

Habitat-Forming Seaweeds in a Changing Climate

Doctoral Thesis

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*“When you’re curious, you find
lots of interesting things to do.”*
– Walt Disney

ABSTRACT

Climate change is an umbrella term encompassing some of the largest and most potent selective pressures currently acting on ecosystems. It can have diverse effects on marine systems; the most powerful of which are changes to salinity through altered patterns of precipitation and evaporation, temperature through increased global temperature, and pH through the dissolution of CO₂ into seawater where it ultimately reacts with water to form carbonate (CO₃²⁻) and hydrogen ions (2H⁺). All these changes may impact marine organisms, in particular above the thermocline and in coastal waters. The studies included in this thesis were all performed in or close to the transition zone between the North Sea and the Baltic Sea. This area is a shallow coastal water mass influenced by the fully oceanic North Sea and the brackish Baltic Sea. Brown seaweeds are important habitat-forming seaweeds in this area, and bladderwrack (*Fucus vesiculosus*) is one of the most widespread and abundant.

The general objective of this thesis is to evaluate the effects of climate change on habitat-forming seaweeds in a coastal area and to experimentally address the complexity caused by the multiple factors changing simultaneously as a consequence of climate change. For example, including both separate and interactive effects of changes in seawater temperature, pH, salinity, and grazing pressure on both adult and early life stages of primarily *Fucus vesiculosus* in the experiments. By conducting field and lab experiments and combining physiological, chemical, and genetic approaches, I detect different aspects of responses to climate induced stress.

My findings show that *F. vesiculosus* responds to climate change variables differently in different populations, and it responds to combinations of variables in ways that are not easily predicted based on experiments with single variables. I found that this seaweed will likely increase in growth by area but not weight under future climate change, and that its ability to induce chemical defence to grazing will be dramatically reduced. Furthermore, I found that *F. vesiculosus* and two other species of brown seaweeds may reduce their calcium content and tissue strength, which leads to increased risk of physical damage from storms and grazing and could result in population declines. This could in turn lead to significant effects on coastal ecosystems, and if these patterns are also true for other habitat-forming species they could have wide-reaching effects.

Keywords: Ocean acidification, warming, freshening, temperature, salinity, pH, pCO₂, *Fucus vesiculosus*, phlorotannins, grazing, tissue resilience, macroalgae.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Klimatförändringar innebär en kraftig utmaning speciellt för marina ekosystem. De mest påtagliga effekterna kommer av förändringar i temperatur, pH och salthalt i haven. Effekter på habitatskapande arter kan ha vittgående konsekvenser för hela ekosystem. *Fucus vesiculosus*, blåstång, har en nyckelroll i strandnära ekosystem. Grunda kustnära ekosystem är speciellt sårbara och känsliga för förändringar eftersom de har mindre vattenvolym. Studierna i denna avhandling utfördes alla i eller nära övergångszonen mellan Nordsjön och Östersjön, en av världens största vattenmassor med brackvatten.

Växthusgaser, som koldioxid, i atmosfären leder till ökade temperaturer. Ökade koldioxidutsläpp leder också till försurning av haven eftersom det bildas kolsyra när koldioxiden löses i vattnet. Salthalten är en annan faktor som påverkas av klimatförändringar; resultatet blir antingen ökad eller sänkt salthalt i olika områden.

Syftet med denna avhandling var att utvärdera effekterna av klimatförändringar på habitatbildande tång i kustområden som påverkas mer än de flesta andra marina områden i världen. Eftersom klimatpåverkan är multifaktoriell har jag inkluderat både separata och interaktiva effekter av havstemperatur, pH, salthalt och betning på både tidiga och vuxna livsstadier av tång, främst blåstång. Genom att kombinera fysiologiska, kemiska och genetiska frågeställningar i både fält- och laboratorie-experiment försökte jag upptäcka olika aspekter av klimatinducerad stress.

Resultaten visade att tångens vävnader påverkas och blir försvagade, vilket visades genom drag- och trycktester. Kalciuminnehållet i vävnaderna minskade och halten av florotanniner, ett ämne som skyddar mot betare, blev lägre när tången utsattes för lägre salthalt. Experiment med betare visade att snäckor som hade utsatts för ökad koldioxidhalt betade mindre.

Tidiga livsstadier av blåstången påverkades av ökad koldioxidhalt, ökad temperatur, eller kombinationen av dessa faktorer, vilket tyder på att deras fortplantning påverkas av klimatförändringar. Denna avhandling visar att klimatförändring, framförallt genom ändrad temperatur, koldioxid och salthalt påverkar habitatbildande tång och att effekten skiljer sig mellan olika populationer och livsstadier av samma art. Ökat pCO_2 ökar tillväxt av vuxna och tidiga livsstadier i populationer från områden med lägre salthalt, medan ökad temperatur har en negativ effekt på tillväxt av tidiga livsstadier oavsett ursprung. Exponering för hög koldioxidhalt ledde till att tången blev känsligare för mekanisk påverkan. Alla tre klimatförändringsvariablerna minskade tångens förmåga att inducera kemiskt försvar och de blev känsligare för betning.

LIST OF PAPERS

This thesis is based on the following papers, which are referred to in the text by their roman numerals:

PAPER I: **Kinnby, A.**, Jonsson, P. R., Ortega-Martinez, O., Töpel, M., Pavia, H., Pereyra, R. T., & Johannesson, K. (2020). Combining an Ecological Experiment and a Genome Scan Show Idiosyncratic Responses to Salinity Stress in Local Populations of a Seaweed. *Frontiers in Marine Science*, 7, 470.

PAPER II: **Kinnby, A.**, White, J.C.B., Toth, G.B., & Pavia, H. (2021). Ocean acidification decreases grazing pressure but alters morphological structure in a dominant coastal seaweed. *PLoS one*, 16(1), e0245017.

PAPER III: **Kinnby, A.**, Cervin, G., Larsson, A.I., Edlund, U., Toth, G.B., & Pavia, H. Increased risk of tissue breakage in habitat-forming seaweeds under ocean acidification. (Manuscript).

PAPER IV: **Kinnby, A.**, Toth, G.B., & Pavia, H. Climate change increases susceptibility to grazers in a foundation seaweed. (In review).

PAPER V: **Kinnby, A.**, Johannesson, K., Cervin, G., & Pavia, H. Effects of ocean acidification and warming on fertilization success and germination in *Fucus vesiculosus*. (Manuscript).

Other papers not included in this thesis:

Kinnby, A., Pereyra, R.T., Havenhand, J.N., De Wit, P., Jonsson, P.R., Pavia, H., & Johannesson, K. (2019). Factors affecting formation of adventitious branches in the seaweeds *Fucus vesiculosus* and *F. radicans*. *BMC Ecology*, 19(1), 22.

Toth, G. B., Harrysson, H., Wahlström, N., Olsson, J., Oerbekke, A., Steinhagen, S., **Kinnby, A.**, White, J., Albers, E., Edlund, U., Undeland, I. & Pavia, H. (2020). Effects of irradiance, temperature, nutrients, and pCO₂ on the growth and biochemical composition of cultivated *Ulva fenestrata*. *Journal of Applied Phycology*, 32, 3243-3254.

