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Press

Estonian Marine Institute, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia.

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The road to wisdom?
Well, it's plain and simple to express:

Err
and err
and err again,
but less
and less
and less.

-Piet Hein

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LIST OF ORIGINAL PUBLICATIONS

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

I. **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*, 934229.

II. **Hall, J.R.**, Herkül, K., Baltar, F., Hepburn, C.D., & Martin, G. (2024). Shifts in macroalgae composition alters carbon flow in Coastal Baltic Sea ecosystems: implications for dissolved organic carbon bioavailability and flux. *Frontiers in Marine Science*, *11*, 1384165.

III. Albert, G., **Hall, J.R.**, Pajusalu, L., Twigg, I. M., Wenley, J., & Martin, G. (2025). The effect of water motion and elevated carbon on two green algae *Ulva intestinalis* and *Cladophora glomerata* DIC acquisition and DOC release in the brackish Baltic Sea. *European Journal of Phycology*, 1–10.

AUTHORS CONTRIBUTIONS

'***' leading contribution, '**' major contribution, '*' minor contribution

	I	II	III
Original Idea	***	***	**
Study Design	***	***	**
Conducting Experiment	***	***	**
Data Collection	***	***	**
Data Analysis	***	***	**
Manuscript Preparation	***	***	**

LIST OF ABBREVIATIONS

AZ – acetazolamide
BBP – bacterial biomass production
BRT – boosted regression tree
C – carbon
CCM – carbon concentrating mechanism
DIC – dissolved inorganic carbon
DOC – dissolved organic carbon
DW – dry weight
HELCOM – (Helsinki Commission), an intergovernmental organization governing the Convention on the Protection of the Marine Environment of the Baltic Sea Area
LDOC – labile dissolved organic carbon
N – nitrogen
P – phosphorous
PAR – photosynthetically active radiation
pH – a measure of acidity or basicity of a solution
POC – particulate organic carbon
TOC – total organic carbon
RDOC – refractory dissolved organic carbon
SDM – species distribution modelling
SLDOC – semi-labile dissolved organic carbon
SRDOC – semi-refractory dissolved organic carbon
URDOC – ultra-refractory dissolved organic carbon
UV – ultraviolet

INTRODUCTION

Macroalgae play a foundational role in marine carbon cycling through their high primary productivity and contribution to both particulate and dissolved organic carbon pools. Although covering less than 0.1% of the ocean floor, macroalgae account for approximately 5–10% of total marine primary production (Krause-Jensen and Duarte, 2016; Duarte et al., 2005). Unlike phytoplankton that typically have rapid turnover rates, macroalgae can form long-living stands with substantial biomass, particularly in kelp forests which can sequester between 120–720 g C m^{-2} yr^{-1} (Krause-Jensen et al., 2018). A large portion of photosynthetically fixed macroalgal carbon is readily released into surrounding waters as dissolved organic carbon (DOC), accounting for up to 40% of total carbon fixation in certain species (Wada et al., 2007, Abdullah & Fredriksen, 2004). The role of macroalgae in coastal carbon cycling is increasingly recognized in the context of climate change mitigation. Their potential capacity for carbon sequestration, particularly in the form of exported biomass and recalcitrant DOC, has led to growing interest in their potential role in "blue carbon" strategies (Macreadie et al., 2019; Krause-Jensen and Duarte, 2016). However, the complex dynamics of carbon cycling in macroalgal systems, including the variable fate of DOC and the influence of environmental factors on carbon fixation and release rates, necessitate research to fully understand their contribution to marine carbon sequestration (Duarte & Cebrián, 1996; Krumhansl & Scheibling, 2012).

