

GERLI ALBERT

Carbon use strategies of macrophyte
communities in the northeastern
Baltic Sea: implications for
a high CO₂ environment



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Carbon use strategies of macrophyte
communities in the northeastern Baltic Sea:
implications for a high CO₂ environment



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Department of Zoology, Institute of Ecology and Earth Sciences,
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LIST OF ORIGINAL PUBLICATIONS

- I** Pajusalu, L., **Albert, G.**, Fachon, E., Hepburn, C. D., Kotta, J., Liversage, K., Paalme, T., Peterson, A., Pritchard, D. W., Põllumäe, A., Torn, K., & Martin, G. (2020) Ocean acidification may threaten a unique seaweed community and associated industry in the Baltic Sea. *Journal of Applied Phycology*. 32:2469–78.
- II** **Albert, G.**, Hepburn, C. D., Pajusalu, L., Paalme, T., Pritchard, D. W. & Martin, G. (2020) Could ocean acidification influence epiphytism? A comparison of carbon-use strategies between *Fucus vesiculosus* and its epiphytes in the Baltic Sea. *Journal of Applied Phycology*. 32:2479–87.
- III** Pajusalu, L., **Albert, G.**, Fachon, E., Hepburn, C. D., Kotta, J., Kõivupuu A., Paalme, T., Pritchard, D. W., Põllumäe, A., Torn, K. & Martin, G. (2023) Species-specific responses of macrophyte production to the increasing CO₂ environment with potential ecosystem implications involved in the Baltic Sea. *Journal of Applied Phycology*. <https://doi.org/10.1007/s10811-023-03047-3>
- IV** **Albert, G.**, Pajusalu, L., Torn, K., Pritchard, D. W., Hepburn, C. D., Paalme, T., Põllumäe, A. & Martin, G. (2023). Comparison of carbon uptake strategies between *Chara aspera* and *Chara tomentosa* growing in the brackish Baltic Sea and in the freshwater lakes of Estonia. Manuscript preprint available at <http://dx.doi.org/10.2139/ssrn.4441208>

AUTHOR’S CONTRIBUTION (*’ denotes a moderate contribution, ‘**’ denotes a high contribution, ‘***’ denotes a leading role).

	I	II	III	IV
Original idea		*	**	***
Study design	*	*	**	**
Performing the experiments	***	***	***	***
Data collection	***	***	***	**
Data analysis	***	***	***	***
Manuscript writing	*	***	**	***

LIST OF ABBREVIATIONS

CCM – carbon concentrating mechanism

DIC/ C_T – (total) the sum of all dissolved inorganic carbon

DW – dry weight

NPP – net primary productivity

PAR – photosynthetically active radiation

pCO_2 – partial pressure of carbon dioxide

A_T (total alkalinity) – the capacity of water to resist acidification and maintain a stable pH level

OA – ocean acidification

pH – a measure of acidity or basicity of a solution, acidic solutions (values < 7) have lower pH values than basic solutions

pH_{NBS} – National Bureau of Standards scale

$\delta^{13}C$ – carbon⁻¹³ stable isotope

P vs. DIC – Photosynthesis versus dissolved inorganic carbon

CA – carbonic anhydrase

1. INTRODUCTION

The ocean's uptake of carbon dioxide (CO₂) contributes to reducing atmospheric CO₂ levels and mitigating climate change. The oceans have already absorbed around 30% of anthropogenic CO₂ emissions, resulting in ocean acidification (OA) (IPCC 2022). The term "ocean acidification" refers to the reaction of carbon dioxide with seawater which causes changes in the carbonate chemistry, leading to higher levels of dissolved carbon dioxide (CO₂) and bicarbonate (HCO₃⁻) and decreased levels of carbonate (CO₃²⁻) (Gattuso and Hansson 2011). As atmospheric CO₂ concentrations are expected to rise further under IPCC emission scenarios, the CO₂ concentration will be approximately 250% higher than it is now, causing the open ocean surface pH to fall by 0.3–0.4 units by the end of the 21st century (IPCC 2022).

The pH declines caused by increasing atmospheric CO₂ are more predictable in open ocean surface waters than in coastal seas (Duarte et al. 2013; Müller et al. 2016). Factors like weathering, river input, eutrophication, upwelling, atmospheric deposition, and remineralization all complicate the carbonate system of coastal watersheds altering local biogeochemistry (Doney et al. 2009; Omstedt et al. 2009, 2010). Additionally, metabolic activity (photosynthesis and respiration) plays a huge role, especially in shallow and sheltered areas (Duarte et al. 2013; Waldbusser and Salisbury 2014). Furthermore, changes in these processes are typically quite slow in the open ocean compared to coastal seas. Long-term ocean monitoring at various locations has shown that pH fluctuations in coastal waters can be ten times greater than in the open ocean (Hofmann et al. 2011).

All the above-mentioned characteristics of coastal seas also apply to the Baltic Sea, which is one of the world's largest estuaries. The Baltic Sea can be divided into the following subregions: the Gulf of Finland, the Gulf of Bothnia, the Gulf of Riga, Baltic Proper (which includes the Gulf of Gdansk), the Danish Straits and the Kattegat (Müller 2018), where over the past decades various processes have caused visible changes. Trends in salinity have been documented using observations dating back to the late 1800s (Gustafsson and Stigebrandt 2007; Mohrholz 2018). In contrast, pH trends in the Baltic Sea have received less attention (Almén et al. 2017). The open ocean's pH and DIC are relatively stable; the DIC is normally around 2.4 mM and the pH around 8 (Cole et al. 2021). The brackish Baltic Sea has a lower concentration of DIC than the ocean (about 1.2–1.5 mM, Raven and Samuelsson 2009; Müller 2016). Based on factors such as lower DIC concentration and low alkalinity in most regions, high freshwater input and lower salinity, it is highly likely that the Baltic Sea is more vulnerable to ocean acidification than the open ocean in general (Omstedt et al. 2010; Kuznetsov and Neumann 2013). It is projected that the surface water pH in the central Baltic Sea will decrease up to 0.5 pH units by the end of this century (HELCOM 2020).

There are also significant geographical differences across the Baltic Sea in salinity patterns which are directly related to alkalinity (higher salinity means

higher alkalinity and hence OA buffering capacity) (Fig. 1b). The dominant composition of the bedrock in the southeastern Baltic Sea is carbonates. River water in this area contains far more dissolved carbonate (which makes water alkaline) than river water in the northern regions of the Baltic Sea, where the bedrock is mostly granite and gneiss (Müller 2018). The water in the Gulf of Riga, for example, has a higher pH than that in Bothnian Bay. As a result, the former is less vulnerable to future ocean acidification than the latter. In addition to the natural variability of Baltic Sea salinity dynamics, climate change is expected to increase precipitation and runoff in the coming century (Saraiva et al. 2019), lowering the proportion of North Sea water and thus the salinity in the brackish Baltic Sea. The total alkalinity of the surface water has already increased in the Baltic Sea. The increase in total alkalinity has compensated for almost half of the CO₂-induced acidification in the central Baltic Sea and almost 100% in the Gulf of Bothnia (Müller 2018). Nevertheless, the increasing alkalinity should not be interpreted as protection against future CO₂-induced acidification (Müller 2018).

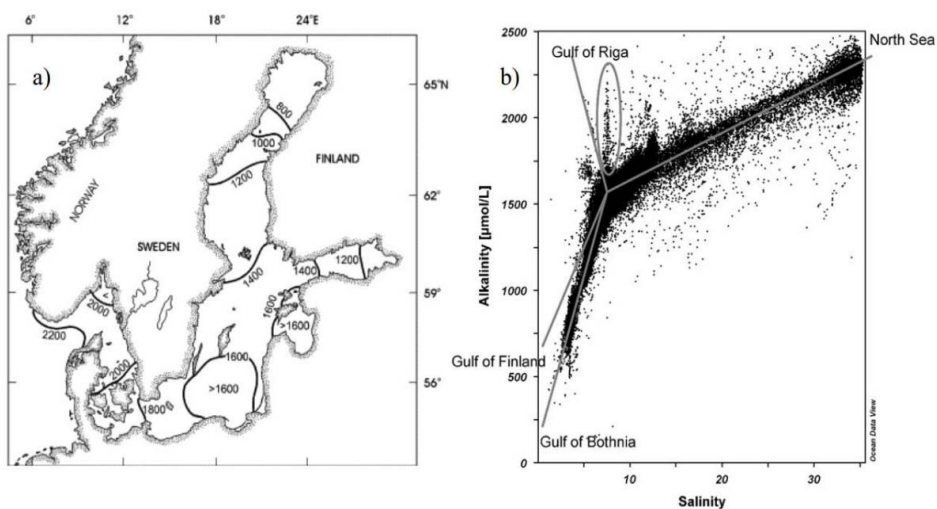


Fig. 1. a) Mean surface water total alkalinity of the Baltic Sea. b) Total alkalinity versus salinity in the Baltic Sea. Straight lines are guidelines, illustrating the mixing regimes. In the figure, the Bothnian Bay and the Bothnian Sea are merged into the Gulf of Bothnia. Encircled data originate from anoxic deep waters (Hjalmarsson et al. 2008).

The past 15 years of OA research on marine organisms has shown a great variety of responses between species, communities, and even life stages within the same species (Kroeker et al. 2010; Bednaršek et al. 2019; Schlenger et al. 2021), and there are no universal pH thresholds that apply to all organisms. Many marine species are vulnerable to the ongoing OA (Kuffner et al. 2008; Wittmann and Pörtner 2013; Brien et al. 2016), while others appear unaffected (Isari et al. 2016; Brien et al. 2016; Clark et al. 2020) or might even benefit from the increasing CO₂ in the environment (Koch et al. 2013; Bergstrom et al. 2019; Noisette et al.