Olsson, J., Toth, G. B., Oerbekke, A., Cvijetinovic, S., Wahlström, N., Harrysson, H., Steinhagen, S., **Kinnby, A.**, White, J., Edlund, U., Undeland, I., Pavia, H., & Albers, E. (2020). Cultivation conditions affect the monosaccharide composition in *Ulva fenestrata*. *Journal of Applied Phycology*, 32(5), 3255-3263.

TABLE OF CONTENTS

Table of Contents

BACKGROUND	1
THE BALTIC ‘TIME MACHINE’	1
EFFECTS OF CLIMATE CHANGE ON THE MARINE ENVIRONMENT	3
HABITAT-FORMING SEAWEEDS	4
REPRODUCTIVE STRATEGIES OF <i>F. VESICULOSUS</i>	5
PHLOROTANNINS	6
SEAWEED-GRAZER INTERACTIONS	7
AIMS OF THE THESIS	8
METHODS	9
MANIPULATION OF SEAWATER PARAMETERS	9
PHYSIOLOGICAL TRAITS.....	10
TISSUE RESILIENCE (BREAKING FORCE, PUNCTURING FORCE, AND RISK FACTOR)	10
GRAZING EXPERIMENTS	11
BIOCHEMICAL COMPOSITION.....	13
MEASUREMENTS ON EARLY LIFE STAGES	13
MAIN RESULTS	14
GROWTH	14
TISSUE RESILIENCE (BREAKING FORCE, PUNCTURING FORCE, AND RISK FACTOR)	14
BIOCHEMICAL COMPOSITION.....	16
SUSCEPTIBILITY TO GRAZERS	17
EFFECTS OF CLIMATE CHANGE ON EARLY LIFE STAGES OF <i>F. VESICULOSUS</i>	17
DISCUSSION, CONCLUSIONS AND FUTURE PERSPECTIVES	18
FUNDING	21
ACKNOWLEDGEMENTS	21
REFERENCES	23

BACKGROUND

Climate change leads to multiple effects caused by simultaneous shifts in several physical factors which will interact with species and ecosystems in complex ways (Teagle and Smale, 2018). In marine systems the effects of climate change include altered salinity, increased temperature, and elevated pCO₂, all of which are currently affecting and will continue to impact marine species and ecosystems. Although this can be a threat to any type of organism, effects on habitat-forming species will have broad consequences for the whole ecosystem, and thus potentially be more serious. One such species is the common brown seaweed bladderwrack, *Fucus vesiculosus*, which forms habitat for other organisms in coastal waters in the northern hemisphere, including Swedish waters.

The Baltic ‘time machine’

The studies included in this thesis were all performed in or close to the transition zone between the North Sea and the Baltic Sea (Fig. 1). The Baltic Sea is a shallow, coastal, mostly enclosed water mass and forms one of the largest bodies of brackish water in the world. It is relatively species-poor due to its low salinity and recent formation after the last ice age (approximately 8500 years ago) (Zillén *et al.*, 2008). This basin is also highly affected by anthropogenic influence through runoff from agricultural and rural areas. Because of its enclosure, it is currently being affected by climate change and local anthropogenic stress combined at a greater rate than other coastal areas. It has been suggested that the condition of the Baltic Sea is already close to the conditions which are projected for other coastal areas by the year 2100, allowing it to function as a ‘time machine’ (Reusch *et al.*, 2018). Studies conducted in this area involve populations of species that are already exposed to considerable stress, and knowledge gained from studies in this area might function as early warnings of what can happen elsewhere in the future.

The present study region is focused along the Swedish west coast, in the transition region between the Baltic Sea and the North Sea where the abiotic conditions represent a mix of both regimes. There are strong surface currents which create an asymmetric barrier to population connectivity: The Jutland current brings North Sea water into the Kattegat and Skagerrak while the Baltic surface current moves brackish water northward (Jonsson *et al.*, 2016). This area demonstrates a salinity regime that is very different from the other parts of the North Atlantic (Fig. 1). The sea surface salinity varies along a strong gradient, increasing from 6-8 psu in the south up to 34-35 psu in the North Sea, and the sea surface temperature can vary widely over the seasons (Nielsen *et al.*, 2016). In the same geographic range, yearly average temperature decreases and stabilizes from south to north (Andersen *et al.*, 2017; Snoeijs-Leijonmalm and Andrén, 2017). Total alkalinity (A_T; a measure of the acid-binding capacity of seawater) impacts how much atmospheric changes in pCO₂ affect the actual pH of seawater (Sundquist, 1991). It is closely coupled to salinity and also follows a gradient increasing from lower alkalinity in the brackish Baltic Sea water to higher, and more stable, alkalinity in the more saline North Atlantic water. These environmental gradients can exert powerful abiotic pressures on the species living there (Pearson *et al.*, 2000).



Figure 1. Map of the study area illustrating the salinity gradient from the eastern North Sea and into the Baltic Sea. Legend indicates the sampling sites that were used in the papers that make up this thesis.

Effects of climate change on the marine environment

Climate change is an umbrella term encompassing some of the largest and most potent selective pressures currently acting on ecosystems (Denman *et al.*, 2011). Climate change can have diverse effects on marine systems, where the most powerful are changes to salinity, temperature, and pH (IPCC, 2007). These environmental factors are fundamental to the ecosystems in the oceans, and all species living there will be affected in one manner or another (Harley *et al.*, 2006). Shallow, coastal systems are particularly vulnerable to such changes because they have less water volume and hence a lower buffering capacity (Harley *et al.*, 2006; Levitus *et al.*, 2009).

One of the largest vectors of climate change is the emission of greenhouse gases, whereof carbon dioxide (CO₂) is the most common. About 40% of the CO₂ increase ultimately dissolves into the oceans (Feely *et al.*, 2004). This CO₂ reacts with water and forms carbonic acid, H₂CO₃, which in turn deprotonates into bicarbonate, (HCO₃⁻), carbonate (CO₃²⁻) and hydrogen ions (2H⁺). The increased concentration of hydrogen ions results in lower pH in the oceans; this is termed ocean acidification (Sabine *et al.*, 2004). The atmospheric CO₂ concentrations are currently 400 µatm and are projected to increase to 1000 µatm by year 2100 (RCP 8.5, IPCC, 2013). The concentration of hydrogen ions in the surface ocean has increased by 30% since the industrial revolution, equivalent to a reduction of 0.1 pH units (Raven *et al.*, 2005). The overall ocean pH is projected to continue to decrease, and expected to drop with another 0.4 units by year 2050 and 0.7 units by year 2300 (Caldeira and Wickett, 2003; Orr *et al.*, 2005). The majority of the dissolved CO₂, and therefore the majority of the pH change, concentrates above the thermocline, resulting in lower pH closer to the surface and eventually changes to deep water as well (Sabine *et al.*, 2004).

As CO₂ and other greenhouse gases are released into the atmosphere by anthropogenic activity, they accumulate in the atmosphere and capture infrared radiation, leading to global temperature increases. This effect is responsible for a 0.1°C increase in mean sea surface temperature per decade during the last 40 years (Taboada and Anadón, 2012) and mean seawater temperatures are projected to continue to rise 2-5°C by the end of this century (IPCC, 2013). However, it is not just the mean values that will increase but also extreme temperature events will become stronger and more frequent. Temperature changes can have powerful direct effects on marine organisms, especially those that do not thermoregulate, such as seaweeds and their most common grazers. Differences in how different species tolerate heat stress as well as their adaptive potential can result in very different outcomes, leading to clear ‘winners’ and ‘losers’ between those that can adapt to a new regime, and those that cannot (Somero *et al.*, 2010).

