the Calvin Cycle during photosynthesis (Raven and Geider 1988). The temperature coefficient Q10 for marine microalgae under light-saturated growth is generally assumed to describe a value near 2, meaning that photosynthesis and the associated cell-division double for each 10 °C increase until unfavorable conditions are reached (Eppley 1972; Raven and Geider 1988). Given that *F. vesiculosus*-associated epiphytes in coastal shallow water zones of the temperate Baltic Sea are adapted to wide temperature ranges across seasons (> 30 °C), it can be assumed that warming by delta 5 °C led to more favorable thermal conditions in spring (rising from 5-7 °C to 10-12 °C) and that the microalgal community was able to make rapid use of the available resources via temperature-driven faster growth which exceeded the counteracting effects of grazing.

The simultaneous manipulation of one abiotic (temperature) and one biotic (grazing) factor in the experiment allowed investigating the relative importance of the direct effects of both factors on microalgal biomass as well as the indirect effects of abiotic change (temperature) through altered trophic interactions (consumption). The results suggest that in spring bottom-up instead of top-down processes constitute a more important driver of

F. vesiculosus-associated microalgal biomass. Related to this, direct effects of seawater warming had a stronger effect on microalgal biomass than indirect effects via altered grazing. It can be assumed that the relative importance of the effective pathways of temperature switches, i.e. that the direct temperature effect on microalgae weakens and indirect temperature effects through altered grazing strengthen, as soon as the carrying capacity of the system is reached and other resources (e.g. nutrients, space, light) limit the accelerated growth and primary biomass accumulation under warming (e.g. O'Connor et al. 2009). However, previous work on the same system showed that the same positive effect of warming on epiphytes (here micro- and filamentous macroepiphytes) can be triggered via indirect effective pathways (i.e. loss of top-down forcing) in summer (Werner et al. early view). In the context of previous experimental work, the present outcome adds another challenging aspect to the overarching goal of understanding and predicting climate change effects on ecosystems by suggesting that the effective pathways of an environmental factor (here direct bottom-up and indirect top-down) and the resulting effects on food web processes and functioning of the system (here the ecological balance between production and consumption) can vary in sign and size in dependence on the trophic state of the system and on season.

Acknowledgments

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Collecting the experimental *F. vesiculosus* systems in the field (Bülk, Kiel Bay).

General conclusion

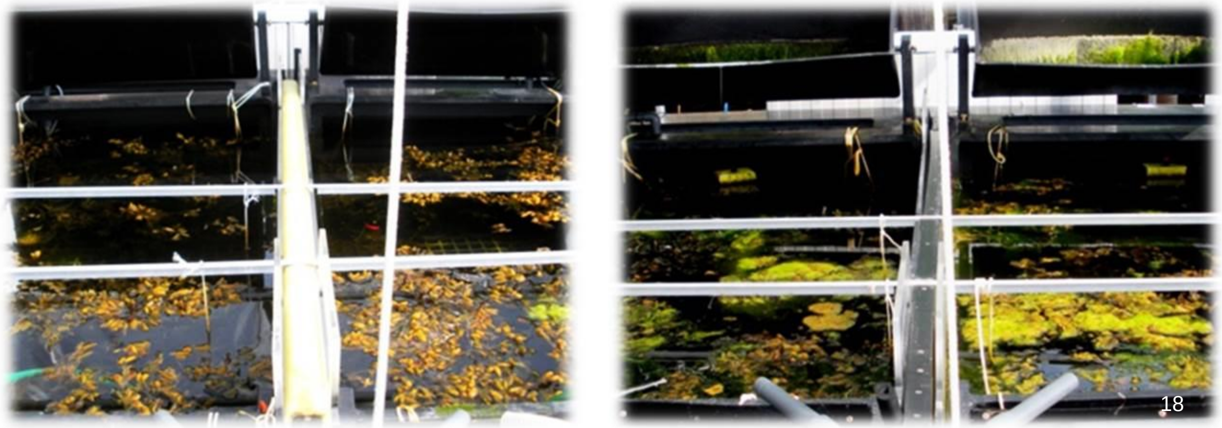
Overall, my studies provide important mechanistic clues about the underlying direct and indirect effective pathways of realistic environmental change in a coastal marine seaweed system. To the best of my knowledge, it is one of the first studies which assessed the seasonal variability of the same environmental factors on the same marine system over the course of one year. The outcome suggests that high seawater CO_2 concentrations predicted for the year 2100 only have minor effects on the tested non-calcifying Baltic Sea seaweed system, which is consistent with findings in Baltic Sea seagrass systems (Eklöf et al. 2012; Alsterberg et al. 2013; Eklöf et al. 2015). In contrast to this, seawater warming alone (global factor), but even more so when combined with nutrient enrichment (local factor), can trigger ecological imbalance in the tested seaweed system by weakening the balancing effect of top-down grazing and/ or by strengthening bottom-up forces that potentially override grazing control. Given that top-down grazing forms a crucial ecological force in coastal vegetated systems in general (e.g. Poore et al. 2012; Montfrans et al. 1984; Eriksson et al. 2009) and considering that coastal and enclosed seas are impacted by anthropogenic nutrient pollution worldwide (Lotze et al 2006; Halpern et al. 2008), the identified driving mechanisms of ecological change, and the detected additive effects of global and local variables may be (to some extent) transferrable to other (temperate) systems or can at least contribute to developing hypotheses for future climate change research on them.

The results of the Chapters I to III clearly show that seawater warming has strong and persistent effects on the tested *F. vesiculosus* system. However, they also show that the sign and size of temperature effects vary with season. I suggest that this seasonal variation in temperature effects can be explained by the seasonal variation in the relative importance of the direct and indirect effective pathways, by which temperature induces ecological change. Related to this, it may be explained by the seasonal variation in the relative importance of the regulating bottom-up and top-down mechanisms in the system.