2022). It has been suggested that many aquatic macrophytes benefit from OA; however, as a result, others may be outcompeted (Beardall and Raven 2004; Cornwall et al. 2017; Pajusalu et al. 2020). Due to the possible consequences for marine ecosystems, OA has been designated as one of the ten priorities for the United Nations Sustainable Development Goal (SDG) No 14 on the conservation and sustainable use of marine resources. The World Meteorological Organisation has also included OA as a headline climate indicator, acknowledging the relationship between rising carbon dioxide levels in the atmosphere and the climate system (Trewin et al. 2021). However, not much research on OA in the Baltic Sea can be found.

The Baltic Sea is species-poor as the existing salinity gradient limits the distribution of both marine and freshwater species. While the total number of recorded macrophytes reaches up to 560 species in the whole Baltic Sea, locally the species diversity can be very low (HELCOM 2020). For example, the Gulf of Riga, with its 71 species, has the lowest macrophyte diversity of all the basins in the Baltic Sea (HELCOM 2020). The main environmental factors structuring the macrophyte communities in the Baltic Sea besides salinity are the substrate and light (Martin 2000; Kautsky et al. 2017). In addition, the macrophytes are subjected to high epiphytic burdens, excessive nutrient concentrations, and poor underwater light conditions (Kersen et al. 2013). Various changes in macrophyte communities over the last few decades could be attributed to one of the Baltic Sea's major issues – eutrophication (HELCOM 2009, 2016; Kõuts 2023). The occurrence of perennial macroalgae has decreased, but the occurrence of fast-growing opportunistic filamentous algae has increased (Vahteri et al. 2000; Eriksson et al. 2002; Råberg 2004). Fast-growing filamentous macroalgae are able to take advantage of high nutrient concentrations or nutrient pulses, increasing their competitive success over perennial algal species (Karez et al. 2004; Korpinen et al. 2007), resulting in epibiosis, i.e., the spatial association between a substrate organism (basibiont) and a sessile organism (epibiont) attached to the basibiont's outer surface without trophically depending on it (Wahl 1989). Nevertheless, epiphytes are frequently observed to have a direct negative impact on the fitness of their hosts (Eriksson and Johansson 2003; Isæus et al. 2004).

Habitat-forming macroalgae are the foundation species of rocky shore habitats, which are prominent in the northern and western archipelago areas of the Baltic Sea coastal zones (Hällfors et al. 1981). Vertical zonation of algae species generates a structurally complex environment that is vital for both juvenile fish and small invertebrates, hence housing a significant portion of biodiversity in Baltic coastal ecosystems (Hällfors et al. 1981; Kautsky et al. 2017). Furthermore, macrophytes are significant as primary producers in trophic food chains, as well as for their nutrient cycling, impact on littoral microclimate and hydrochemical processes, and influence on sediment dynamics. Additionally, through carbon uptake and storage, submerged macrophytes have shown promising potential for mitigating climate change (Kennedy et al. 2010; McLeod et al. 2011; Krause-Jensen and Duarte 2016).

The macrophytes growing in the northeastern brackish Baltic Sea are macroalgae, charophytes, seagrass, and other angiosperms. Charophytes (*Chara* spp.) are a type of algae that have complex thalli and are rooted to soft-bottom sediment by rhizoids (Schubert and Blindow 2003). They can form very dense canopies in oligotrophic, calcareous lakes and ponds, as well as in sheltered bays of the Baltic Sea (Schubert and Blindow 2003). Benthic macroalgae predominate along rocky shores in the Baltic Sea, with bladderwrack *Fucus vesiculosus* being the most significant species in shallow-water hard-bottom algal communities in the NE Baltic (Torn et al. 2006; Kautsky et al. 2017; Jonsson et al. 2018). Filamentous macroalgae are widely distributed in the shallow coastal zones of the Baltic Sea and are known to form drifting mats (Arroyo et al. 2012), as well as grow as epibionts on substrate organisms (Wahl 1989). The red macroalgae, among all macrophytes, inhabit the deepest water layers, with *Furcellaria lumbri-calis* being the main habitat-forming species (Bučas et al. 2009). The unattached form of *F. lumbri-calis* grows on the soft bottom of Kassari Bay, forming a unique community in association with the red macroalga *Coccolytus truncatus* (Kersen 2013). The only seagrass in the NE Baltic Sea, *Zostera marina* is considered a keystone species on sandy bottoms (Boström et al. 2014). Submerged angiosperms are widespread on soft-bottom substrates and often coexist with *Z. marina* in mixed communities (Gustafsson 2013).

So far, macrophyte research in the Baltic Sea has primarily focused on how salinity, light, temperature, and nutrient load define the patterns of biomass and productivity of these important primary producers (Martin et al. 2006; Paalme et al. 2011; Jonsson et al. 2018; Barboza et al. 2019). The impacts of OA on macrophytes are still poorly studied, as existing research has yielded inconsistent findings (Pajusalu et al. 2016; Takolander et al. 2017; HELCOM 2021). Research mostly conducted in the ocean has shown that many macrophytes possess a CCM (carbon concentrating mechanism), which enables the use of bicarbonate (HCO_3^-) for photosynthesis. Since approximately 90% of the DIC ($\approx 35\%$ and pH 8.2) in seawater is in the form of bicarbonate and only 1% is CO_2 , the species that possess CCMs have a photosynthetic advantage (Cornwall et al. 2017). However, while CO_2 simply diffuses into the cell, the use of HCO_3^- is more complex. It involves active uptake and transport of HCO_3^- either by using intracellular or periplasmic carbonic anhydrases (CA) to convert HCO_3^- into CO_2 or secretion of H^+ to acidify the area of their boundary layer, locally shifting the DIC equilibrium to the creation of CO_2 to enhance dissociation of HCO_3^- to CO_2 (Giordano et al. 2005; Koch et al. 2013), therefore the process is energetically costly. CCMs are thought to have developed in response to historical carbon-limited environments (Meyer and Griffiths 2013), and they are found in a wide range of taxonomically and spatially varied species with varying underlying physiological mechanisms (Hepburn et al. 2011; Cornwall et al. 2017). Given that elevated CO_2 reduces the carbon deficit caused by slow CO_2 diffusion rates in seawater, photosynthesis and growth of macrophytes may improve. However, macrophytes with a CCM might not respond to increased CO_2 levels or respond only if the elevated CO_2 levels enable the CCM to downregulate thus allowing the energy to be used for other

purposes. Non-CCM macrophytes (that rely solely on diffusive CO₂), particularly red macroalgae, are expected to benefit from increasing dissolved CO₂ (Hepburn et al. 2011; Diaz-Pulido et al. 2016; Cornwall et al. 2017). In general, ocean acidification may benefit macrophytes that lack CCMs or have CCMs with low affinities for DIC by alleviating CO₂ constraints. The varied responses of macrophytes, both with and without CCMs, to rising CO₂ levels, could have an impact on interspecific competition and community structures in the future high CO₂ world.

Objectives and hypotheses

The overall aim of this doctoral thesis was to evaluate the impacts of elevated carbon in the common macrophytes in the coastal ecosystems of the northeastern part of the Baltic Sea to anticipate potential changes under future climate. This was achieved by studying the most prevalent macrophyte species, which, as primary producers, play a significant role in trophic food chains and nutrient cycling, provide habitat, and influence littoral microclimate, hydrochemical processes, and sediment dynamics. To understand and compare how different macrophyte species and communities might respond to predicted changes in seawater carbonate chemistry in the brackish Baltic Sea, carbon uptake mechanisms were studied. The abovementioned issues are addressed in four main hypotheses (**H1–H4**):

- The main expectation was that macrophytes in the northeastern Baltic Sea possess various types of carbon-concentrating mechanisms (CCMs) and exhibit different responses to varying dissolved inorganic carbon (DIC) concentrations (**H1**).
- It has been proposed that morphologically simple algae, such as the filamentous macroalgae, often appear to lack effective CCMs (Hepburn et al. 2011). Thus, it was hypothesised that the benefits of acidification are greater for filamentous species rather than species with more complex morphology (e.g., *Charophytes*, *Fucus*, *Zostera*, and other angiosperms studied in this thesis), which possess a CCM (**H2**).
- Furthermore, non-CCM macroalgae, particularly red macroalgae that thrive in low-light environments, are expected to benefit the most from OA due to reduced costs of carbon uptake as a result of greater CO₂ availability (Hepburn et al. 2011; Diaz-Pulido et al. 2016; Cornwall et al. 2017). Specifically, it was hypothesised that red macroalgae do not possess CCMs and therefore benefit the most from increasing CO₂ compared to other studied macrophyte groups (**H3**).
- Different aquatic habitats could have significantly different chemical, physical, and biological properties (McKinley et al. 2011; Shao et al. 2015). Thus, we hypothesised that the same species (e.g., *Chara aspera* and *C. tomentosa*) growing in freshwater lakes and the brackish Baltic Sea have significantly different carbon uptake mechanisms (**H4**).

2. MATERIAL AND METHODS

2.1 Study system

The seawater carbon system is characterized by four measurable parameters and at least two of these are needed in order to quantitatively determine the carbon system related to ocean acidification. These parameters are total dissolved inorganic carbon (C_T , the sum of all inorganic carbon species dissolved in seawater), total alkalinity (A_T), partial pressure of carbon dioxide (pCO_2), and the negative decadic logarithm of proton concentration (pH), which refers to H^+ activity or concentrations depending on the pH-scale used. C_T is defined as $C_T = [CO_2] + [HCO_3^-] + [CO_3^{2-}]$ (Dickson et al. 2007). The term A_T in seawater comes from continental weathering processes and is delivered to the sea via riverine input on a global scale. It is named “the backbone” of the marine CO_2 system, which governs the rate of ocean acidification. Generally, the alkalinity in the ocean is stable ($\sim 2200\text{--}2300 \mu\text{mol kg}^{-1}$) (Dickson et al. 2007); however, in the Baltic Sea, it varies greatly between different geographical locations (Fig. 1a). North Sea water has typical ocean A_T concentrations ($\sim 2250 \mu\text{mol kg}^{-1}$) which is much higher than the average Baltic Sea A_T of approximately $1530 \mu\text{mol kg}^{-1}$ (calculated by dividing the total A_T pool of $\sim 33,000 \text{ Gmol}$ (Gustafsson et al. 2014) by the total water volume of $\sim 21,600 \text{ km}^3$) (Hjalmarsson et al. 2008).