Salinity is another environmental factor that will be affected by climate change, resulting in either an increase or a decrease in different areas (Jenkins, 1999; Wentz *et al.*, 2007). In temperate regions, including the Baltic Sea, increased precipitation as well as increased river flow and coastal run-off is expected to result in a decreased salinity (Wentz *et al.*, 2007; van de Waal *et al.*, 2009; Jonsson *et al.*, 2018). Especially the Baltic Proper will be affected since in the north where the river outflow is greatest the salinity is already very low. Salinity affects

many physiological functions in all marine organisms through changes in osmotic stress, so fluctuations in salinity are powerful stress factors (Gagnaire *et al.*, 2006; Tomanek, 2011).

In addition, coastal waters are highly variable and dynamic environments which can present many challenges to any organism that lives there, such as seaweeds. One type of challenge is seasonal storms and the powerful wind and waves that follow them (Gaylord, 1999). These storms represent powerful destructive events, and are predicted to become more regular and increase their strength under climate change (Hawkins *et al.*, 2009; Bindoff *et al.*, 2007). The waves generated by these storms can impose as much stress on seaweeds as hurricane force winds impose on trees; just as losses to tree canopy can have broad ecosystem effects, so too can losses to the seaweed canopy (Martone *et al.*, 2012).

Habitat-forming seaweeds

The availability of habitat, especially complex habitats that can provide structure, enhance biodiversity, and increase the available niche space, is critical to the overall productivity of an ecosystem and the organisms that inhabit it. In marine ecosystems seaweeds (macroalgae), especially large, brown seaweeds such as kelps and furoids, form three-dimensional, complex habitats that provide refuge, shelter, and food to many species (Smale *et al.*, 2013). It has been well-established that such a habitat-forming function is of great ecological importance, but also can have powerful economic effects by nurturing the ecosystem functions of nearshore waters (Costanza *et al.*, 1997). The studies that make up this thesis are focused on three such species of brown seaweeds:

Saccharina latissima is one of the dominant kelp species in the study area, and grows subtidally in wave-sheltered and somewhat exposed areas across the North Atlantic, and is of great ecological importance (Bekkby and Moy, 2011). In our study area it can be found growing from approximately 2-20m on hard substrates in semi-exposed locations (Hanelt *et al.*, 1997).

Ascophyllum nodosum is an intertidal and subtidal furoid seaweed that functions as an important primary producer and habitat-forming seaweed in North Atlantic Basin (Cardoso *et al.*, 2017). The furoids are benthic key players inhabiting rocky intertidal areas in both sheltered and exposed areas in the littoral zone in the North Atlantic Sea, the North Pacific Ocean, the North Sea and the Baltic Sea (Bergström *et al.*, 2005; Lima *et al.*, 2007). In the study area, *A. nodosum* grows in sheltered sites immediately below the water surface down to 1.5m on hard substrates.

Fucus vesiculosus, commonly known as bladder wrack, is a brown seaweed belonging to the order Fucales. It is the predominant seaweed in the Baltic Sea and grows on hard substrates and cobbles, forming floating vesicles only in more sheltered areas. While it grows intertidally though most of its range, *F. vesiculosus* grows subtidally and is only exposed to air during extreme low water events along the Swedish coastline where there is no significant tidal influence. Throughout these atidal areas, wave action, wind direction and air pressure can affect the sea level (Johannesson, 1989), so it must still be able to tolerate drying out for intermittent periods.

Reproductive strategies of *F. vesiculosus*

Sexual reproduction is the norm for *F. vesiculosus* throughout its distributional range. It is a dioecious, perennial species with external fertilization (Bergström *et al.*, 2005). Gametes are produced in conceptacles that are situated on the receptacles at the tips of individual branched fronds (Fig. 2). The conceptacles contain either oogonia, with egg cells, or antheridia, with sperm cells. When the conceptacles have matured, they contain eight eggs per oogonium or 64 spermatozooids per antheridium (Graiff *et al.*, 2017). For gamete release to succeed and fertilization to occur in the water column, it is crucial that the seaweeds are located close to each other, that the release of gametes is synchronized, and that the weather is calm (Serrão *et al.*, 1996; Pearson *et al.*, 1998). The release of the gametes is determined by the time of day and month (Andersson *et al.*, 1994). All *Fucus* spp. lack a planktonic motile stage which means that the fertilized egg will settle shortly after gamete release. The egg, as well as the zygote, are negatively buoyant to facilitate the settling process (Pearson and Brawley, 1996). While some turbidity is necessary for the mixing of the gametes, too vigorous water motion will not only dilute the sperm but also have detrimental effects on the zygote; the fertilization itself may be successful but early development sheer-stress-induced damage can stop development at the 64-cell stage, thus reducing fertilization success (Mead and Denny, 1995).

Low salinities, such as found in the central, northern, and eastern regions of the Baltic, have been associated with increased polyspermy in marine organisms such as oysters and seaweeds, which reduces the success of sexual reproduction (*e.g.*, Togo and Morisawa, 1999). Marine organisms often have a protective mechanism against polyspermy, generally termed polyspermy block, that stops the entry of more than one sperm through depolarization of the egg membrane upon penetration by the first sperm. This depolarization is caused by sodium (Na^+) influx, which likely explains why the block against polyspermy is less effective in waters with low salinity, while it is functional in higher salinities (Serrão *et al.*, 1999).

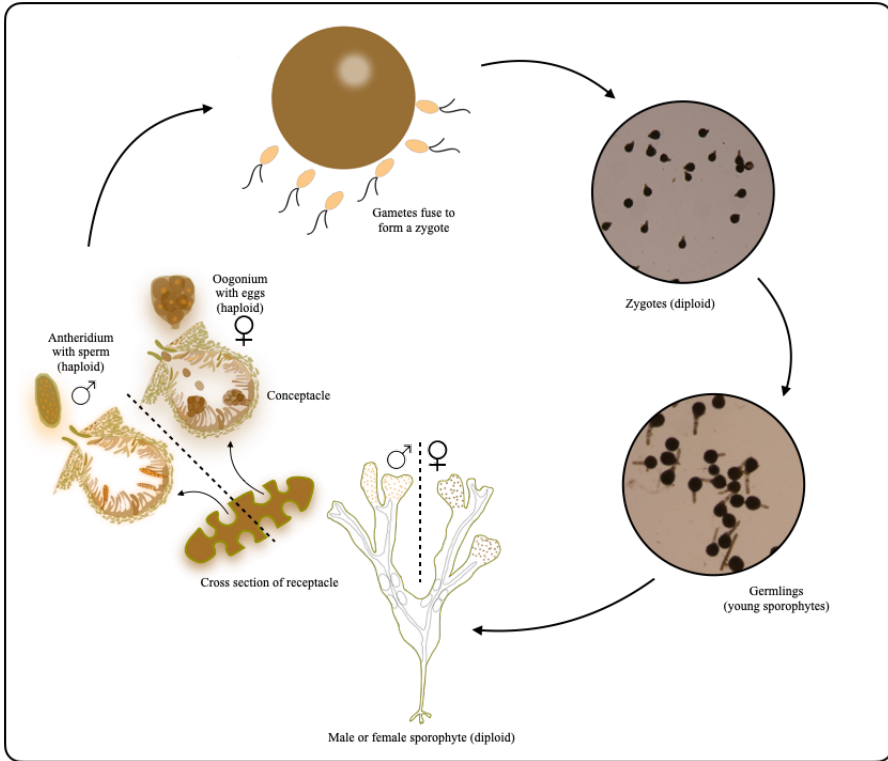


Figure 2. Schematic diagram of the life cycle of *Fucus vesiculosus* showing diploid adult sporophytes, haploid gametes, and stages of fertilization and development.