Mesograzers constitute an important structuring force in coastal marine *F. vesiculosus* systems as they mediate the competitive dominance of epiphytes and other annual algae and thereby promote the maintenance and recruitment of the perennial foundation species (e.g. Worm 2000; Eriksson et al. 2009). In line with this, and consistent with findings in other aquatic or even terrestrial studies (Post and Pedersen 2008; O'Connor 2009; Sommer and Lewandowska 2011; Kratina et al. 2012; Alsterberg et al. 2013; Falkenberg et al. 2014), the results in Chapter I and II show that direct temperature effects on grazers play an important role with regard to the overall temperature effect on the system. Particularly in summer and winter, temperature-induced altered performance of grazers (direct effect) led to cascading (subsequent indirect) effects on epiphytes and the foundation seaweed (Chapter I). It has to be noted, though, that most studies, including mine in Chapter I and II, could not quantitatively partition direct temperature effects on grazers and algae from indirect temperature effects via altered grazer – algae interactions. My follow-up study in Chapter III therefore focused on disentangling both effective pathways of warming in the same experimental system. In line with metabolic theory (Brown et al. 2004; Allen et al. 2005), the study showed that both, metabolic processes of mesograzers and photosynthesis of microalgae, are directly enhanced by warming (inferred from abundance, biomass and growth rates), provided that temperatures do not exceed the thermal tolerance window of either one. It is therefore possible that in summer the conjunction of both, indirect effects (release from grazing pressure) and direct effects (accelerated growth of epiphytes and thermal stress on *F. vesiculosus*) led to the observed epiphytic overgrowth and biomass decline of the foundation species *Fucus* (Chapter I). In the context of the seasonally variable importance of the system's regulating mechanisms (see below), however, altered grazing (i.e. the indirect temperature effect) seems to constitute the main driver of change in the system in summer, whatsoever. In winter, indirect temperature effects via altered grazing clearly represented the most important driver of temperature effects on the foundation seaweed (see below). In contrast to this, direct positive temperature effects on algal biomass were the dominant driver of change in spring (Chapter III, see below),

The seasonal variation in the relative importance of the direct and indirect effects of temperature seems interlinked with the seasonal pattern in the systems' regulating mechanisms, i.e. with the seasonal variation in the relative importance of regulating top-down and bottom-up forces. In summer, maintaining ecosystem processes in coastal marine systems of the southwestern Baltic Sea are generally characterized by strong top-down control, because grazer abundance is high and autotrophic production is increasingly limited by resource depletion. It is plausible that disruption of the main regulating mechanism by warming represented the most important driver of the cascading (indirect) effect on the system (see above). In winter, bottom-up and top-down processes are generally less intense, because autotrophic productivity and heterotrophic activity are low due to decreasing temperatures and light intensities. In winter, seawater warming only affected top-down control, leading to indirect negative effects on the foundation seaweed through intensified grazing (Chapter I). In contrast to this, ecosystem processes in spring are characterized by strong bottom-up regulation as resource-replete conditions fuel high autotrophic productivity, thereby establishing the standing biomass for higher trophic levels. In this bottom-up controlled state of the system in spring, temperature-enhanced grazing did not counteract temperature-enhanced algal growth and biomass production (Chapter III). A similar effect occurred under moderate nutrient enrichment during the warm summer season (Chapter II) and was also observed in field studies on eutrophication effects in the Baltic Sea (Lotze et al. 2000). In summer, strengthened bottom-up forces (nutrient enrichment) led to overcompensation of grazer control and hence to increased biomass of competitively dominant microepiphytes or other fast-growing annual algae (Chapter II, Lotze et al. 2000). Combined warming and moderate enrichment (Chapter II) amplified this effect in summer by shifting the control of epiphytes towards weaker-top down grazing (temperature effect) and stronger bottom-up forces (enrichment and temperature).

Overall, these findings demonstrate a high context-dependency of global climate change effects on an ecosystem and thereby clearly show that our understanding of the basic underlying ecosystems processes and patterns forms a prerequisite for testing, predicting and managing future ecological change in marine ecosystems. Moreover, the results point out that ecological impact of global climate change may be underestimated if local perturbation is disregarded and, thus underline the chance and responsibility of local ecosystem management. Regarding the Baltic Sea, nutrient pollution has been one of the most severe environmental problems for coastal ecosystems (Elmgren 1989; Jansson and Dahlberg 1999; HELCOM 2014) and nutrient reduction measures implemented in international agreements such as the Water Framework Directive (WFD, European Parliament, 2000) or the Baltic Sea Action Plan (BSAP, HELCOM 2007a) have only been partially successful so far. Future climate change projections for the Baltic Sea region suggest an increase of nutrient influxes to coastal waters due to proceeding industrial agriculture and changes in precipitation patterns (BACC 2008, 2015). My findings strongly encourage the establishment of a good ecological status with respect to eutrophication in the Baltic Sea. Due to the oceans large thermal inertia, seawater temperature will continue to rise even if stringent greenhouse gas mitigation measures were bindingly implemented (RCP 2.6) and the 2 °C warming goal was met. Efforts to reduce local perturbation (such as eutrophication) may mediate otherwise amplified pressure on ecosystems and may, thus, promote the resistance and functioning of marine ecosystems under proceeding global climate change.



Development of the experimental *F. vesiculosus* systems in the Kiel Outdoor Benthocosms in an ambient (left) and a high (right) temperature treatment after about ten weeks of experimental runtime in summer 2013.