The water samples (250 ml) for the carbonate system calculations were collected from the studied species sites: Väike Strait (**III**, **IV**), Küdema Bay (**III**), Kõiguste Bay (**II**, **III**), Kassari Bay (**I**, **III**), Kihelkonna Bay (**III**) (Fig. 2), lake Seljajärv, (**IV**) and lake Äntu Sinijärv (**IV**) at the depth of 0.5 m using laboratory glass bottles which were filled carefully to avoid any air bubbles. The samples were preserved at $4 \text{ }^\circ\text{C}$ until the analysis following HELCOM draft guidelines for sampling and determination of total alkalinity (HELCOM 2016). Triplicate subsamples were used for the total alkalinity analysis by potentiometric titration using a Metrohm 848 Titrino Plus. For the calculation of the carbonate system, A_T (total alkalinity) and pH_{NBS} (National Bureau of Standards scale) were measured, and summer (June–August) average pH and temperature were used for C system calculations, which were executed using $CO_2\text{SYS}$ software (Lewis and Wallace 1998) (Table 1).

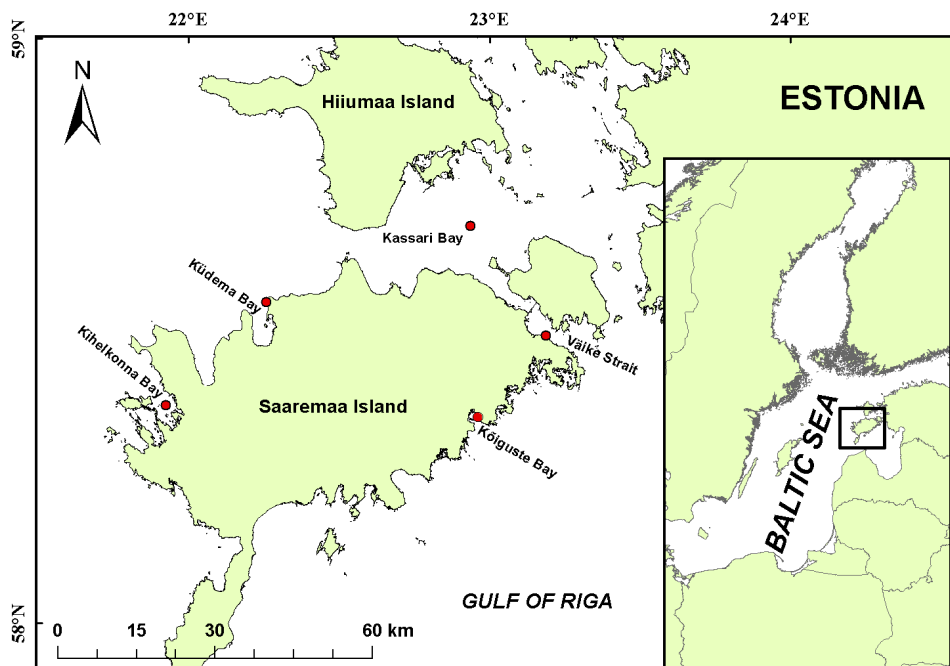


Fig. 2. Locations of sample collection sites in the West Estonian Archipelago, NE Baltic Sea (I–IV).

Table 1. Carbonate chemistry of Väike Strait (III, IV), Küdema Bay (III), Kõiguste Bay (I, III), Kassari Bay (I, III), Kihelkonna Bay (III), lake Seljajärv (IV) and lake Äntu Sinijärv (IV).

Sampling site	Väike Strait	Küdema Bay	Kõiguste Bay	Kassari Bay	Kihelkonna Bay	Seljajärv	Äntu Sinijärv
pH _{NBS}	8.3	8.3	8.3	8.3	8.3	8.00	7.88
A _T (μmol kg ⁻¹)	1600	1800	1800	1900	2000	3016	4048
pCO ₂ (μatm)	303	341	343	362	382	1387	3727
HCO ₃ ⁻ (μmol kg ⁻¹)	1421	1600	1604	1694	1783	2995	4034
CO ₃ ²⁻ (μmol kg ⁻¹)	32	92.2	91	96	101	10	7
CO ₂ (μmol kg ⁻¹)	11.3	12.8	12.9	13.6	14.3	107	287
DIC (μmol kg ⁻¹)	1514	1705	1708	1803	1899	3112	4329

pCO₂, HCO₃⁻, CO₃²⁻, CO₂, and DIC were calculated based on A_T and pH_{NBS} using CO₂sys.

2.2 Studied macrophytes

Macrophytes for this study (laboratory experiments) were collected around Saaremaa Island in the West Estonian Archipelago Sea (northern Baltic Sea) in five different bays (Fig. 2; Table 2). All studied specimens from brackish water were collected by scuba diving (**I–IV**) and from freshwater lakes using a hook (**IV**) (Table 2). The study focuses on the dominant macrophyte species in different benthic communities in the northeastern part of the Baltic Sea (according to the Phytobenthos database of the Estonian Marine Institute, University of Tartu) (**I, II, III** and **IV**; Table 2, Fig 3). For this thesis such frequent/important macrophytes were combined into groups as follows: *Chara*; *Fucus*; filamentous macroalgae; red macroalgae attached and unattached forms; *Zostera* and other angiosperms) (**III**). In addition, the same two studied *Chara* species that inhabit the brackish Baltic Sea, also inhabit freshwater lakes of Estonia (Seljajärv and Äntu Sinijärv), therefore, a carbon uptake mechanism comparison of the same species growing in different habitats was also explored (**IV**).

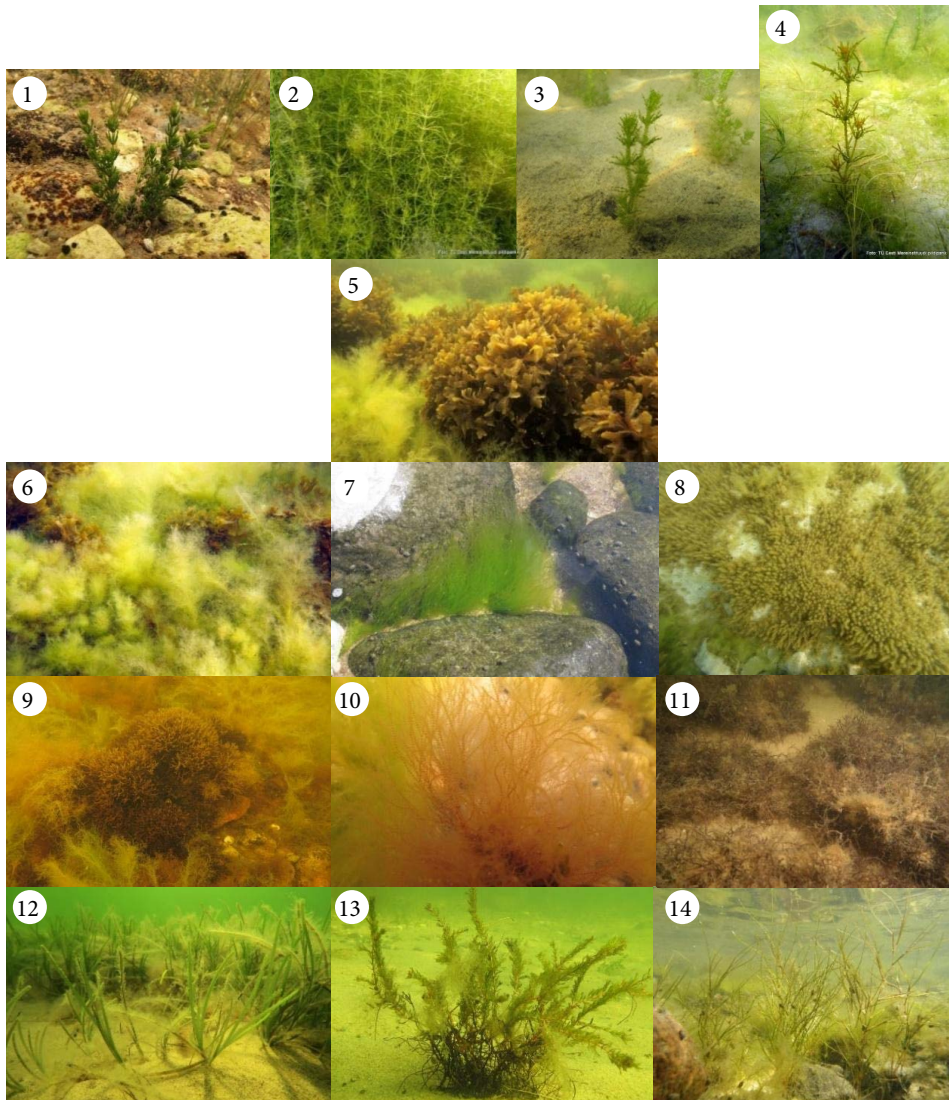


Fig. 3. Studied macrophyte species: 1. *Chara connivens* 2. *C. aspera* 3. *C. canescens* 4. *C. tomentosa* 5. *Fucus vesiculosus* 6. *Cladophora glomerata* 7. *Ulva intestinalis* 8. *Pylaiella littoralis* 9. *Furcellaria lumbricalis* (attached) 10. *Ceramium tenuicorne* 11. *Furcellaria lumbricalis* and *Coccotylus truncatus* (unattached) community 12. *Zostera marina* 13. *Myriophyllum spicatum* 14. *Stuckenia pectinata* (photos downloaded from the Estonian Marine Institute photo library).