Phlorotannins

Phlorotannins are secondary polyphenolic metabolites unique to brown seaweeds, with multiple roles at both cellular and organismal levels (Pavia *et al.*, 1999). They are chemically similar to tannins found in vascular plants (Schoenwaelder, 2002; Henry and Van Alstyne, 2004; Wiencke *et al.*, 2004; Roleda *et al.*, 2006). Phlorotannins can be placed into six groups determined by their chemical structure, which is always based around polymers of phloroglucinol (1,3,5-trihydroxybenzene) (Ragan and Glombitza, 1986). Immediately after fertilization these phenolics are the first components of the primary cell wall to be secreted, and they remain active in the fastest growing tips of developing rhizoids (Schoenwaelder, 2002). They also appear to function as adhesives to help settlement, help the seaweed to resist damage from heavy metals, and may also act as a form of polyspermy block (Schoenwaelder, 2002). In addition to these functions, phlorotannins are also part of the brown seaweeds' defense against UV radiation and chemical defense against grazing (Pavia *et al.*, 1997; Pavia and Toth 2000a; Henry and Van Alstyne, 2004). Chemical defenses can be constitutive and/or inducible. Constitutive defenses are always present in the organism, whereas inducible defense is triggered by a stimulus, *e.g.*, the synthesis of phlorotannins is induced by grazing. In addition to their inducibility as a response to grazing, variation in phlorotannin content in brown

seaweeds have also been linked to salinity (Nylund *et al.*, 2012), nitrogen and light availability (Yates and Peckol, 1993; Arnold *et al.*, 1995; Pavia and Toth 2000b), life-history stage (Steinberg, 1989), and season (Steinberg, 1995).

To date, there have been very few studies directly considering the effects of climate change, such as ocean acidification or increased temperature, on phlorotannin production. However, Swanson and Fox (2007) found an enhanced production of phlorotannins under elevated levels of pCO₂.

Seaweed-grazer interactions

One of the major ecological interactions for all seaweeds is grazing, which is mediated by many interacting effects, for example: the metabolism of the grazers, the population density of grazers, the biochemical make-up of the seaweed including nutritional profile and defensive compounds, such as phlorotannins. All of these factors may be affected by climate change. For example, the palatability of *F. vesiculosus* has been shown to reduce under warming and reduce strongly under the combined effects of warming and acidification (Raddatz *et al.*, 2017); changes to the tissue toughness of *F. vesiculosus* have also been reported in response to low salinity and warming (Rothäusler *et al.*, 2017). The intertidal seaweed grazer community along the Swedish west coast and the eastern North Sea is composed of littorinid snails and crustaceans, and is more diverse than in the Baltic Sea where it is dominated by *Idotea baltica* (Wikström *et al.*, 2006; Leidenberger *et al.*, 2012; Nylund *et al.*, 2012). As predator-prey interactions change in the face of the changing climate, it may affect community structure as predation influences the grazing patterns of prey species (Kroeker *et al.*, 2014).

AIMS OF THE THESIS

The general objectives of this thesis were to evaluate the effects of climate change on habitat-forming seaweeds in a coastal area where climate change is inducing environmental changes faster than in most other marine areas in the world. In order to represent the multi-factor changes that are the consequence of climate change, I included both separate and interactive effects of seawater temperature, pH, salinity, and grazing pressure on both adult and early life stages, focusing primarily on *Fucus vesiculosus*. By conducting field and lab experiments and combining physiological, chemical, and genetic approaches, I aimed to detect different aspects of responses to climate-induced stress. The specific aims of each study are detailed as follows:

PAPER I: To investigate the effects of a moderate salinity decrease on growth, phlorotannin content, and photosynthetic activity in populations of *F. vesiculosus* from different ambient salinities along a natural gradient, and to interpret the results in light of population genetic differences.

PAPER II: To investigate the effects of elevated pCO₂ on adult individuals of *F. vesiculosus* and the generalist grazer *Littorina littorea*, considering both direct physiological effects on the seaweed and the indirect effects through the interaction with the grazer.

PAPER III: To investigate the effects of ocean acidification on three habitat-forming seaweeds by assessing effects on growth, thallus breaking strength, and drag, under both lab and field conditions.

PAPER IV: To investigate how increased stress from temperature, salinity, and pCO₂ affects *F. vesiculosus* growth, biochemical composition and susceptibility to the specialized grazer *Littorina obtusata*.

PAPER V: To investigate the effects of high temperature and elevated pCO₂, on fertilization success, size of germlings, sperm motility, and sperm velocity in populations of *F. vesiculosus* from different ambient salinities.

METHODS

Here I summarize the most fundamental methods used throughout this thesis, while further details are given in the individual papers (Fig. 3; example of experimental set-up).

Manipulation of seawater parameters

Accurate and reliable manipulation throughout the experiments is fundamental when investigating the effects of seawater pCO₂, salinity, and temperature. To control the pCO₂ present in flow-through seawater (**paper II, paper III, paper IV**), I used a combination of CO₂ scrubbed air and pure CO₂ to deliver a target pCO₂ as controlled by a pH computer (Aqua Medic) and verified using an independent, calibrated Li-850 CO₂/H₂O gas analyzer (Li-Cor). The CO₂ analyzer was calibrated with custom mixed gas, 970 ppm (Linde Gas AB, Sweden). The pH was recorded using HANNA instruments pH electrode HALO probe (HI-1102) calibrated with NBS pH 4.01, 7.01, and 10.01 standards (HANNA instruments) before each measurement. Total alkalinity was estimated from salinity using long-term salinity:alkalinity relationship data for this location ($r=0.94$; data obtained from SMHI <https://www.smhi.se/data/oceanografi/datavardskap-oceanografi-och-marinbiologi/sharkweb>) (Eriander *et al.*, 2016) and pH_T was calculated from the temperature, salinity, pCO₂, and total alkalinity using CO₂calc (Robbins *et al.*, 2010). To obtain specific pCO₂ values for the fertilization experiments (**paper V**), the experiment was conducted in small chambers with air with the specific pCO₂ required distributed into them.

To control the salinity in flow-through seawater (**paper I**) conductivity monitoring controllers (AQUA MEDIC) were used to control the release of freshwater into a constant flow of seawater. When the conductivity rose above a set threshold a solenoid valve opened to increase the flow of freshwater and reduce the salinity of the overall system. In **paper IV** reduced salinity was achieved by setting the treatment to a constant 4 psu lower than the ambient.