Outlook

In this thesis I did not account for carry-over effects as the experimental systems were renewed at the onset of each seasonal experiment. However, ecological impacts of global and local climate change factors most likely operate for longer time scales but seasons. In order to clarify the resistance of the *F. vesiculosus* system in consequence of the changes described, it would be of high interest to test if the consequences of altered regulating mechanisms in one season carry over into the following ones and manifest over time, ultimately leading to subtle but lasting re-organization in terms of composition and functioning. For instance, it seems possible that temperature-enhanced grazing on the foundation species *F. vesiculosus* in winter causes reduced fitness at the beginning of the following growing season and, thus, leads to higher competitive dominance of epiphytes. At the same time, temperature-strengthened bottom-up forcing and overcompensation of grazing in spring may weaken as soon as other resources (nutrients) become limiting again (depending on the eutrophication status). A cross-seasonal (December - June) experiment has just been launched in the Kiel Outdoor Benthocosms, potentially completing this series of seasonal experiments by providing answers to the remaining question of carry-over effects.

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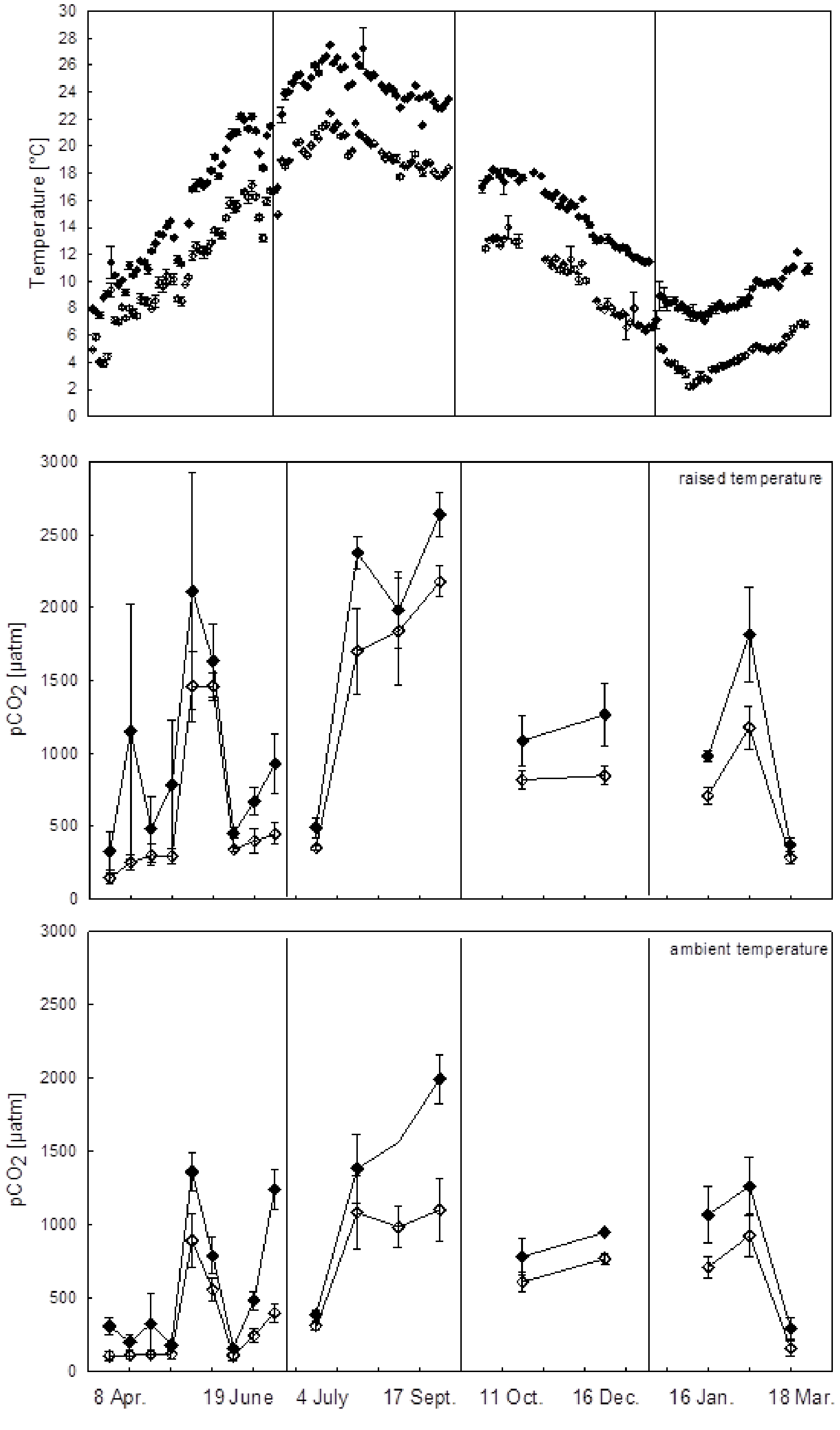
Figure I	Doney, S.C., and D.S. Schimel. 2007. Carbon climate system coupling on timescales from the Precambrian to the Anthropocene. Annu Rev Environ Resour 32: 31-66.
Figure II	Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver, and M. Wehner. 2013. Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Foto 1	*Fucus vesiculosus*, Rolf Nyström; rolfsbild.se
Foto 2	*Gammarus* spp., Roberto Petracini; elacuarista.com
Foto 3	*Idotea* spp., Ingo Arndt; geo.de
Foto 4	*Littorina* spp., Paul Morris; gbif.org
Foto 5	*Spirogyra* spp., n.n.; aquarium.kosmos.de
Foto 6	*Elachista fucicola*, Anne Frijsinger & Mat Vestjens; meerwasser-lexikon.de
Foto 7	*Chladophora* spp., n.n.; visayards.com
Foto 8	*Pilayella littoralis*, Dr. Joe Costa; buzzardsbay.org
Foto 9	*Pilayella* spp., n.n.; balticseaweed.com
Foto 10	epiphytic red algae, n.n.; naszbaltyk.pl
Foto 11	*Eunotia* spp., n.n.; photomacrography1.net
Foto 12-14	*Asterionella* spp., *Licmophora* spp., *Cocconeis* spp., Franziska J. Werner

Foto 15	Kiel Outdoor Benthocosms, Pewe R-Mediabase
Foto 16	Two benthocosm tanks, Angelika Graiff
Foto 17	Field work, Angelika Graiff
Foto 18	Response of the experimental systems, Franziska J. Werner

Appendix

Chapter I

Appendix I-A. Display of the seawater temperature [°C] and pCO_2 [µatm] treatments in the four seasonal experiments from early summer 2013 to winter/ spring 2014.