Table 2. The groups, species and taxonomic group of studied macrophytes, locations where they were collected, and the paper in which each species was examined

Group	Species	Taxonomic group	Site name	Collection depth	Paper
<i>Chara</i>	<i>Chara connivens</i> Salzm. ex-Braun		Väike Strait	1.5 m	III
	<i>Chara aspera</i> Willd.	Charophytes	Väike Strait+ Seljajärv	1.5 m+0.4m	III, IV
	<i>Chara canescens</i> Loisel.		Väike Strait	1.5 m	III
	<i>Chara tomentosa</i> L.		Väike Strait+ Äntu Simjärv	1.5 m+0.4 m	III, IV
<i>Fucus</i>	<i>Fucus vesiculosus</i> L.	brown macroalgae	Küedema Bay	1 m	II, III
Filamentous macroalgae	<i>Cladophora glomerata</i> (L.) Kütz	green macroalgae			III
	<i>Ulva intestinalis</i> L.	green macroalgae	Küedema Bay	0.5 m	III
	<i>Pylaiella littoralis</i> (L.) Kjellm	brown macroalgae			II, III
	<i>Furcellaria lumbricalis</i> (Hudson) J.V. Lamouroux			5 m	III
(unattached forms)	<i>Ceramium tenuicorne</i> (Kützing) Waern		Kõiguste Bay		II, III
	<i>Furcellaria lumbricalis</i> (Hudson) J.V. Lamouroux	red macroalgae			I, III
<i>Zostera</i>	<i>Coccolylus truncatus</i> (Pallas) M.J. Wynne & J.N. Heine		Kassari Bay	7 m	I, III
Other angiosperms	<i>Zostera marina</i> L.	seagrass	Kihelkonna Bay	3 m	III
	<i>Myriophyllum spicatum</i> L.				III
	<i>Stuckenia pectinata</i> (L.) Börner	angiosperms	Kõiguste Bay	1 m	III

2.3 Experiments

Photosynthesis vs. dissolved inorganic carbon (P vs. DIC) curves and pH drift experiments were conducted at the Estonian Marine Institute's Kõiguste field station on Saaremaa Island. The carbon isotope ($\delta^{13}\text{C}$) analysis was conducted at the University of Tartu, Institute of Chemistry.

Photosynthesis vs. DIC curves

The idea of the P vs. DIC experiment was to provide characteristics of carbon acquisition for the studied macrophytes under different DIC concentrations by using the oxygen evolution method. The exact methodology (Beardall and Roberts 1999) is described in papers I–IV.

pH drift experiment

The pH drift method is a quick and efficient way to examine the carbon metabolism of macrophytes. Macrophytes that solely fix CO_2 (obligate CO_2 consumers) cannot elevate the pH above a specific point since carbon speciation and acidity are mutually exclusive. In the northeastern brackish Baltic Sea at pH levels of 9–9.2 (depending on salinity and alkalinity variability) and above, the concentration of CO_2 is too small to support photosynthetic activity for obligate CO_2 users. The exact methodology (Maberly 1990; Hepburn et al. 2011; Cornwall et al. 2017) is described in papers I–IV.

Carbon isotope ($\delta^{13}\text{C}$) analysis

Carbon isotope ($\delta^{13}\text{C}$) tissue analysis was performed on macrophytes to identify each species' carbon acquisition reliance on diffusive CO_2 supply vs. carbon concentrating mechanism (CCM). $\delta^{13}\text{C}$ values less than -30‰ , in general, imply a reliance on diffusive CO_2 supply and the absence of a functional CCM. $\delta^{13}\text{C}$ values greater than -10‰ suggest the presence of an active CCM. Macrophytes having $\delta^{13}\text{C}$ tissue values between -30‰ and -10‰ are expected to use a variety of carbon uptake techniques. The exact methodology (Raven et al. 2002) is described in papers I–IV.

Measurements of carbonate chemistry in natural macrophyte communities

The natural fluctuations of pH and CO_2 concentration ($\mu\text{mol kg}^{-1}$) were measured in five different macrophyte communities (*Chara*, *Fucus*, *Furcellaria* (unattached form), *Zostera* and other angiosperms) (Fig. 1; Table 1). These carbonate chemistry parameters, as well as water temperature and salinity, were measured continuously among the vegetation using an optical CO_2 sensor (AMT Analysenmesstechnik GmbH, Germany) with an external interface to CTD probe systems (Sun & Sea Technology GmbH, Germany). In July 2018, measurements were

taken at each site for a full 24-hour cycle with a sampling frequency of 20 minutes. Using an ODYSSEY PAR logger, the irradiance among vegetation was quantified as photosynthetically active radiation (PAR). Measurements were recorded for one week on various days at each site, and weather conditions were similar throughout the study period.

2.4 Statistical methods

The R statistical software platform was used to conduct the statistical analysis for the P vs. DIC experiment in publications **I–IV** (R Core Team 2017). The Michaelis–Menten curve (Johnson and Goody 2011) was fitted to plots of photosynthetic rate vs. DIC concentration. The Michaelis–Menten equation is $P = P_{\max} / \text{DIC} + K_{0.5}$, where P_{\max} is the point at which the maximum photosynthetic rate of the organism is reached, and $K_{0.5}$ is the concentration of DIC at which the photosynthetic rate of the organism is half of P_{\max} (Johnson and Goody 2011). The lme4 package in R was used in a maximum likelihood, non-linear mixed effects modelling approach (Bates et al. 2015). This approach allowed a single model to be used, whilst accounting for species-level (fixed factor) and individual-level (random factor, replicate incubation id) variability in P_{\max} and $K_{0.5}$. Within-species comparisons of P_{\max} and $K_{0.5}$ were made using simultaneous t-tests, using the R package multcomp (Hothorn et al. 2008). For the pH drift experiment, the final (48-hour) pH values were compared using a two-way ANOVA post hoc-test and two-tailed t-test (**I–IV**). For this thesis, the Kruskal–Wallis H test was used to (R Core Team 2022) analyze variations in pH compensation points (48-hour values) among studied macrophyte groups. Spearman’s Rank-Order correlation was conducted to explore the relationship between pH compensation points and $\delta^{13}\text{C}$ values of studied species. For all statistical analyses, a probability of 0.05 was used to determine statistical significance.

3. RESULTS

3.1 Laboratory experiments

Ceramium tenuicorne had a significantly higher P_{\max} than all other studied species (post-hoc test, $p < 0.001$) and *Z. marina* had significantly higher P_{\max} values than *C. aspera* (post-hoc test; $p = 0.010$), *F. lumbricalis* (unattached) ($p = 0.026$), *F. vesiculosus* ($p = 0.040$), *P. littoralis* ($p = 0.031$), and *C. tomentosa* ($p = 0.032$) (Figure 4; Table 3). In addition, *C. truncatus* had a significantly higher P_{\max} value than *F. lumbricalis* (post-hoc test; $p < 0.001$).

A significant difference between the $K_{0.5}$ values was found between *Z. marina* and *C. tenuicorne* (post-hoc test; $p = 0.002$), *F. vesiculosus* (post-hoc test; $p = 0.002$), *P. littoralis* ($p = 0.003$) *C. truncatus* (post-hoc test; $p = 0.003$). The $K_{0.5}$ values also differed significantly between *F. lumbricalis* (unattached) and *C. truncatus* (post-hoc test; $p < 0.001$), *P. littoralis* (post-hoc test; $p < 0.001$), *F. vesiculosus* (post-hoc test; $p < 0.001$), *C. tenuicorne* (post-hoc test; $p < 0.001$). No other statistically significant differences in P_{\max} or $K_{0.5}$ were observed.

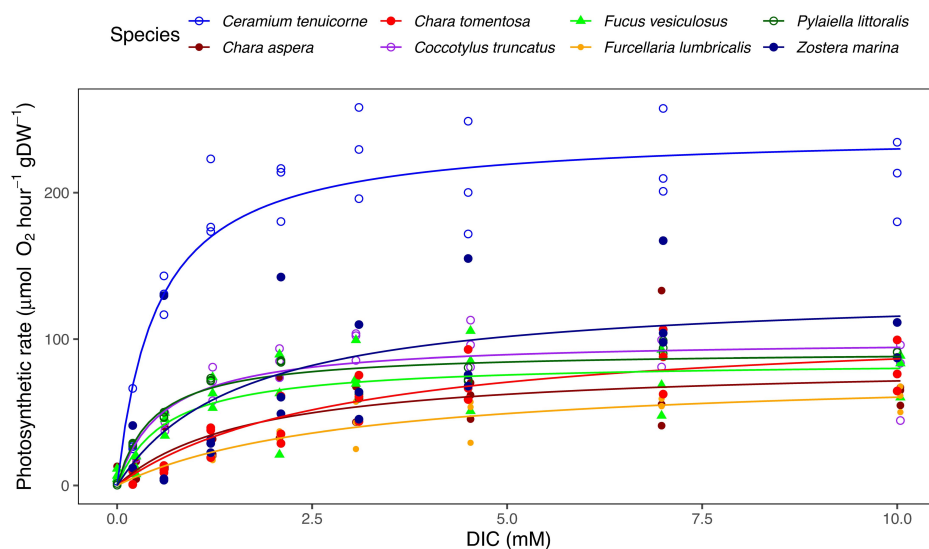


Fig. 4. The photosynthetic rate (P_{\max}) of *C. tenuicorne*, *C. tomentosa*, *F. vesiculosus*, *P. littoralis*, *C. aspera*, *C. truncatus*, *F. lumbricalis* (unattached), and *Z. marina* ($n=3$ per species) at different concentrations of dissolved inorganic carbon (mM).