In experiments with flow-through seawater submersible heaters were used to increase the temperature (**paper IV**). To obtain specific temperatures during conditioning of seaweeds they were cultured in temperature-regulated rooms at the Tjämnö Marine Laboratory (**paper V**). During fertilization experiments specific temperatures were obtained using incubator cabinets (**paper V**).



Figure 2. Experimental set-up of header tanks that can distribute experimentally controlled seawater with specific salinity, pCO₂, and/or temperature as used in the greenhouse facility at Tjärnö Marine Laboratory.

Physiological traits

Growth of adult thalli was assessed in a number of ways throughout the thesis: by weight, by length, or by area. In **paper I** growth was measured as length increase in apical tips using images taken at the beginning and end of the experiment. In **paper II**, **paper III**, and **paper IV** growth was measured as percent increase in area, also using images taken at the beginning and end of the experiments, and percent increase in weight using a standardized blotting procedure. All image analyses for length and area were done in ImageJ (Schneider *et al.*, 2012).

In **paper I**, **paper II**, and **paper III** the efficiency of photosystem II was measured in the tissue that had formed during the experiment using a diving PAM (pulse amplitude-modulated fluorometer; Walz, Effeltrich, Germany). The tissue was dark-adapted for 10 minutes using a leaf clip, and the fiber optic tip was held at a fixed distance from the seaweed using a silicone spacer. Wherever possible all measurements were taken at a similar time of day throughout each experiment.

Tissue resilience (breaking force, puncturing force, and risk factor)

In **paper II** and **paper III** breaking force (sometimes called pull-to-break force) was assessed by placing a seaweed thallus in a bench vise between two protective wooden plates (Fig. 4a). A similar pair of wooden plates were anchored to the apical tip of the thallus using a clamp,

and these two sets were then pulled apart, slowly increasing the force applied until the tissue failed. The force was measured using a dynamometer (Lutron FG-5020, Taiwan). This was performed three times per individual in apical tissue of *F. vesiculosus* and *A. nodosum*, but only once for apical tissue of *S. latissima* and basal tissue in all species (due to morphological constraints). The equipment used was identical for all replicates.

In **paper III** puncturing force was measured by placing the seaweed thallus flat on a wooden work surface and gradually increasing the force applied by a dynamometer (Lutron FG-5020, Taiwan) fitted with a blunt tip until the tissue failed (Fig. 4b). These measurements were performed three times each for both apical and basal tissue of each individual. The same surface and tip were used for all measurements.

A risk factor was calculated for seaweeds in **paper III** using measured drag (Fig. 4c) and breaking forces according to the formula (from Martone, 2006):

$$R=F_d/F_b$$

Where R= risk factor, F_d = drag force, and F_b = breaking force.

Grazing experiments

In **paper II** and **paper IV** the susceptibility to grazing of the *F. vesiculosus* thalli grown in the different treatments was measured in feeding trials using snail grazers placed together with pieces of seaweeds in small containers (200 mL) with constant flow-through from the treatments. To control for autogenic changes in mass (growth) during the experiment that was not caused by the grazing of the snails, each container with seaweed pieces and herbivores was paired with a control container without herbivores containing part of the thallus of the same individual of seaweed. The wet weight of all seaweed pieces was determined at the start and at the end of the experiment by using a standard blotting procedure, and the wet weight change of each seaweed piece was calculated by subtracting the weight at the end of the experiment from the starting weight. The herbivore consumption of seaweeds exposed to different treatments was determined by subtracting the weight change in the autogenic control containers (those containers with seaweed but no grazers) from the wet weight change of the grazed seaweeds. In **paper II** feeding preference of the grazer was also examined by placing two seaweed pieces (one grown under ambient conditions and the other under experimental treatment conditions) in each container with herbivores and comparing the wet weight change of each of those two pieces to each other (Peterson and Renaud, 1989).

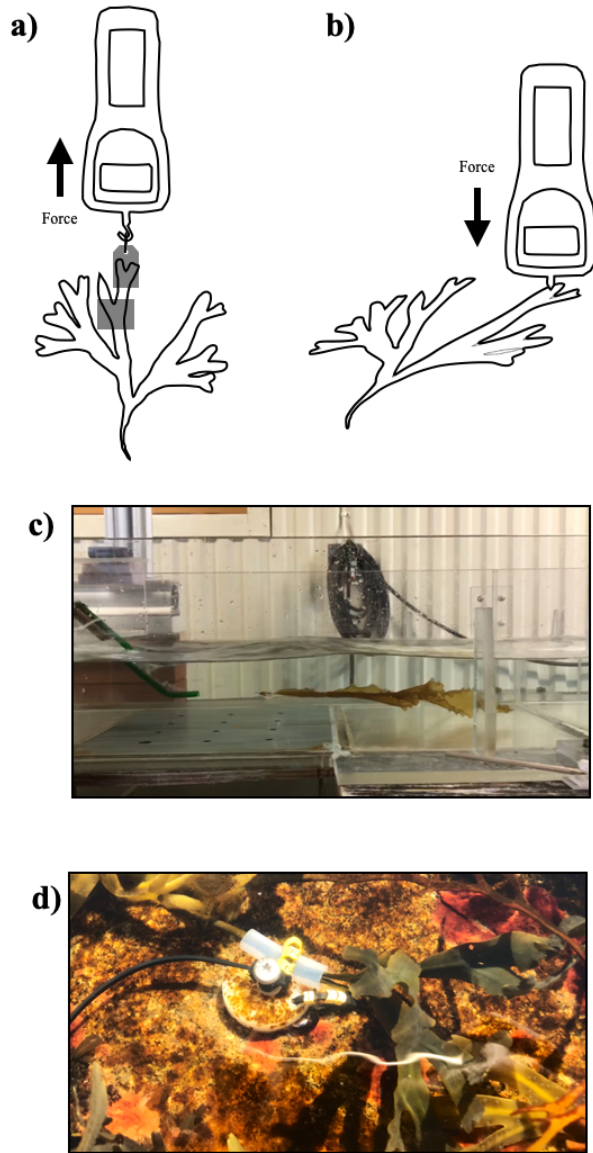


Figure 3. Description of methods used in **paper II** and **III**. a) Dynamometer in place to measure breaking force in pull-to-break tests, gray panels represent pairs of wooden blocks gripping the seaweed and allowing gradual force to be applied using the dynamometer. b) Dynamometer in place to measure puncturing force in push-to-puncture test. c) Photo of an individual of *S. latissima* in the flume tank attached to a dynamometer measuring drag force. d) Photo of an individual of *Fucus vesiculosus* after being re-attached to the substrate in the field during the transplant experiment in **paper III** (Fig. 4d).

Biochemical composition

In **all papers** biochemical composition was analyzed in various ways. These analyses were performed using apical tissue, tissue which grew during the experiments, which was frozen at - 60°C immediately following the experiment, freeze dried, homogenized to a powder, and then analyzed according to the desired measurement. In **paper I**, **paper II**, and **paper IV** the phlorotannin content in *F. vesiculosus* was analyzed colorimetrically using the Folin-Ciocalteu method (Van Alstyne, 1995). In **paper II** the carbon (C) and nitrogen (N) content as well as the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the samples were analyzed with an elemental analyzer coupled to an isotope ratio mass spectrometer. In **paper IV** the samples for C, N, and $\delta^{13}\text{C}$ were instead sent to the Stable Isotope Facility at University of California Davis for analysis using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer (IRMS). In **paper III** samples for ion composition were analyzed using ICP-OES (inductively coupled plasma – optical emission spectrometry).