Appendix I-B List of the initial total and species specific amount of grazers distributed per experimental unit in early summer, late summer, fall/ winter and winter/spring. The amount of grazers added varied between experiments according to the natural variability of their abundance across seasons.

	Total grazers added per exp. unit	*Littorina littorea*	*Idotea* spp.	*Gammarus* spp.
Early summer	119	39	50	30
Late summer	358	143	22	193
Fall/ winter	130	35	69	26
Winter/ spring	218	30	39	149

Appendix I-C Description of the effects of increased seawater [CO_2] in late summer and fall/ winter

In our study effects of [CO_2] were weak and inconsistent in that they occurred only in late summer and fall/ winter. That is, [CO_2] increased the biomass of *Fucus vesiculosus* and the per capita biomass of *Idotea* spp. in late summer, however, the proportion of explained total variances (ω^2) by [CO_2] was low (Table 1, Appendix I-D). An interaction effect of [CO_2] x temperature affected the total biomass of grazers in late summer (Figure 1n) but it explained only a very low amount of the total variance (ω^2, Table 1, Appendix I-D). Likewise the generally very low biomass of macroepiphytes in fall/ winter was significantly affected by an interaction effect of [CO_2] and temperature (Table 1, Appendix I-D).

Appendix I-D ANOVA and MANOVA results for the late summer experiment explaining the effects of seawater [CO_2], temperature and their interaction on total grazer abundance (ab), total grazer biomass (bm), the biomass (bm) of microepiphytes, macroepiphytes and *Fucus vesiculosus* (*Fucus*), individual grazer species abundance (*L. littorea* ab, *Idotea* spp. ab, *Gammarus* spp. ab) and on the per capita biomass (per capita bm) of each grazer species. Omega squared (ω^2) indicates the effect size of the factors. Sample size (*n*) was twelve.

Late summer				
Variable	**Factor**	**F $_{(1, 8)}$**	***p*-value**	**ω^2**
Total grazer ab	CO_2	1.25	0.30	
	Temp	21.39	**<0.01**	0.63
	CO_2 x Temp	0.67	0.43	
SQRT total grazer bm [g AFDW]	CO_2	0.31	0.59	
	Temp	152.01	**<0.001**	0.90
	CO_2 x Temp	6.45	**<0.05**	0.03
Ln microepiphyte bm [pg C]	CO_2	0.76	0.41	
	Temp	22.30	**<0.01**	0.66
	CO_2 x Temp	0.30	0.60	
Ln macroepiphyte bm [g FW]	CO_2	1.17	0.31	
	Temp	6.28	**<0.05**	0.31
	CO_2 x Temp	0.49	0.50	
Ln *Fucus* bm [g FW]	CO_2	14.22	**<0.01**	0.10
	Temp	114.92	**<0.001**	0.82
	CO_2 x Temp	0.18	0.68	
Ln *Idotea* spp. ab	CO_2	0.54	0.48	
	Temp	40.54	**<0.001**	0.78
	CO_2x Temp	0.80	0.40	
SQRT *Gammarus* spp. ab	CO_2	2.14	0.18	
	Temp	9.94	**<0.05**	0.40
	CO_2 x Temp	1.23	0.30	
Ln *L. littorea* ab	CO_2	2.70	0.14	
	Temp	0.38	0.55	
	CO_2 x Temp	0.16	0.70	
LN per capita bm *L. littorea* [mg AFDW]	CO_2	1.40	0.27	
	Temp	7.78	**<0.05**	0.32
	CO_2 x Temp	2.88	0.13	
Per capita bm *Idotea* spp.[mg AFDW]	CO_2	5.82	**<0.05**	0.27
	Temp	2.94	0.12	
	CO_2 x Temp	0.05	0.82	
Per capita bm *Gammarus* spp. [mg AFDW]	CO_2	1.04	0.34	
	Temp	2.04	0.19	
	CO_2 x Temp	0.09	0.77	

Appendix I-E ANOVA and MANOVA results for the fall/ winter experiment explaining the effects of seawater [CO_2], temperature and their interaction on total grazer abundance (ab), total grazer biomass (bm), the biomass (bm) of microepiphytes, macroepiphytes and *Fucus vesiculosus* (*Fucus*), individual grazer species abundance (*L. littorea* ab, *Idotea* spp. ab, *Gammarus* spp. ab) and on the per capita biomass (per capita bm) of each grazer species. Omega squared (ω^2) indicates the effect size of the factors. Sample size (*n*) was twelve.