Table 3. The half-saturation constant ($K_{0.5}$ [DIC]) and maximum photosynthetic rates (P_{max}) of *C. tenuicorne*, *C. tomentosa*, *F. vesiculosus*, *P. littoralis*, *C. aspera*, *C. truncatus*, *F. lumbricalis* (unattached), and *Z. marina* \pm SE (n=3 per species)

	$K_{0.5}$ [mM DIC]	P_{max} ($\mu\text{mol O}_2 \text{ h}^{-1} \text{ gDW}^{-1}$)
<i>Ceramium tenuicorne</i>	0.50 \pm 0.10	241.28 \pm 10.41
<i>Chara tomentosa</i>	2.82 \pm 0.40	90.28 \pm 10
<i>Fucus vesiculosus</i>	0.52 \pm 0.14	88.86 \pm 19.1
<i>Pylaiella littoralis</i>	0.56 \pm 0.13	93.33 \pm 9.7
<i>Chara aspera</i>	2.79 \pm 1.01	83.88 \pm 9.5
<i>Coccotylus truncatus</i>	0.57 \pm 0.20	114 \pm 8.2
<i>Furcellaria lumbricalis</i>	3.22 \pm 0.16	71.69 \pm 13.9
<i>Zostera marina</i>	2.11 \pm 0.71	152.21 \pm 19.4

The results from the pH drift experiments indicated that all studied species in the brackish Baltic Sea (n=3 per species) within the six study groups raised pH above 9.2 (Fig. 5), suggesting that they can all use HCO_3^- for photosynthesis. The pH compensation points varied from 9.31 to 10.51. The pH compensation point of red macroalgae was substantially lower than that of filamentous algae (Kruskal–Wallis H test, $p < 0.001$) and *Chara* group ($p < 0.001$); however, there was no significant difference when compared to the other studied macrophyte groups ($p > 0.05$) (Fig. 5). *Chara* and filamentous algae had higher pH compensation points compared to the other studied species. In addition, *Zostera* and other angiosperms had higher pH compensation points compared to *Fucus* and red macroalgae. There was a correlation between pH compensation points and $\delta^{13}\text{C}$ values of the studied macrophyte species (Spearman $R = 0.34$, $p < 0.05$) (III). There was no significant difference found between the pH compensation points of freshwater *C. aspera* 8.99 \pm 0.14 (n=3) and *C. tomentosa* 9.45 \pm 0.1 (n=3) (Two-tailed t-test: $t=1.1043$, $p=0.3316$). However, the pH compensation points of the brackish Baltic Sea *C. aspera* and *C. tomentosa* were significantly higher than the same species growing in the freshwater lakes (Two-way ANOVA: $f=17.39$, $p=0.003$) (IV).

The carbon isotope ($\delta^{13}\text{C}$) values of studied species (n=3 per species) ranged between -30 and -10‰ . The only exception was the red macroalgal species *C. truncatus* which had a $\delta^{13}\text{C}$ value of $-36.20 \pm 0.11\text{‰}$ (mean \pm SE). The seagrass *Zostera* had the highest mean $\delta^{13}\text{C}$ value, followed by other angiosperms, *Fucus* and *Chara* (Fig. 5). Compared to other studied species, filamentous macroalgae had a more negative mean $\delta^{13}\text{C}$ value, and red macroalgae had a substantially more negative mean $\delta^{13}\text{C}$ value, with large differences between species (Fig. 5) (III). The carbon isotope values between brackish *C. aspera* $-13.11\text{‰} \pm 0.26$ (mean \pm SE, n=3), and *C. tomentosa* $-13.88\text{‰} \pm 0.22$ (n=3), were considerably different compared to freshwater *C. aspera* $-30.23\text{‰} \pm 0.27$ (n=3) and *C. tomentosa* $-32.33\text{‰} \pm 0.90$ (IV).

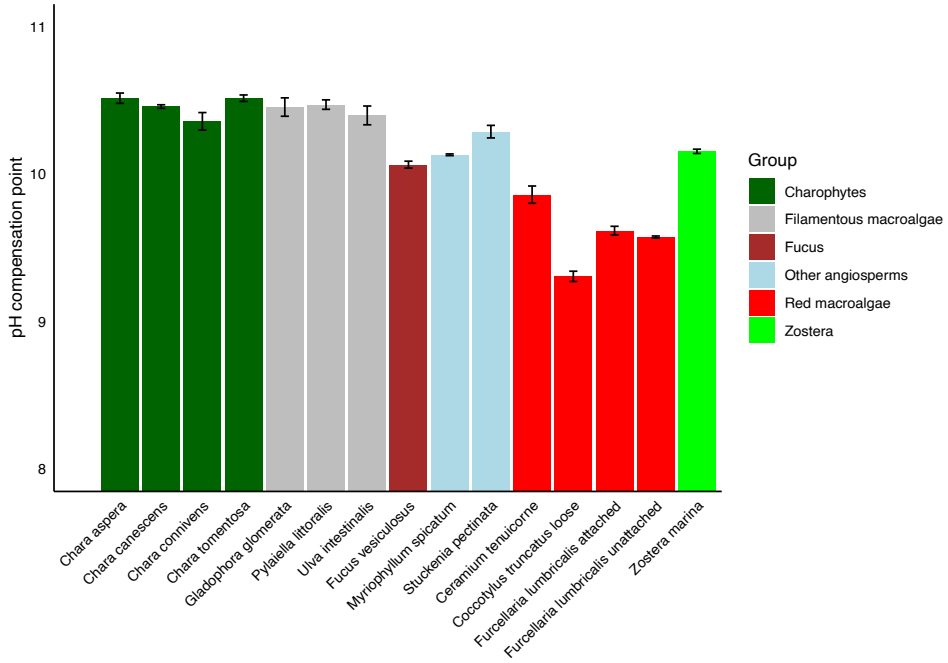


Fig. 5. Comparison of pH compensation points of the studied macrophyte groups.

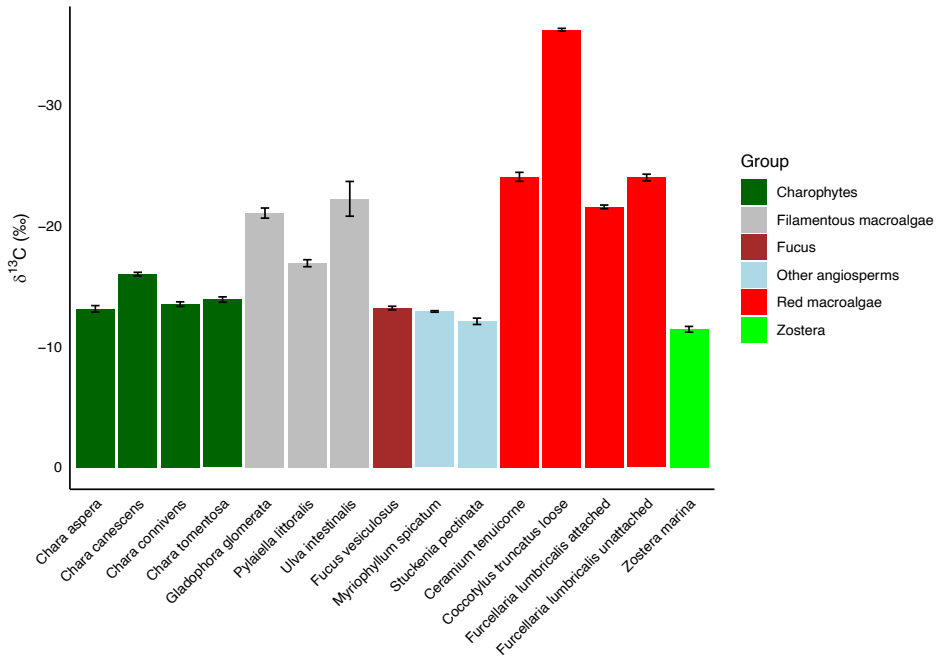


Fig. 6. Comparison of carbon stable isotopes ($\delta^{13}\text{C}$) of the studied macrophyte groups.

3.2 Measurements of carbonate chemistry in natural macrophyte communities

The diurnal fluctuation in pH was the highest in the (other) angiosperm and charophyte community, where it fluctuated by 0.9 (mean pH 7.91) and 0.8 pH units (mean pH 9.78), respectively, during the active vegetation period (Fig. 6a). The diurnal fluctuations in *Fucus*, *Furcellaria* (unattached), and *Zostera* communities were similarly varying between pH 8.31–8.95, pH 8.26–8.73 and pH 8.03–8.75, respectively. As a rule, pH values peaked around noon and decreased at night in natural communities (Fig. 6a). The diurnal fluctuations in pH values were inverse to the fluctuations in CO₂ concentrations (mg L⁻¹) (Fig. 6a, b).

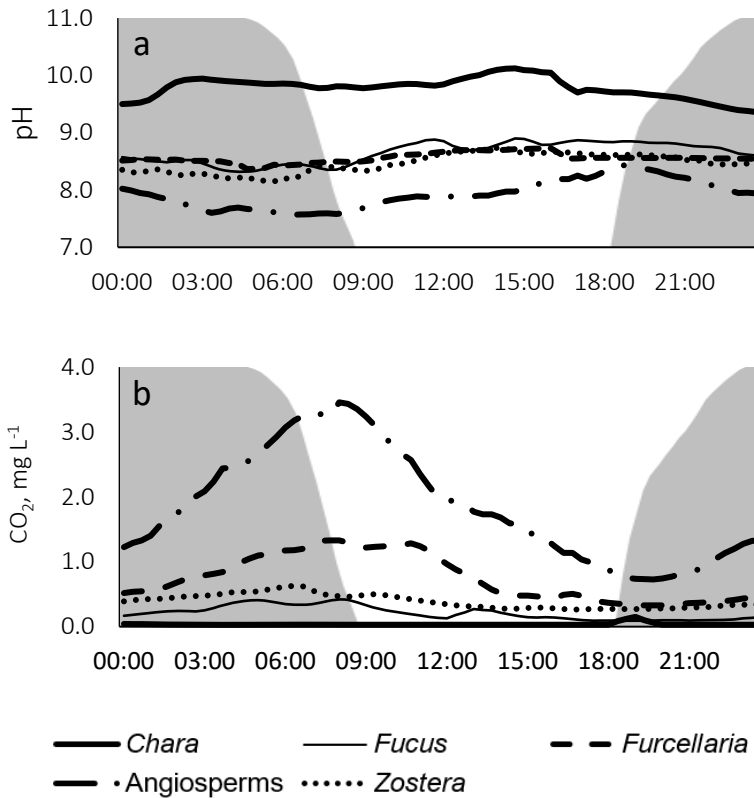


Fig. 6. The diurnal fluctuations in (a) pH values and (b) CO₂ concentrations for specified study groups in July (continuous recordings). The grey background indicates light conditions measured at a 2-meter depth during a cloudless day (*Chara* community).