Measurements on early life stages

In **paper V** the effects of high temperature, elevated pCO₂, and their interaction on early life stages of *F. vesiculosus* were investigated. Six populations of *F. vesiculosus* from a coastal salinity gradient were used and fertilization success, size of germlings, as well as sperm motility and velocity were assessed in a fully crossed design. Zygotes were exposed to ambient (15°C) or high (18°C) temperature and ambient (400 μatm) or elevated (1100 μatm) pCO₂. In short, for each population six crosses with 3 males and 3 females (*i.e.*, a total of 18 individuals) were used in the experiment. Gametes from males and females were allowed to release and the concentration of gametes from each individual was determined. In the experiment equal proportions from each individual were used. Gametes were mixed in respective treatment waters and placed in incubators. Fertilization success was measured after 15 hours after fertilization and length of germlings were measured 5 days later.

MAIN RESULTS

Growth

It was found that growth responses to reduced salinity varied by population (**paper I**). Populations from marine origin maintained growth when exposed to reduced salinity whereas populations from intermediate salinities grew less in reduced salinity than in their ambient salinity. One of two populations of brackish origin maintained growth whilst one other ceased growth almost completely. The average area growth rates under elevated pCO₂ were higher than growth under ambient conditions (**papers II & III**; Fig. 5). However, thallus weight did not differ significantly between seaweeds grown under ambient elevated pCO₂ conditions. When seaweeds were exposed to changes in more than one climate variable, it was observed that elevated pCO₂ had a positive effect on seaweed growth at ambient temperature, but not at elevated temperature, while growth increased in low salinity at ambient but not high temperature, regardless of pCO₂-level (**paper IV**).

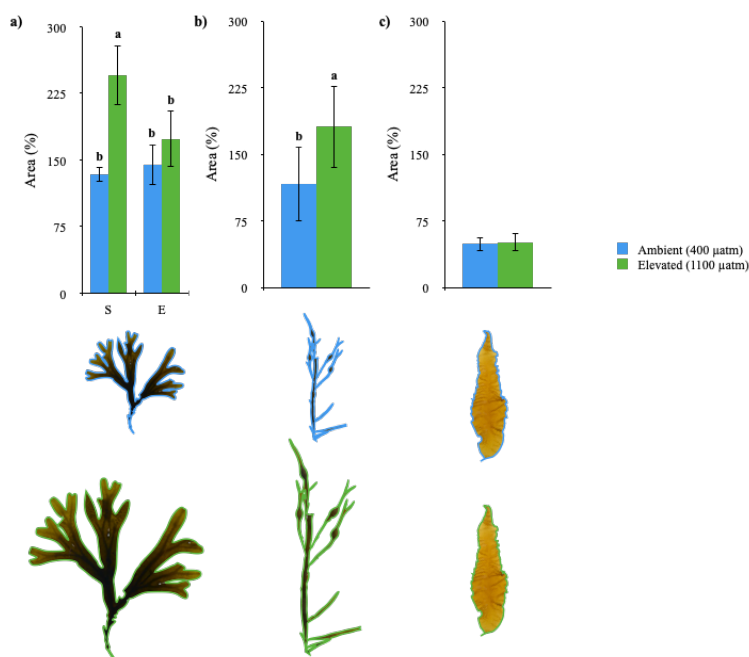


Figure 4. Effects on growth by area of elevated pCO₂ on three habitat-forming seaweeds; a) *F. vesiculosus*, b) *A. nodosum*, c) *S. latissima*. Values are means ± 95% CI. Photos represent growth trends for the respective species under experimental or control conditions, but are not to scale.

Tissue resilience (breaking force, puncturing force, and risk factor)

Resilience, measured as the force required to either break or puncture the thallus, was significantly reduced in apical tissue but not in basal tissue of *F. vesiculosus* and *Saccharina latissima* (**paper III**; Fig. 6). These results corresponded to an increase in risk factor, which

was calculated from the tissue resilience. A similar change was observed in *Ascophyllum nodosum*, in both breaking and puncturing force on apical tissue, but also puncturing force on basal tissue. Changes in risk factor were only found on apical tissue. Furthermore, it was found that *F. vesiculosus* from exposed sites was significantly less likely to survive after being exposed to elevated pCO₂, a pattern which was not observed for individuals from sheltered sites (**paper III**). Furthermore, SEM (scanning electron microscope) analysis showed that there were clear morphological differences in the tissue structure between seaweeds grown under elevated and ambient pCO₂ levels. Tissue of individuals grown under elevated pCO₂ had a less dense matrix with open spaces forming within the tissue compared to seaweeds grown under ambient conditions that had a more tightly packed tissue matrix (Fig. 7).

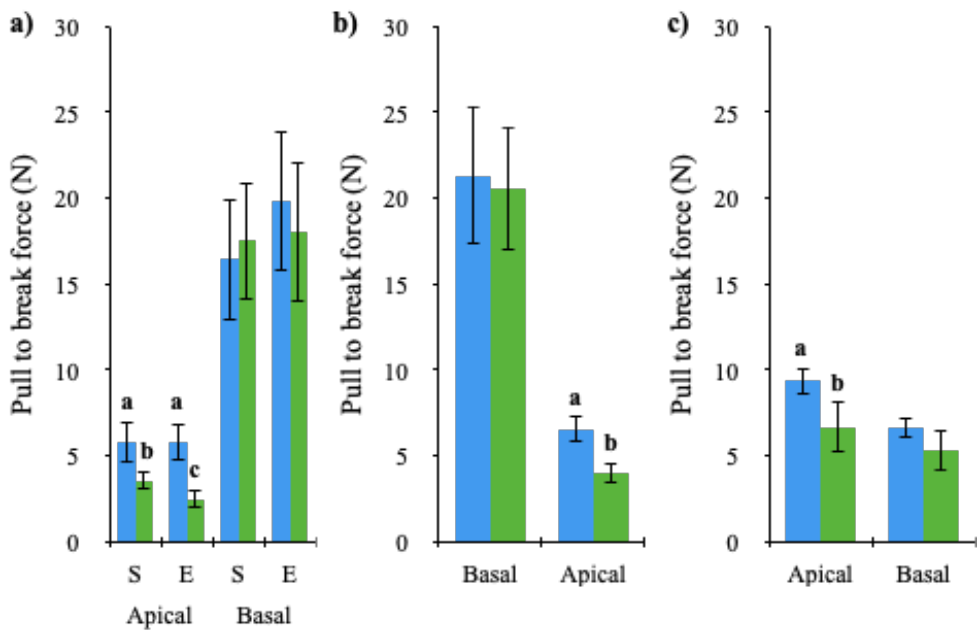


Figure 5. Effects of elevated pCO₂ on tissue resilience measured in a pull-to-break test in three species of habitat-forming seaweeds; a) *F. vesiculosus*, b) *A. nodosum*, c) *S. latissima*. Values are means ± 95% CI.