Fall/ winter				
Variable	**Factor**	**$F_{(1, 8)}$**	***p*-value**	**ω^2**
Total grazer ab	CO_2	0.05	0.83	
	Temp	15.80	**<0.01**	0.59
	CO_2 x Temp	0.43	0.53	
Total grazer bm [g AFDW]	CO_2	0.18	0.68	
	Temp	39.81	**<0.001**	0.77
	CO_2 x Temp	1.16	0.31	
Ln *Idotea* spp. ab	CO_2	0.09	0.77	
	Temp	7.44	**<0.05**	0.38
	CO_2 x Temp	0.44	0.53	
Gammarus spp. ab	CO_2	0.03	0.88	
	Temp	8.58	**<0.05**	0.39
	CO_2 x Temp	1.62	0.24	
L. littorea ab	CO_2	1.87	0.21	
	Temp	2.55	0.15	
	CO_2 x Temp	1.87	0.21	
Ln per capita bm *L. littorea* [mg AFDW]	CO_2	0.10	0.76	
	Temp	0.11	0.75	
	CO_2 x Temp	0.32	0.59	
Ln per capita bm *Idotea* spp.[mg AFDW]	CO_2	0.00	0.97	
	Temp	132.42	**<0.001**	0.93
	CO_2 x Temp	0.00	0.96	
Per capita bm *Gammarus* spp. [mg AFDW]	CO_2	1.23	0.30	
	Temp	3.58	0.09	0.17
	CO_2 x Temp	0.94	0.36	
Ln microepiphyte bm [pg C]	CO_2	0.82	0.39	
	Temp	0.00	0.96	
	CO_2 x Temp	0.26	0.62	
Ln macroepiphyte bm [g FW]	CO_2	0.11	0.75	
	Temp	0.23	0.64	
	CO_2 x Temp	11.27	**<0.01**	0.50
SQRT *Fucus* bm [g FW]	CO_2	0.25	0.63	
	Temp	5.67	**<0.05**	0.31
	CO_2 x Temp	0.01	0.93	

Appendix I-F ANOVA and MANOVA results for the winter/ spring experiment explaining the effects of seawater [CO_2], temperature and their interaction on total grazer abundance (ab), total grazer biomass (bm), the biomass (bm) of microepiphytes, macroepiphytes and *Fucus vesiculosus* (*Fucus*), individual grazer species abundance (*L. littorea* ab, *Idotea* spp. ab, *Gammarus* spp. ab) and on the per capita biomass (per capita bm) of each grazer species. Omega squared (ω^2) indicates the effect size of the factors. Sample size (*n*) was twelve.

Winter/ spring				
Variable	**Factor**	**F $_{(1, 8)}$**	***p*-value**	ω^2
Ln total grazer ab	CO_2	0.06	0.81	
	Temp	62.43	**<0.001**	0.84
	CO_2 x Temp	1.30	0.29	
Ln total grazer bm [g AFDW]	CO_2	0.15	0.70	
	Temp	19.25	**<0.01**	0.64
	CO_2 x Temp	0.02	0.88	
Idotea spp. ab	CO_2	0.02	0.90	
	Temp	4.71	0.06	0.24
	CO_2 x Temp	1.61	0.24	
Ln *Gammarus* spp. ab	CO_2	0.05	0.83	
	Temp	59.29	**<0.001**	0.84
	CO_2 x Temp	1.03	0.34	
L. littorea ab	CO_2	1.17	0.31	
	Temp	0.09	0.77	
	CO_2 x Temp	0.15	0.71	
Per capita bm *Idotea* spp. [mg AFDW]	CO_2	1.72	0.23	
	Temp	21.74	**<0.01**	0.62
	CO_2 x Temp	0.91	0.37	
SQRT per capita bm *Gammarus* spp. [mg AFDW]	CO_2	0.02	0.89	
	Temp	10.0	**<0.05**	0.46
	CO_2 x Temp	0.61	0.46	
Per capita bm *L. littorea* [mg AFDW]	CO_2	2.89	0.13	
	Temp	0.00	0.99	
	CO_2 x Temp	2.62	0.14	
Ln microepiphyte bm [pg C]	CO_2	0.00	0.97	
	Temp	0.97	0.35	
	CO_2 x Temp	1.13	0.32	
Ln macroepiphyte bm [g FW]	CO_2	0.26	0.62	
	Temp	0.09	0.77	
	CO_2 x Temp	0.19	0.68	
Fucus bm [g FW]	CO_2	1.87	0.21	
	Temp	0.03	0.87	
	CO_2 x Temp	1.37	0.27	

Appendix I-G ANOVA and MANOVA results for the early summer experiment explaining the effects of seawater [CO_2], temperature and their interaction on total grazer abundance (ab), total grazer biomass (bm), the biomass (bm) of microepiphytes, macroepiphytes and *Fucus vesiculosus* (*Fucus*), individual grazer species abundance (*L. littorea* ab, *Idotea* spp. ab, *Gammarus* spp. ab) and on the per capita biomass (per capita bm) of each grazer species. Omega squared (ω^2) indicates the effect size of the factors. Sample size (*n*) was twelve.