4. DISCUSSION

This research indicates that common submerged macrophytes found in the Baltic Sea, such as macroalgae, charophytes, seagrass, and other angiosperms, likely have carbon-concentrating mechanisms (CCMs) (I–IV). All studied species, apart from red macroalga *C. truncatus* (II), have the capacity to take up both types of carbon forms (CO_2 and HCO_3^-) for photosynthesis (I–IV). It was also found that macrophytes' primary productivity is frequently limited by carbon availability during their active growth period; therefore, an additional CO_2 supply could enhance their primary productivity. However, there was considerable diversity in carbon uptake discrimination among the species analysed (I–IV) in the six groups (III).

The *Chara* group indicated that bicarbonate is the primary carbon source used for photosynthesis. However, due to the current low CO_2 availability in the natural community during their active growth period, *Chara* spp. could gain from rising CO_2 levels by downregulating the CCM operation (III, IV). Secondly, for perennial brown alga, *F. vesiculosus*, the $\delta^{13}\text{C}$ and pH compensation values indicate HCO_3^- utilisation; due to its high affinity for CO_2 and relatively low photosynthetic increase with increasing DIC concentrations, the benefit from elevated CO_2 levels for *F. vesiculosus* is not significant in the future (II, III). Thirdly, the study focused on three dominant fast-growing filamentous macroalgae in the northern Baltic Sea: *U. intestinalis*, *C. glomerata* (greens) (III), and *P. littoralis* (brown) (II). Different forms of CCMs are most likely present in the examined filamentous macroalgae. Brown filamentous algae have a CCM with a high affinity for DIC (carbon-saturated CCM species) (II), and greens (III) downregulate CCM operation when a sufficient CO_2 concentration is available for photosynthesis. This means that among the studied filamentous macroalgae, greens will likely get a higher advantage from increasing CO_2 than brown algae *P. littoralis*, and the greens will be the second “winners” after red macroalgae within the studied groups (III). Our findings indicate that red macroalgae prefer to use CO_2 over HCO_3^- as a carbon source (I, II, III). They appear to downregulate HCO_3^- when a sufficient amount of CO_2 is available. Consequently, red macroalgae are expected to benefit from elevated CO_2 more than the other studied groups (III). (III). The seagrass *Z. marina* and other studied angiosperms (*M. spicatum* and *S. pectinata*) have similar CCMs (III), which is consistent with previous research indicating angiosperms' effective use of HCO_3^- (Maberly and Madsen 2002, Hussner et al. 2016). However, the current DIC availability in the Baltic Sea may still limit the photosynthesis of *Z. marina*. Therefore, there could be a photosynthetic gain for *Z. marina* from increasing CO_2 , particularly if the CCM could be down-regulated (III).

This study demonstrates that macrophytes in the NE Baltic Sea have different carbon utilisation mechanisms, and as a result display various responses to elevated carbon (e.g., mainly no or positive responses). However, the seasonal fluctuations of light and nutrients mediate the effects of ocean acidification in macroalgae (Xu

and Gao 2012; Gao et al. 2020) and other organisms (Xu and Gao 2012; Gao et al. 2020) and should be taken into consideration when the results of laboratory experiments are extrapolated to natural ecosystems (Takolander et al. 2017). In this study, we found that *F. vesiculosus* and *P. littoralis* have very similar CCMs (II), as implied by P_{\max} and $K_{0.5}$ values, indicating similar photosynthetic response to elevated CO_2 ; however, this knowledge could lead to premature conclusions if we do not consider other factors. As an example, research suggests that *P. littoralis* might experience advantages from warming in the context of climate change. If there is a decline in ice cover, more light may be available for photosynthesis during the early spring when surface water remains cold. This shift in peak abundance of *P. littoralis* to an earlier timeframe could have significant implications for other species, including the reproduction and settlement of fucoids and other algae (Berger et al. 2003; Råberg et al. 2005).

Additionally, the metabolic activity (photosynthesis and respiration) of macrophytes has a significant impact on the carbonate chemistry in shallow coastal waters. In this study, the highest pH fluctuation occurred in angiosperm (0.9 pH units) and charophyte (0.8 pH units) communities (Fig. 4a), and it is higher than projected by the year 2100 (IPCC 2022, HELCOM 2021). Similarly, Middelboe and Hansen (2007) found that the diurnal and seasonal pH variability in macroalgal habitats could exceed one unit. Frequently, during spring, summer, and autumn, when photosynthetic activity removes carbon from seawater, the pH in the region remains high, usually around 9 or above, while in winter, pH values are lower, approximately around 8. This pH pattern may be disrupted by the stochastic upwelling of CO_2 -rich water, as observed in previous studies (Saderne et al. 2013), and with future climate change, the frequency and intensity of such events may increase due to the deeper waters absorbing more atmospheric carbon (Omstedt et al. 2012). Consequently, seagrass and macroalgal habitats frequently maintain high pH levels, potentially serving as refuge habitats against ocean acidification and becoming more important, especially for calcifying species (Takolander et al. 2017). The basis for any future predictions is the knowledge of the current carbonate system in different marine habitats. In this study, we calculated the carbonate system of all sites where the studied species (I–IV) were collected (Table 1). First, it should be highlighted that the alkalinity in all studied sites in the West Estonian Archipelago Sea (northern Baltic Sea) is lower (1600–2000 $\mu\text{mol kg}^{-1}$) than in the ocean (~2200–2300 $\mu\text{mol kg}^{-1}$) (Dickson et al. 2007). Meaning that in the studied sites, the OA buffering capacity is lower than in the ocean (Table 2). Another important buffering factor is the salinity of the water. In our studied sites, the salinity was significantly lower (5–7‰) than in the ocean (35‰) which makes the brackish Baltic Sea more vulnerable to acidification.

The most remarkable difference in carbonate chemistry was described between the Baltic Sea and freshwater lakes. We found that the same charophyte species *C. aspera* and *C. tomentosa* growing in the brackish Baltic Sea and Estonia's freshwater lakes have different carbon uptake mechanisms. The reason for different CCM operations between brackish and freshwater charophytes is probably due to their local adaptation differences. The freshwater lakes act as a CO_2 source rather

than a sink; therefore, they do not need to use HCO_3^- for photosynthesis because energetically inexpensive CO_2 is in abundance (IV). In the Baltic Sea, a substantial difference in carbonate chemistry was found between the Väike Strait, where the group *Chara* grows (III, IV), and Kihelkonna Bay, where the seagrass *Z. marina* monospecific stand is represented (III). All the other studied sites (inhabited by the rest of the studied groups: red macroalgae, filamentous macroalgae, other angiosperms, and *Fucus*) had relatively similar carbon values. This is also consistent with the *in-situ* carbonate chemistry measurements. The lowest CO_2 concentrations were measured in the *Chara* community, and the highest CO_2 concentrations were in the angiosperm community, as found in the carbonate system calculations. Likewise, similar trends are visible in other studied communities. These short-term *in-situ* measurements also indicate a varying DIC availability in different communities which is consistent with the carbonate system calculations, varying between 1.5–1.9 mM. However, the magnitude of pH changes depends on the carbon use strategies of macrophytes and on the dominant species in the community as well as the community biomass.

As an additional factor, the Baltic Sea is highly eutrophicated. Despite significant reductions in anthropogenic nitrogen and phosphorus inputs over recent decades, improvements in key indicators of eutrophication have not been observed, as evidenced by the continuous increase in phosphorus pools (Kõuts et al. 2021, 2023). Studies have suggested that *P. littoralis* thrives in eutrophic conditions, and therefore, the projected increase in nutrient inputs for the future (Meier et al. 2012) could potentially lead to intensified *P. littoralis* blooms, especially when water temperatures remain optimal for the species (Takolander et al. 2017). However, our research demonstrated that the carbon (II) and nutrient uptake of *P. littoralis* was similar to *F. vesiculosus* but significantly different from *U. intestinalis* (authors' unpublished data). In this study, we found that filamentous algae (*U. intestinalis*, *C. glomerata*) (III) had more negative isotope values than the groups *Zostera*, *Fucus*, and other angiosperms, which indicates a higher possibility of CCM downregulation. Furthermore, Middelboe and Hansen (2007) and Pajusalu et al. (2013) observed the highest photosynthetic stimulation of *U. intestinalis* by CO_2 . Therefore, when CO_2 and nutrient concentrations increase, the opportunistic filamentous alga *U. intestinalis* could outcompete slow-growing facultative CCM species in hard bottom shallow-water areas, especially perennial species (e.g., *F. vesiculosus*) (III), without the possibility of downregulating CCM operation.

Fucus vesiculosus is the most extensively studied macrophyte species in the Baltic Sea in the context of OA, but the findings from various studies still show some contradictions. Some research indicates either no response on a short-term basis (Pajusalu et al. 2013) or a very weak response (Werner et al. 2016) to elevated carbon. On the other hand, three studies (Gutow et al. 2014; Al-Janabi et al. 2016; Werner et al. 2016) reported negative effects, with one of these studies linking the decline in *Fucus* biomass to the combination of CO_2 treatment and elevated temperature (Werner et al. 2016). Additionally, two studies found beneficial effects (Nygård and Dring 2008; Al-Janabi et al. 2016). As mentioned

earlier, our studies (II, III) indicate that *F. vesiculosus*, a perennial brown alga with slow metabolism, will not experience significant photosynthetic benefits under future CO₂ conditions. As a result, lower competitive fitness for this species under future climate conditions could lead to shifts in the distribution of *F. vesiculosus* habitat, with implications for species richness. *Fucus vesiculosus* habitat is the most species-rich macroalgal habitat in the Baltic Sea, and a reduction of *F. vesiculosus* will inevitably lead to a reduction in species richness (Schagerström et al. 2014).