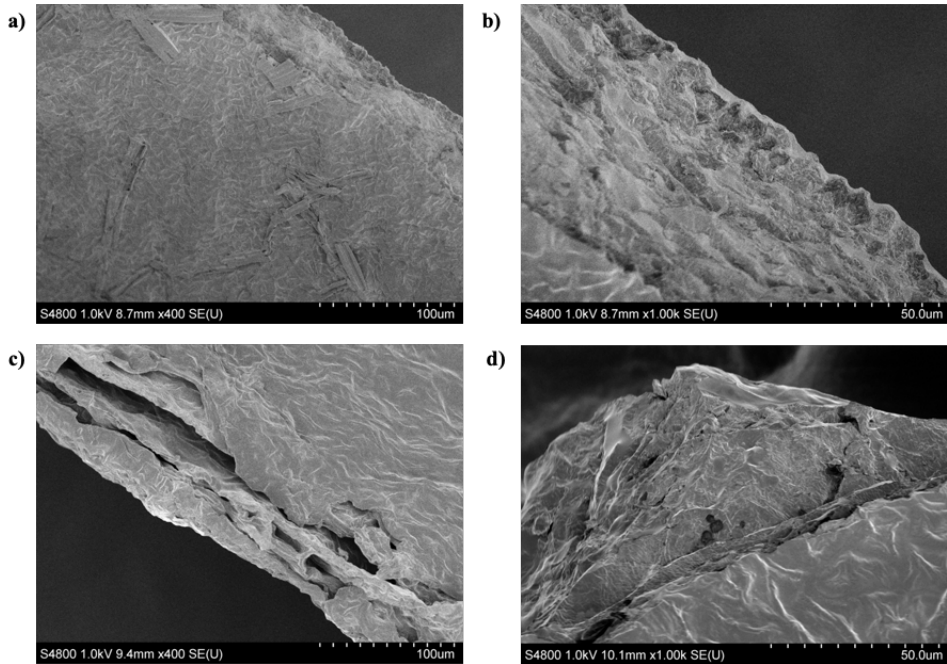


Figure 6. SEM images of (a-b) *Fucus vesiculosus* with exposed origin grown under ambient pCO₂ and (c-d) *F. vesiculosus* with exposed origin grown under elevated levels of pCO₂. Magnifications: (a,c) x400 and (b,d) x1000. Photos: Ulrica Edlund.

Biochemical composition

The calcium content of seaweed tissue was shown to be lower in *F. vesiculosus* and *A. nodosum* when exposed to elevated pCO₂ but not in *S. latissima* (**paper III**). It was observed that *F. vesiculosus* from sheltered sites had lower calcium content than individuals from exposed sites, and this pattern held true in both ambient and elevated pCO₂ conditions. Magnesium content followed the same pattern, although the differences between exposure origin were only a trend.

Phlorotannin content significantly decreased in four of six populations when exposed to reduced salinity (**paper I**), as well as in seaweeds exposed to elevated levels of pCO₂ compared to ambient levels of pCO₂ (**paper II**). Seaweeds grown under high temperature, reduced salinity, and elevated pCO₂ in an orthogonal design were used in a grazing experiment where it was found that seaweeds grown under ambient conditions had noticeably higher phlorotannin content in grazed tissue compared to ungrazed tissue. This increase in phlorotannin content following grazing was not found in any of the seaweeds grown under to any of the climate change conditions (**paper IV**).

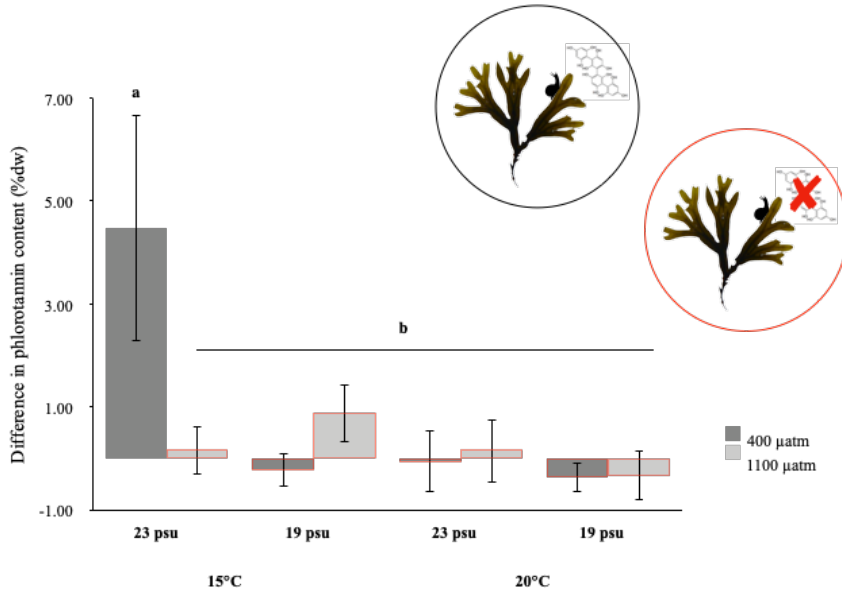


Figure 7. Difference in phlorotannin content of the same individual of *Fucus vesiculosus* between ungrazed and grazed tissue by *Littorina obtusata* after exposure to different levels of temperature (ambient and high), salinity (ambient and low), and pCO₂ (ambient and elevated) as fixed, orthogonal factors. Letters denote statistically significant post hoc groupings (SNK post hoc test, p<0.05). Values are means ± 95% CI, n=10. Red outline indicates an experimentally manipulated treatment and black outline indicates ambient conditions.

Susceptibility to grazers

Snails exposed to elevated pCO₂ consumed less seaweed than snails exposed to ambient conditions (**paper II**). We found an interaction between salinity and pCO₂ on consumption by snail grazers (**paper IV**); seaweeds grown in low salinity became 83% more susceptible to grazing compared to seaweeds grown under ambient conditions. Furthermore, at ambient salinity seaweeds exposed to elevated pCO₂ became 74% more susceptible to grazing (**paper IV**).

Effects of climate change on early life stages of *F. vesiculosus*

In all populations studied, early life stages of *F. vesiculosus* were affected by increased pCO₂, increased temperature, or the combination of these factors, although no two populations reacted identically (**paper V**). For fertilization success, the two most marine populations were negatively affected by elevated pCO₂ while the remaining four populations were positively affected, although this was somewhat mitigated by increased temperature. For germling length, the three least marine populations all showed increased growth at elevated pCO₂, while only one of the three more marine populations showed the same effect. High temperature generally affected germling growth negatively. The measured effects on percent motile sperm and sperm velocity varied strongly by population, including directly conflicting effects from temperature on sperm velocity in two populations.

DISCUSSION, CONCLUSIONS AND FUTURE PERSPECTIVES

This thesis shows that climate change through alterations in salinity, pCO₂, and temperature have effects on habitat forming seaweeds that differ between life stages and among geographically close populations of the same species. In general, elevated levels of pCO₂ enhanced growth in adult life stages and germlings from seaweed populations in less saline habitats, while high temperature had a negative effect only on germling growth, regardless of origin. This negative effect of high temperature might be a consequence of *F. vesiculosus* being adapted to colder, temperate areas, but also because early life stages are often more vulnerable to even small changes in temperature. Notably, exposure to elevated pCO₂ also led to the adult seaweeds breaking more easily due to mechanical force, using both pull-to-break and push-to-puncture tests. Furthermore, all three climate change variables reduced the ability of the seaweeds to induce chemical defense, *i.e.*, produce more phlorotannins, and consequently the seaweeds became more susceptible to grazers. Despite the enhanced growth found under some climate scenarios, the reduced breaking strength in combination with the impairment of chemical defense production might lead to reduction in seaweed biomass under future climate change conditions, which would reduce the available habitat and food in coastal ecosystems for many organisms.