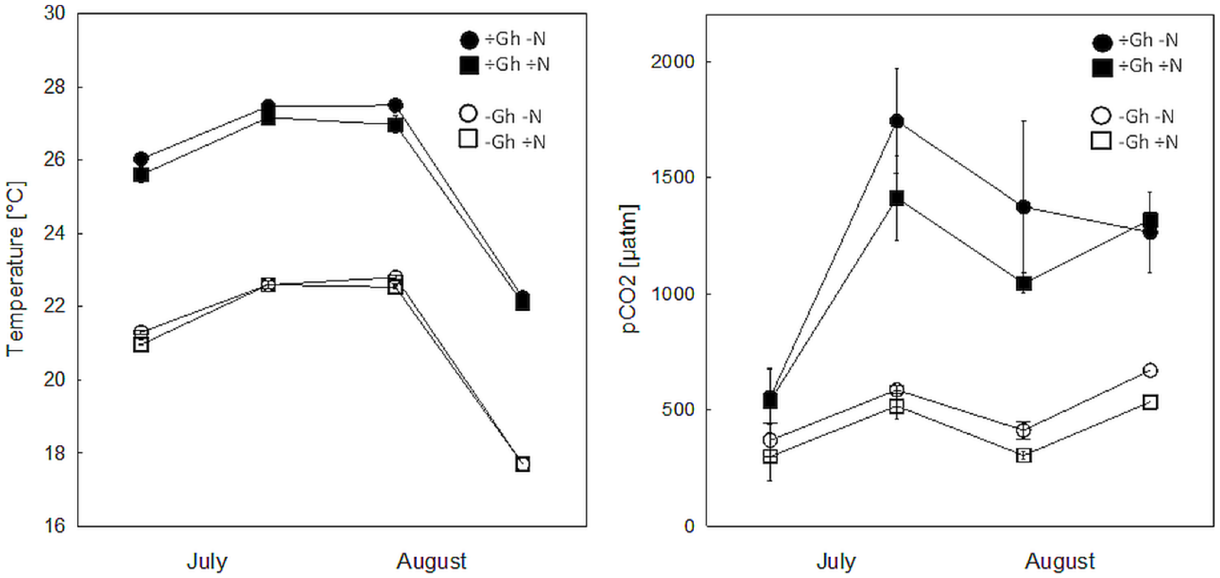
Early summer				
Variable	**Factor**	**F $_{(1, 8)}$**	***p*-value**	ω^2
Total grazer ab	CO_2	0.34	0.58	
	Temp	1.99	0.19	
	CO_2 x Temp	0.49	0.50	
Ln total grazer bm [g AFDW]	CO_2	1.64	0.24	
	Temp	2.07	0.19	
	CO_2 x Temp	0.03	0.88	
Ln *Idotea* spp. ab	CO_2	0.39	0.55	
	Temp	55.03	**<0.001**	0.83
	CO_2 x Temp	0.54	0.48	
Gammarus spp. ab	CO_2	0.02	0.89	
	Temp	0.25	0.63	
	CO_2 x Temp	0.11	0.75	
L. littorea ab	CO_2	0.00	0.97	
	Temp	1.43	0.26	
	CO_2 x Temp	0.75	0.41	
Ln per capita bm *Idotea* spp.[mg AFDW]	CO_2	0.02	0.90	
	Temp	13.73	**<0.01**	0.55
	CO_2 x Temp	0.26	0.62	
Per capita bm *Gammarus* spp. [mg AFDW]	CO_2	1.75	0.22	
	Temp	1.69	0.23	
	CO_2 x Temp	0.00	0.98	
Per capita bm *L. littorea* [mg AFDW]	CO_2	1.88	0.21	
	Temp	0.12	0.73	
	CO_2 x Temp	0.77	0.41	
Microepiphyte bm [pg C]	CO_2	1.01	0.34	
	Temp	0.15	0.71	
	CO_2 x Temp	1.09	0.32	
Fucus bm [g FW]	CO_2	1.96	0.19	
	Temp	3.17	0.11	
	CO_2 x Temp	0.38	0.55	
Macroepiphyte bm [g FW]	CO_2	0.20	0.66	
	Temp	31.56	**<0.001**	0.72
	CO_2 x Temp	1.55	0.25	

Appendix I-H Results of Pearson's correlation computed for response variables that were significantly affected by elevated seawater temperature in late summer, fall/ winter and early summer. Listed are only the results showing a significant or a trend of a significant correlation.

Factor	***n***	**r (x,y)**	**t**	***p*-value**
Late summer				
Total grazer ab, Ln microepiphytes bm [pg C]	12	-0.76	-3.67	**<0.01**
Total grazer bm [g AFDW], Ln microepiphytes bm [pg C]	12	-0.81	-4.39	**<0.01**
Total grazer ab, Ln macroepiphyte bm [g DW]	12	-0.33	-1.12	0.29
Total grazer bm [g AFDW], Ln macroepiphyte bm [g DW]	12	-0.60	-2.38	**<0.05**
Total grazer ab, *Fucus* bm [g FW]	12	0.60	2.35	**<0.05**
Total grazer bm [g AFDW], *Fucus* bm [g FW]	12	0.87	5.66	**<0.001**
Fucus bm [g FW], Ln microepiphyte bm [pg C]	12	-0.69	-3.05	**<0.05**
Fucus bm [g FW], Ln macroepiphyte bm [g DW]	12	-0.77	-3.87	**<0.01**
Ln *Idotea* spp. ab, Ln microepiphyte bm [pg C]	12	-0.81	-4.42	**<0.01**
SQRT *Gammarus* spp. ab, Ln microepiphyte bm [pg C]	12	-0.70	-3.12	**0.01**
Idotea spp. per capita bm [mg AFDW], Ln *Fucus* bm [g FW]	12	0.70	3.13	**0.01**
Ln *L. littorea* per capita bm [mg AFDW], Ln Fucus bm [g FW]	12	0.71	3.18	**<0.01**
Fall / winter				
Ln *Idotea* spp.per capita bm [mg AFDW], SQRT *Fucus* bm [g FW]	12	-0.56	-2.16	0.055
Early summer				
Ln *Idotea* spp. ab, Ln macroepiphyte bm [g FW]	12	0.58	2.24	**<0.05**

Chapter II

Appendix II-A Display of the temperature [°C] and pCO$_2$ [µatm] levels combined in the greenhouse (Gh) treatment. Shown are the measurements for all treatment combinations: high temperature/ pCO$_2$ (+Gh) are represented by the filled symbols. Ambient temperature/ pCO$_2$ (-Gh) are represented by the open symbols. Moderate nutrient enrichment (+N) is represented by the squares.



Appendix II-B Mean concentration of the dissolved inorganic nutrients nitrate (N), phosphate (P), silicate (Si) in the ambient and the nutrient enrichment treatment. Nutrient enrichment comprised a doubling of the natural mean concentrations of the dissolved inorganic nutrients in the Kiel Fjord averaged over the respective months July and August over the past seven years.

	Dissolved inorganic nutrients [µmol L^{-1}]			
	July		August	
	ambient	enriched	ambient	enriched
NO$_3$	0.9	1.5	1.1	1.9
PO$_4$	0.5	1.0	0.6	1.3
SiO$_4$	15.4	28.8	18.7	35.3

Appendix II-C List of the total and species specific amount of grazers added to each experimental unit at the onset of the experiment.