However, extrapolating results from short-term experiments (in natural systems) or laboratory experiments to nature has numerous challenges. The contradicting results in the Baltic Sea as well as in other ecosystems could be a result of other affecting variables that have not been taken into consideration. For example, if photosynthesis is limited by nutrient availability, a carbon increase would only have a minor effect as Liebig's law of the minimum states: the growth only occurs at the rate permitted by the most limiting factor (Sprengel 1840). Nevertheless, when nutrients do not limit, photosynthesis should increase if there is no light limitation. For instance, the impact of light on the carbon metabolism of algae becomes evident in the distribution of carbon uptake strategies among natural macroalgal communities: macroalgae that solely depend on the diffusive uptake of CO₂ (non-CCM species, mostly red macroalgae) show a positive correlation with increasing depth because the presence of limited light reduces the energy available for operating a CCM (Hepburn et al. 2011; Lovelock et al. 2020). However, even coexisting species from the same taxonomic group could respond differently to future elevated CO₂ due to significantly different CCMs (I). Our research (I) indicates a possible change in the balance of the unique unattached loose-lying red macroalgal community formed by *F. lumbricalis* and *C. truncatus*. This community is commercially important as the chemical compounds in *F. lumbricalis* are used for furcellaran (hydrocolloid, extracted from algae) production (Tuvikene et al. 2010; Tuvikene and Robal 2015). However, the predicted increase in CO₂ concentrations likely favours *C. truncatus* (non-CCM species) over *F. lumbricalis* (CCM species). This will lead to a lower quality of the product and impact commercial exploitation (I).

Moreover, the predicted changes in salinity and temperature (IPCC 2022) will further impact macrophytes directly or indirectly, and when the factors change simultaneously, it is even more difficult to predict future changes, especially at the community or ecosystem level. The effects of OA on macrophytes regarding the whole brackish Baltic Sea remain uncertain. However, based on previous literature (Koch et al. 2013; Middelboe and Hansen 2007; Pajusalu et al. 2015, 2016) and this study (I–IV), the findings suggest a potential increase in primary productivity, especially in red macroalgae (III). Additionally to elevated CO₂, coastal eutrophication promotes the dominance of fast-growing filamentous green algae at the expense of fucoids (Berger et al. 2003; Orav-Kotta and Kotta 2004). Consequently, the vital ecosystem functions provided by perennial species (e.g., *F. vesiculosus*) are at risk.

Information on the impacts of OA on Baltic Sea organisms is gradually accumulating. While most studies have focused on individual species, recent evidence on community responses has started to emerge (Takolander et al. 2017). In order to better understand the first signs of acidification, particularly the potentially contrasting trends among different areas, it is crucial to expand existing marine monitoring programs by including inorganic carbon system parameters (A_T , pH, pCO_2 , DIC) and ensuring high-quality measurements (Takolander et al. 2017; Müller 2018). Secondly, considering that there is a high diurnal and annual fluctuation of pH (Middelboe and Hansen 2007; Pajusalu et al. 2016), experiment thresholds should reflect the above pH values, which the species are already experiencing today when describing the possible impacts of future acidification. These are the key elements for overcoming contradicting results. Last, there is a great need for multi-stressor experiments; this could give us a better understanding of the potential changes in complicated ecosystems such as the brackish Baltic Sea. However, considering the vast number of species, it is an inconceivably difficult task. A more feasible approach would be focusing on reference organisms, keystone species, and ecosystem engineers, identifying common patterns, concentrating on the species, processes, and ecosystems that are most vulnerable or resilient to possible change, and encompassing a wide range of processes, from subcellular to ecosystem dynamics and biogeochemical cycling.

5. CONCLUSIONS

- As hypothesised (**H1**), macrophytes in the northeastern Baltic Sea possess various types of carbon-concentrating mechanisms (CCMs) and exhibit different responses to varying dissolved inorganic carbon (DIC) concentrations, consequently, this leads to diverse responses at elevated CO₂ concentrations in future.
- As hypothesised (**H2**), there was a considerable difference in DIC acquisition, pH compensation points, and carbon stable isotope values between morphologically simple algae, such as filamentous macroalgae, and morphologically complex algae. Thus, increasing CO₂ concentrations may cause shifts in the species composition of macrophyte communities by replacing the perennial macroalgae (e.g., *Fucus vesiculosus*) with fast-growing filamentous algal species. This leads to a reduction in species richness as *F. vesiculosus* habitat is the most species-rich macroalgal habitat in the Baltic Sea.
- As hypothesised (**H3**), red macroalgal species that typically grow in deeper waters had considerable differences in CCM operation compared to other studied groups, therefore, red macroalgal species will likely benefit the most from future elevated CO₂ concentrations.
- As hypothesised (**H4**), the same species (e.g., *Chara aspera* and *C. tomentosa*) growing in totally different carbonate chemistry environments use significantly different carbon uptake mechanisms.
- Macroalgae *Furcellaria lumbricalis* (unattached) and *Coccolytus truncatus* growing together in the same habitat have significantly different CCMs, indicating that the share of *F. lumbricalis* in the community might decrease under increasing CO₂ conditions. This will lead to a lower quality of the product and impact commercial exploitation (**I**).
- In general, non-CCM and CCM species whose photosynthesis is limited by current DIC availability and species capable of downregulating their CCM operation, will show the largest positive response to elevated CO₂.

SUMMARY

The ocean's ability to absorb CO₂ enables the reduction of atmospheric CO₂ levels and the mitigation of anthropogenic climate change. The oceans have already assimilated approximately 30 per cent of CO₂ emissions, resulting in ocean acidification. When carbon dioxide reacts with seawater, carbonate chemistry changes significantly, resulting in higher concentrations of dissolved carbon dioxide (CO₂) and bicarbonate (HCO₃⁻) and reduced concentrations of carbonate (CO₃²⁻). As atmospheric CO₂ concentrations continue to rise in accordance with IPCC emission scenarios, the surface water pH in the central Baltic Sea will decrease by up to 0.5 pH units by the end of this century. Furthermore, long-term monitoring of the ocean in various locations has revealed that pH fluctuations in coastal waters can be up to ten times greater than in the open ocean. The Baltic Sea is more susceptible to ocean acidification than the open ocean due to factors such as low DIC concentration and low alkalinity in most regions, high freshwater intake, low salinity, etc.

Research has revealed a diversity of responses across species, populations, and even life stages within the same species due to the impacts of ocean acidification, and there are no universal pH thresholds applicable to all organisms. Many aquatic macrophytes have been hypothesized to benefit from OA, but others may be displaced consequently. According to studies, numerous macrophytes have a CCM (carbon concentrating mechanism) that enables them to use bicarbonate (HCO₃⁻) for photosynthesis. However, the species that lack CCM likely gain a photosynthetic advantage because 90% of the DIC is bicarbonate and only 1% is CO₂. Therefore, photosynthesis and macrophyte growth may improve due to the fact that increased CO₂ levels mitigate the negative effects of slow CO₂ diffusion rates in seawater. Macrophytes with a CCM might not respond to higher CO₂ concentrations unless the higher CO₂ concentrations cause the CCM to downregulate (allowing the energy to be used for other purposes).

Different responses of macrophytes (with and without CCMs) to rising CO₂ levels may influence interspecific competition and community structure. Due to a lack of research on OA in the Baltic Sea, the purpose of this doctoral dissertation was to evaluate the effects of elevated carbon on common macrophytes in the coastal ecosystems of the northeastern part of the Baltic Sea in order to predict possible changes. Carbon use strategies in macrophytes were determined by analysing the carbon isotopes (δ¹³C), pH drift experiments, and photosynthesis versus dissolved inorganic carbon. Additionally, in-situ measurements of pH and CO₂ were conducted in the natural macrophyte communities. Furthermore, the carbonate system was calculated for each of the sites where the studied species were collected. According to the findings, common submerged macrophytes in the Baltic Sea, such as macroalgae, charophytes, seagrass, and other angiosperms, possess carbon-concentrating mechanisms (CCMs) (I–IV). Apart from the red macroalga *C. truncatus* (II), all of the investigated species (I–IV) can absorb both CO₂ and HCO₃⁻ for photosynthesis. While all tested species showed evidence of

CCMs, differential levels of CCM activity indicate varying levels of competitive fitness in a future CO₂-high environment (I–IV).

The carbonate chemistry in shallow coastal waters is highly influenced by the metabolic activity (photosynthesis and respiration) of macrophytes. Submerged macrophytes already live in an environment with considerable pH variability in the shallow brackish Baltic Sea. For example, the maximum amount of pH fluctuation measured up to 0.9 pH units in an angiosperm community, which is more than projected for seawater by the year 2100. Based on the carbonate system calculations, it was found that the alkalinity of the West Estonian Archipelago was lower (1600–2000 mol kg⁻¹) than that of the ocean (2200–2300 mol kg⁻¹). In other words, the OA buffering capacity of the studied sites is less than that of the ocean. The greatest differences were discovered between Väike Strait, where the group *Chara* grows (III, IV), and Kihelkonna Bay, where the group Angiosperms is represented (III). Carbon values at all other analysed sites (inhabited by the remaining studied groups: red macroalgae, filamentous macroalgae, *Zostera*, and *Fucus*) were similar. This is also consistent with the results of in-situ carbonate chemistry measurements: the *Chara* community had the lowest CO₂ concentrations based on carbonate system calculations, while the angiosperm community had the highest CO₂ concentrations. Similarly, comparable trends can also be observed in other studied groups.

Elevated carbon will benefit charophytes (*Chara* spp.) in sheltered areas of the shallow coastline of the northern Baltic Sea. Simultaneously, the predicted change in seawater carbon chemistry is likely to cause shifts in the distribution of habitat-forming species. *Fucus vesiculosus* habitat is the most species-rich macroalgal ecosystem in the Baltic Sea, and the reduction of its extent will result in a fall in species richness. The benefits and degree of the algal response to elevated CO₂ levels are also affected by other factors, such as nutrient availability. In the Baltic Sea, eutrophication is a major issue, leading to high growth rates of filamentous epiphytes. A combination of elevated CO₂ and increased nutrient concentrations might tip the balance towards fast-growing filamentous species, despite the similarities in their carbon physiology. Under elevated CO₂ conditions, we estimate losses of the drifting form of the *F. lumbricalis* community due to competition with *C. truncates*. This could set a constraint to the exploitation of these species to preserve the community in the future.