In general, the results from this thesis show that growth by area increased under elevated pCO₂, most often in *F. vesiculosus*, but also in *A. nodosum*, while growth by weight did not. Previous work on the growth of *F. vesiculosus* under elevated pCO₂ has shown mixed results, from unaltered (Ober and Thornber, 2017; Takolander *et al.*, 2019), reduced (Gutow *et al.*, 2014), to a tendency to increase (Graiff *et al.*, 2015). The results from this thesis suggest that increased temperature had no conclusive effect on growth of adults, but a generally negative effect on germling growth of *F. vesiculosus*. Alestra and Schiel (2015) found a similar reduction in growth at increased temperature amongst three species of Arctic seaweeds, while Al-Janabi *et al.* (2016) found an increase in growth at increased temperature in *F. vesiculosus* germlings, during the summer. The studies included in this thesis suggest that this variation, which has been previously documented at regional or continental scales, persists even at local scales and could account for the lack of consensus from previous work. Evidence from previous studies on the effects of salinity on *F. vesiculosus* has shown reduced growth (Rugio *et al.*, 2018). In agreement with this, it was found that decreased salinity had generally negative effects on growth that varied by population, and, in one example, co-varied with genetic differences in calcium binding protein (**paper I**). This protein has previously been shown to be linked to salinity tolerance in land plants (Veena *et al.*, 1999), and the results from this study preliminarily suggest evidence of local adaptation in seaweed populations (**paper I**).

When different combinations of the three climate variables (pCO₂, temperature, and salinity) were allowed to interact, the results indicated complex interactions that are difficult to predict based on the manipulation of individual variables (**paper IV**). In early life stages these effects were not consistent but varied between populations (**paper V**). Earlier work examining the effects of multiple interacting variables have shown effects such as tissue necrosis (salinity and temperature, Takolander *et al.*, 2017) and reduced growth (salinity and temperature, Rugiu *et*

al., 2018). Moreover, interactions have been shown to mitigate the effects of changes to a single variable (temperature and pCO₂, Mensch *et al.*, 2016) and that these effects vary over seasons (Wahl *et al.*, 2020; Saha *et al.*, 2019). Overall, the data and results are still too scattered to draw rigid conclusions, and more work is needed to understand these complex interactions.

Studies investigating effects of ocean acidification on habitat-forming seaweeds showed that tissue resilience decreased using both pull-to-break and push-to-puncture tests when seaweeds had been grown under elevated pCO₂ (**paper II & III**). For *F. vesiculosus* and *A. nodosum* this effect was seen in apical (freshly grown) tissue, while basal tissue resilience was reduced in push-to-puncture strength only. This corresponds with an increased risk suggesting that these species are more likely to suffer damage from mechanical stress such as from grazing or wave action. Interestingly, this was paralleled by the formation of voids in the tissue matrix of seaweeds grown under elevated pCO₂ that were not present in seaweeds grown under ambient pCO₂. This reduced tissue strength could potentially lead to widespread damage and population decline as weather patterns tend towards more powerful storms under climate change (Hawkins *et al.*, 2009; Bindoff *et al.*, 2007). It could also interact with the simultaneous reduction in the seaweed's ability to induce chemical defense and leave them especially vulnerable to grazing pressure.

Phlorotannin production was reduced when the seaweeds were exposed to reduced salinity, although this effect varied by population (**paper I**). There was also a small reduction in phlorotannin production when seaweeds had been exposed to elevated pCO₂, but the most powerful results found were that all three climate change variables, in isolation or in any combination, dramatically affected the ability of *F. vesiculosus* to induce chemical defense, *i.e.*, the production of phlorotannins. Exposure to lower salinity has been shown experimentally to reduce phlorotannin content (Connan and Stengel, 2011), while in natural populations phlorotannin content has been shown to be higher in low salinity populations (Nylund *et al.*, 2012). This was hypothesized to be due to more intense grazing pressure in that ecosystem, and changes to the biochemical composition of seaweeds can alter ecological interactions such as grazing. Grazing experiments showed that *F. vesiculosus* became more susceptible to grazers when seaweeds were exposed to elevated pCO₂ or reduced salinity, regardless of temperature (**paper IV**). This contrasts with previous work by Raddatz *et al.* (2017), who found that palatability was reduced under warming, and especially under the combination of high temperature and elevated pCO₂.

The effects of high temperature and elevated pCO₂ on early life stages of seaweeds are of particular concern. In marine invertebrates, for example, early life stages have been shown to be more vulnerable to climate change than adult stages (*e.g.*, Byrne *et al.*, 2009; Przeslawski *et al.*, 2015). It was found that both germling growth and fertilization success reacted differently in different populations, and some populations reacted completely opposite to others (**paper V**). This is the first reported measurement of the effects of ocean acidification on fertilization success in seaweeds, and the results revealed that effects strongly differ between populations. It was also shown that in populations from less marine origin, high temperature had a negative effect on fertilization success (**paper V**); this could have implications in the

future for these populations that are already living close to the edge of their tolerance range for other environmental variables. However, elevated levels of pCO₂ enhanced fertilization success in low salinity populations although antagonistic effects from temperature changes may reduce these benefits. Fertilization and germling development are critical life stages for individual survival and population sustainability, and much more research is needed to understand the effects of projected future climate change on early life stages of seaweeds at both the population and species levels.

There were both positive and negative effects on growth, but these may be overshadowed by the more powerful effects on other response variables. Seaweeds grown under future climate change scenarios became more susceptible to grazers which could be due to the strong reduction in the seaweeds' ability to induce chemical defense by producing phlorotannins. Furthermore, seaweeds grown under future ocean acidification conditions showed a decreased tissue resilience against mechanical damage. This could possibly be due to the increased growth rate observed under these conditions, and this reduced toughness may also make seaweeds more vulnerable to grazing. It is yet to be determined if germlings of seaweeds that grow faster under elevated pCO₂ also become weaker or if it affects their ability to adhere to the substrate. Together, increased susceptibility to grazers and reduced tissue resilience imply that climate change may lead to a future net decline in populations of habitat-forming seaweeds, which may have large negative consequences on associated organisms that depend on this habitat-forming species for shelter and food. These effects could either be localized to specific populations or widespread, especially when combined with predicted increases to storm frequency and power.

In all studies where multiple populations were included, it was found that the responses measured varied by population (**paper I & V**) and were even linked to genetic differences between populations (**paper I**). Such high variation between nearby populations suggests that taking local adaptation into account is critical to understand the underlying patterns, and consequently for management decisions. Moreover, the responses to alterations in different climate change variables counteracted each other in ways that would have been difficult to predict from single variable experiments. This highlights the importance of not just studying single climate change variables, but also their interactive effects, as well as local adaptation to different environmental conditions in different populations of one species. Furthermore, it also reinforces previous research that different life stages respond differently to similar stressors.

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