Total amount of mesograzers added per exp. unit	*Littorina littorea*	*Idotea* spp.	*Gammarus* spp.
257	147	26	84

Appendix II-D ANOVA and MANOVA results explaining the effects of the greenhouse treatment and nutrient enrichment and their interaction on total grazer abundance (ab), total grazer biomass (bm), individual grazer species' biomass (*Idotea* spec. bm, *Gammarus* spec.bm, *L. littorea* spec.bm), the biomass (bm) of microepiphytes, macroepiphytes and *Fucus vesiculosus* (Fucus). Omega squared (ω^2) indicates the effect size of the factors.

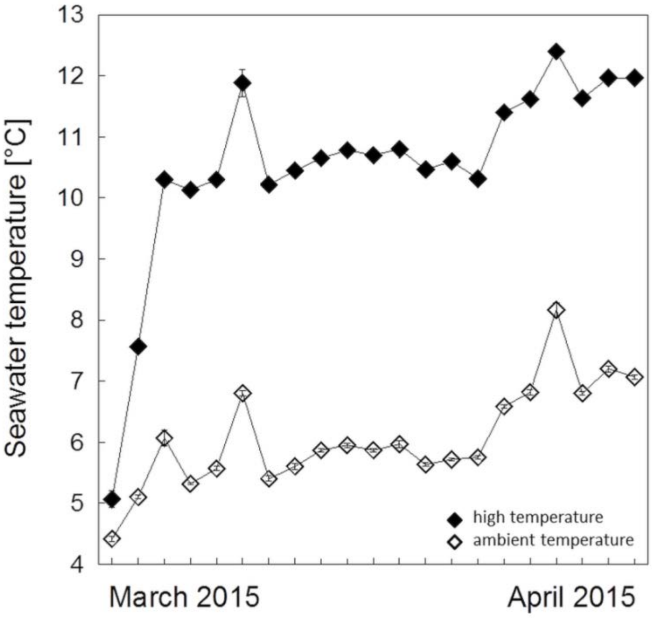
Variable	**Factor**	**$F_{1,8}$**	***p***	**ω^2**
Total grazer ab (log)	Gh	1.02	0.34	
	Nutr	0.63	0.45	
	Gh x Nutr	0.52	0.49	
Total grazer bm [g AFDW]	Gh	2.93	0.13	
	Nutr	0.24	0.64	
	Gh x Nutr	0.26	0.62	
Idotea spec. bm [log AFDW]	Gh	51.20	**<0.001**	0.83
	Nutr	0.16	0.70	
	Gh x Nutr	0.03	0.86	
Gammarus spec. bm [log AFDW]	Gh	12.72	**<0.05**	0.49
	Nutr	1.52	0.25	
	Gh x Nutr	0.47	0.51	
L. littorea bm [AFDW]	Gh	1.17	0.31	
	Nutr	0.17	0.69	
	Gh x Nutr	0.35	0.57	
microepiphyte bm [log Chla μg/L]	Gh	9.5	**<0.05**	0.29
	Nutr	10.59	**<0.05**	0.33
	Gh x Nutr	0.21	0.66	
macroepiphyte bm [g FW]	Gh	3.63	0.09	0.19
	Nutr	0.32	0.59	
	Gh x Nutr	1.25	0.30	
Fucus bm [log g FW]	Gh	56.99	**<0.001**	0.75
	Nutr	1.6	0.24	
	Gh x Nutr	6.74	**<0.05**	0.08

Appendix II-E Results of Pearson's correlation calculated for response variables that were significantly affected by the greenhouse treatment and/or nutrient enrichment. Listed are only the results showing a significant or a trend of a significant correlation.

Factor	***n***	***r* $_{(x,y)}$**	***t***	***p***
Fucus bm [log g FW], Microepiphyte bm [log µg Chla L^{-1}]	12	-0.629	-2.5588	**0.038**
Fucus bm [log g FW], Macroepiphyte bm [g DW]	12	-0.567	-2.1823	0.054
Fucus bm [log g FW], *Idotea* spp. bm [log AFDW]	12	0.884	5.9818	**0.0001**
Fucus bm [log g FW], *Gammarus* spp. bm [log AFDW]	12	0.639	2.6272	**0.025**
Microepiphyte bm [log µg Chla L^{-1}], *Idotea* spp. bm [log AFDW]	12	-0.6641	-2.809	**0.018**
Microepiphyte bm [log µg Chla L^{-1}], *Gammarus* spp. bm [log AFDW]	12	-0.3186	-1.0633	0.312
Macroepiphyte bm [g DW], *Idotea* spp. bm [log AFDW]	12	-0.5058	-1.8545	0.093
Macroepiphyte bm [g DW], *Gammarus* spp. bm [log AFDW]	12	-0.6976	-3.0792	**0.012**

Chapter III

Appendix III-A Display of the seawater temperature [°C] in ambient and high temperature treatments over the course of the experimental runtime from March 5th to April 15th 2015.



Appendix III-B ANOVA results explaining the effects of temperature (temp) on total grazer abundance (ab) and total grazer biomass (bm) [mg AFDW without shell] as well as on the abundance (ab) and the per capita biomass (per capita bm) [mg AFDW individual^{-1} without shell] of each grazer species (*L. littorea, Gammarus* spp. and *Idotea* spp.). Sample size (n) was six.

Variable	**Factor**	**MS**	**$F_{1,4}$**	***p***
Total grazer ab	temp	4266.7	15.5907	**0.02**
Total grazer bm	temp	914311	13.70588	**0.02**
Gammarus spp. ab	temp	5766.00	12.68647	**0.02**
Gammarus spp. per capita bm	temp	0.085211	0.0742	0.79
Idotea spp. ab	temp	13.5000	3.8571	0.12
Idotea spp. per capita bm	temp	73.506	15.3737	**0.02**
L. littorea ab	temp	48.17	2.0352	0.23
L. littorea per capita bm	temp	3260.04	20.8761	**0.01**

Appendix III-C ANOVA results explaining the effects of temperature (temp) and grazers and their interaction on microalgal total biomass [µg cm^{-2} chlorophyll a] and on microalgal growth [µg cm^{-2} chlorophyll a day^{-1}]. Sample size (n) was twelve.