Angiosperms that are common in sheltered soft-bottom environments and frequently form mixed communities with *Z. marina* indicate a steady range in the future environment. *Z. marina* photosynthesis is projected to improve under elevated CO₂ conditions in the northern Baltic Sea, where the species thrives at its lowest salinity levels. As a result, the macrophyte range is projected to expand significantly in the shallowest and deepest regions of the vegetated zone, while *F. vesiculosus* populations are expected to decline. If eutrophication continues in the Baltic, underwater light conditions will deteriorate, as increased turbidity is one of the main effects of eutrophication. Thus, OA may benefit some species that live in low-irradiance situations in the coastal zone, and it may be able to mitigate some of the negative consequences of eutrophication if macroalgae can

photosynthesise more efficiently under low-irradiance conditions. Many studies investigating the effects of climate change on marine organisms are short-term and modify only one species or element of interest. In reality, different abiotic components of climate change, such as salinity, temperature, and pH, interact with each other and influence the complex biotic ecosystem.

SUMMARY IN ESTONIAN

Läänemere makrofüütide süsiniku omastamise strateegiad, suureneva CO₂ kontsentratsiooniga keskkonnas

Merevee suutlikkus absorbeerida süsinikdioksiidi (CO₂) võimaldab vähendada atmosfääri CO₂ taset ja leevendada inimtekkelisi kliimamuutusi. Hinnanguliselt on maailmameri omastanud ligikaudu 30 protsenti atmosfääri paisatud CO₂ heitkogustest, mille tulemusena merevesi hapestub. Kui süsinikdioksiid reageerib mereveega, muutub karbonaatkeemia märkimisväärselt: lahustunud süsinikdioksiidi (CO₂) ja vesinikkarbonaadi (HCO₃⁻) kontsentratsioon suureneb ning karbonaadi (CO₃²⁻) kontsentratsioon väheneb. Kuivõrd IPCC stsenaariumite järgi atmosfääri CO₂ kontsentratsioon tõuseb jätkuvalt, on prognoositud, et Läänemere keskosa pinnavee pH langeb selle sajandi lõpuks kuni 0,5 pH-ühiku võrra. Lisaks on merevee pikaajaline seire näidanud, et rannikuvetes võib pH kõikumine olla kuni kümme korda suurem kui avameres. Liiatigi on Läänemeri madala aluselise ning vähese soolsuse tõttu merevee hapestumisele vastuvõtlikum kui avamerevesi tervikuna.

Teadustöödest selgub, et merevee hapestumise mõju võib erinevatele liikidele olla nii positiivne, negatiivne kui neutraalne. Üks viis mõistmaks merevee hapestumisega seotud muutusi, on kindlaks teha milliseid süsiniku vorme ja strateegiaid makrofüüdid kasutavad fotosünteesi käigus. Makrofüütide hulgas on kolme erinevat tüüpi süsiniku vormide kasutajat: ainult HCO₃⁻ kasutajad, ainult CO₂ kasutajad ja vetikad, kes kasutavad mõlemat eelnimetatud süsiniku vormi. Enamikel makrovetikatel on olemas süsiniku kontsentreerimise mehhanism (CCM) ning nad kasutavad fotosünteesi käigus süsinikuallikana peamiselt HCO₃⁻, mille kontsentratsioon vees on palju kõrgem kui lahustunud CO₂. Siiski, HCO₃⁻ aktiivne omastamine kasutades CCM-i on energiakulukas. Uuringud on näidanud, et vetikad eelistavad fotosünteesis kasutada vees lahustunud CO₂, mis pääseb raku difusiooni teel, energiat kulutamata. Arvatakse, et CCM-iga vetikad on juba valdavalt küllastunud tänapäeva süsiniku taseme juures ning seega on tulevikus vähem mõjutatud merevee hapestumisest. Tulevikus on aga eelistatud seisus need vetikaliigid, kes on n-ö puhtad CO₂ kasutajad, kuivõrd ennustumusmodelite järgi võib aastaks 2100 CO₂ kontsentratsioon merevees suureneeda kuni ca 250%. Süsiniku kontsentreerimise mehhanismiga makrofüüdid ei pruugi reageerida suuremale CO₂ kontsentratsioonile, välja arvatud juhul, kui liigid suudavad CCM-i ümber reguleerida (võimaldades energiat kasutada muudel eesmärkidel, näiteks kasvaks). See, mis suunas ja mil määral CO₂ tõus merevees mõjutab liikidevahelist konkurentsi ja koosluse struktuuri, sõltub sellest, kas liik omab CCM-i või mitte ning millised täpsemalt on need mehhanismid.

Merevee hapestumist üleüldiselt on Läänemeres uuritud võrdlemisi vähe võrreldes ookeaniga. Lisaks on leida ainult üksikuid töid hapestumise mõjudest makrofüütidele. Käesoleva doktoritöö peamine eesmärk oli hinnata merevee hapestumise mõjusid rannikumere makrofüütidele, et prognoosida võimalikke

muutus liigi ja koosluste tasemel. Selleks uuriti Eesti rannikualal kasvavate peamiste makrofüütide süsiniku omastamise strateegiaid. Määrati makrofüütide stabiilsed süsiniku isotoobid ($\delta^{13}\text{C}$), uuriti makrofüütide võimekust pH-d muuta ja fotosünteesilist võimekust erinevatel lahustunud anorgaanilise süsiniku (DIC) kontsentratsioonidel. Lisaks teostati looduslikes makrofüütide kooslustes pH ja CO_2 *in situ* mõõtmised. Samuti võeti proovid iga uuritava liigi kasvukohast ning arvutati karbonaatkeemia näitajad. Töös leiti, et Läänemere makrofüüdid, nagu makrovetikad, määndvetiktaimed, merihein (*Z. Marina*) ja teised veealused katte-seemnetaimed, omavad süsiniku kontsentreerimise mehhanismi (I–IV). Kõik uuritud liigid välja arvatud makrovetikas *C. truncatus* (II), on võimelised omastama fotosünteesi käigus nii CO_2 kui ka HCO_3^- (I–IV). Ehkki kõik uuritud liigid näitasid süsiniku kontsentreerimise mehhanismide olemasolu, viitavad meie tulemused väga selgetele erisustele CCM mehhanismides.

Antud töö põhitulemused:

- Läänemere makrofüütidel esineb erinevat tüüpi süsiniku kontsentreerimise mehhanisme (CCM) ja sellest tulenevalt ka erinevaid reaktsioone CO_2 taseme tõusule (H1).
- Teine hüpotees (H2) leidis kinnitust: morfoloogiliselt lihtsamad vetikad nagu niitjad makrovetikad saavad CO_2 küllusest rohkem kasu kui keerukama ehitusega vetikad. Seega, suurenev CO_2 kontsentratsioon võib põhjustada muutusi makrofüütide koosluste liigilises koosseisus ning mitmeaastased makrovetikad nagu *Fucus vesiculosus* võivad asendada kiirekasvuliste vetika liikidega. See omakorda vähendaks märkimisväärselt elurikkust, kuna kooslus, mida pakub *F. vesiculosus* on liigirikkamaid elupaiku Läänemeres.
- Nagu oletasime (H3), paistab tõusev CO_2 kontsentratsioon olevat kõige kasulikum enamasti sügavamas vees elavatele punavetika liikidele, kes kasutavad teiste uuritud liikidega võrreldes väga erinevat CCM-i.
- Leidsime, et kooskõlas hüpoteesiga (H4), sama liiki (nt *Chara aspera* ja *C. tomentosa*), kuid täiesti erinevas karbonaatkeemilises keskkonnas elutsevad organismid kasutavad erinevaid süsiniku omastamise mehhanisme.
- Samas elupaigas koos kasvavad makrovetikad *Furcellaria lumbricalis* ja *Coccolytus truncatus* kasutavad oluliselt erinevaid CCM-e, viidates *F. lumbricalise* vähenemisele ja *C. truncatuse* osakaalu suurenemisele CO_2 kontsentratsiooni tõustes. Selle tulemusena väheneb tööstuslikult kasutatava produkti kvaliteet.
- Üldiselt võib järeldada leitud tulemuste põhjal, et kõige positiivsemat reaktsiooni lahustunud anorgaanilise süsiniku tõusule näitavad ilma CCM-ita liigid ja CCM-iga liigid kelle fotosüntees on praeguse lahustunud anorgaanilise süsiniku kontsentratsiooni juures piiratud, ning liigid, kes suudavad oma CCM-i toimimist piirata (ümber reguleerida).

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Publications

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- Pajusalu, L., Albert, G., Fachon, E., Hepburn, C.D., Kotta, J., Kõivupuu A., Paalme, T. et al. 2023. Species-specific responses of macrophyte production to the increasing CO₂ environment with potential ecosystem implications involved in the Baltic Sea. *Journal of Applied Phycology*. *Accepted for publication 17.07.2023*
- Hall, J.R., Albert, G., Twigg, I.M., Baltar, F., Hepburn, C.D. & Martin, G. (2022). The production of dissolved organic carbon by macroalgae and its consumption by marine bacteria: Implications for coastal ecosystems. *Frontiers in Marine Science*. 9.
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Publikatsioonid

Albert, G; Pajusalu, L; Torn, K; Hepburn, D.C; Daniel, W.P; Põllumäe, A; Martin, G. (2022). Comparison of carbon uptake strategies between *Chara aspera* and *Chara tomentosa* growing in the brackish Baltic Sea and in the freshwater lakes of Estonia. *Under revision*

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Rahvusvahelistel konverentsidel osalemine

- Albert, G., Pajusalu L., Martin, G. The effects of Ocean Acidification on macroalgal communities in the coastal areas of the NE Baltic Sea. 24th International Seaweed Symposium, 19.02–24.02.2023 Tasmania, Australia ([posterettekanne](#))
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