Variable	**Factor**	**MS**	**$F_{3,8}$**	***p***
Microalgae total biomass	temp	924.05	9.419	**0.015**
	grazer	421.15	4.293	**0.072**
	temp x grazer	4.398	0.045	0.839
Microalgae growth	temp	0.002	8.973	**0.018**
	grazer	0.001	4.489	0.067
	temp x grazer	0.00006	0.290	0.605

Appendix III-D A priori planned comparisons explaining the effects of grazers and temperature on microalgal total biomass [µg cm^{-2} chlorophyll a] and the effects of temperature on microalgal growth [µg cm^{-2} chlorophyll a day^{-1}] . Grazer effects on microalgal total biomass were tested by comparing none-grazed with grazed treatments in either ambient (i.e. -G vs. +G) or high temperature (i.e. +T-G vs- +T+G) treatments. Temperature effects on microalgal total biomass and growth were tested by comparing ambient and high temperature treatments under either none-grazed (i.e. -G vs. +T-G) or grazed (i.e. +G vs. +T+G) conditions.

Variable	Comparison	MS	$F_{1,8}$	***p***
Microalgal total biomass	-G vs. +G	255.81	2.608	0.145
	+T+G vs. +T-G	169.74	1.73	0.225
	+G vs. +T+G	527.97	5.382	**0.049**
	-G vs. +T-G	400.47	4.082	0.078
Microalgae growth	+G vs. +T+G	4.27	6.65	**0.033**
	-G vs. +T-G	1.67	2.603	0.145

Danksagung

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Curriculum Vitae

Name:	Franziska Julie Werner
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1985 – 1989	Grundschule Ambachtal, Herborn-Burg
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Studium

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2007	Erstes Staatsexamen Englisch, Biologie, Bilingual Education (Subject Matter Teaching in English)
2004 – 2005	Hawai’i Pacific University, Honolulu, Hawai’i, USA Marine Biologie, Englisch
2008 – 2010	Institut für Meereswissenschaften (IFM-GEOMAR), Kiel Biologische Ozeanographie
2010	Master of Science (MSc)
Seit Sept. 2012	Promotion am GEOMAR Helmholtz Zentrum für Ozeanforschung, Kiel Experimentelle Ökologie und Nahrungsnetze Thema: Effekte des Klimawandels (Erwärmung und Ozeanversauerung) auf das küstennahe *Fucus vesiculosus* Ökosystem der südwestlichen Ostsee (BMBF, BIOACID II)

Publikationen

Werner, F.J., B. Matthiessen. 2013. Temperature indirectly affects benthic microalgal diversity by altering effects of top-down but not bottom-up control. Oikos.122: 53-62.

Brakel, J., F.J. Werner, V. Tams, T.B.H. Reusch, A.-C. Bockelmann. 2014. Current European Labyrinthula zosterae are not virulent and modulate seagrass (Zostera marina) defense gene expression. PLOS ONE DOI: 10.1371/journal.pone.0092448.

Werner, F.J., A. Graiff, B. Matthiessen. 2015. Temperature effects on seaweed-sustaining top-down control vary with season. Oecologia *(online first)*.

Werner, F.J., A, Graiff, B. Matthiessen. *(in review).* Even moderate nutrient enrichment negatively adds up to global climate change effects on a habitat-forming seaweed system.

Werner, F.J., B. Matthiessen. *(in review)*. Warming has stronger direct than indirect effects on Fucus vesiculosus-associated microalgal biomass in spring.

Auszeichnungen

2005	Mark David Bauer Awards for Environmental Writing (Research), Hawai'i Pacific University, Honolulu, Hawai'i, USA
2012	Best Poster Award, 3rd Young Scientists Excellence Cluster Conference, Kiel

Description of the individual scientific contribution to the multiple-author publications and experimental work

The chapters of this thesis are partly published (chapter I) or in review (chapter II and III) in scientific journals and contain multiple authorships. The list below serves as a clarification of my personal contribution to the publications.

Chapter I:
Temperature effects on seaweed-sustaining top-down control vary with season.
Authors: Franziska Julie Werner, Angelika Graiff, Birte Matthiessen
Published in *Oecologia* (online first)
Contribution: FJW, BM, and AG designed the study. FJW and AG conducted the experiments and analyzed the data. BM provided funding and intellectual input to the analysis. FJW and BM discussed the results. FJW wrote the manuscript with contributions from BM.

Chapter II:
Even moderate nutrient enrichment negatively adds up to global climate change effects on a habitat-forming seaweed system
Authors: Franziska Julie Werner, Angelika Graiff, Birte Matthiessen
Under Review in *Limnology and Oceanography*
Contribution: FJW, BM, and AG designed the study. FJW and AG performed the experiments and analyzed the data. BM provided funding and intellectual input to the analysis. FJW and BM discussed the results. FJW wrote the manuscript with contributions from BM.

Chapter III:
Warming has stronger direct than indirect effects on *Fucus vesiculosus*-associated microalgal biomass in spring
Authors: Franziska Julie Werner, Birte Matthiessen
Under Review in *Marine Ecological Progress Series*
Contribution: FJW and BM discussed the ideas for this study. FJW conducted the experiment. BM provided funding and intellectual input to the analysis. FJW and BM discussed the results. FJW wrote the manuscript with contributions from BM.

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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation, abgesehen von der Beratung meiner Betreuer, selbstständig von mir angefertigt wurde und dass sie nach Form und Inhalt meine eigene Arbeit ist. Sie ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden und wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Biologische Meereskunde erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.