General Background and Ecology of Macroalgae

Macroalgae, more commonly known as seaweeds, are photosynthetic, macroscopic, multicellular organisms encompassing three distinct evolutionarily lineages related to their dominant pigmentation and comprising of the phyla Ochrophyta (brown seaweeds), Chlorophyta (green seaweeds) and Rhodophyta (red seaweeds) (Hurd et al., 2014; Leliaert et al., 2012; Brodie et al., 2017). With the world's seas absent of ferns, mosses, gymnosperms and almost all angiosperms (excluding seagrasses) the marine environment is dominated by these evolutionarily primitive groups (Hurd et al., 2014). The evolutionary diversity of macroalgae is intrinsically linked to the endosymbiotic events that gave rise to their plastids (Keeling, 2013; Archibald, 2015). Through primary endosymbiosis approximately 1.5 billion years ago, a free-living cyanobacterium was engulfed and incorporated within a heterotrophic eukaryote, giving rise to three major lineages: the glaucophytes, the green lineage (ancestral to both green algae and terrestrial plants), and the red lineage (Keeling, 2010; Yoon et al., 2017). Subsequent secondary endosymbiotic events, involving the uptake of unicellular red and green algae by other eukaryotes, led to further diversification (Nowack, 2018; Sibbald & Archibald, 2020). The brown algae arose through this process, sharing a common ancestor with diatoms within the stramenopiles (Dorrell et al., 2017; Yang et al., 2012).

Macroalgae exhibit remarkable morphological diversity, ranging from simple filamentous forms to complex parenchymatous structures (Graham et al., 2016; Charrier et al., 2012). Unlike vascular plants, which demonstrate relatively uniform tissue construction, seaweeds display various architectural strategies (Hurd et al., 2014). Their construction can be uniseriate (single row of cells), pluriseriate (multiple rows), pseudoparenchymatous (adhering filaments forming tissue-like structures), or truly parenchymatous (primarily in brown algae) (Charrier et al., 2012; Hurd et al., 2014). This morphological plasticity allows them to adapt to various marine environments and ecological niches (Hurd et al., 2014). This is reflected in the cell wall composition and structure in macroalgae which are uniquely adapted to the marine environment (Popper & Tuohy, 2010). Their walls contain abundant matrix polysaccharides, often highly sulfated, which provide structural integrity while allowing flexibility in wave-swept environments (Michel et al., 2010; Kloareg & Quatrano, 1988). Brown algae produce alginates and fucoidans (Deniaud-Bouët et al., 2017), red algae synthesize agars and carrageenans (Usov, 2011; Rioux & Turgeon, 2015), while green algae share cellulose with their terrestrial relatives (Domozych et al., 2012; Popper & Tuohy, 2010). These cell wall components not only provide structural support but also play crucial roles in water retention, ion exchange, and protection against environmental stresses (Kloareg & Quatrano, 1988; Raven & Hurd, 2012).

The distribution and zonation of macroalgae in marine environments reflect complex interactions between their physiological capabilities and environmental pressures (Davison & Pearson, 1996; Harley et al., 2012). In intertidal zones, species demonstrate distinct vertical distributions, with different taxa adapted to varying degrees of desiccation stress, wave action, and light exposure (Dring & Brown, 1982; Lubchenco, 1980). This zonation extends into the subtidal region, where light availability becomes the primary limiting factor (Markager & Sand-Jensen, 1992; Steneck et al., 2002). Tropical, temperate, and polar regions each harbour distinctive assemblages of macroalgae, adapted to their respective environmental challenges (Lüning, 1991). Macroalgae function as ecosystem engineers in marine environments, creating complex three-dimensional habitats that support diverse communities of organisms (Graham, 2004; Steneck et al., 2002). Large brown algae, particularly Laminariales (kelps), form underwater forests that modify light regimes, water flow patterns, and local chemistry, while providing shelter and sustenance for numerous marine species (Dayton, 1985; Mann, 1982). In tropical regions, macroalgae are integral components of coral reef ecosystems, contributing to primary production, nitrogen fixation, and calcium carbonate deposition (McCook et al., 2001; Dubinsky & Stambler, 2010).

DOC and its Role in the Marine Environment

Dissolved organic carbon (DOC) is operationally defined as the fraction of organic carbon that passes through a filter with a nominal pore size of 0.22–0.7 μm (Søndergaard & Middelboe, 1995; Sharp, 2002). Organic carbon retained by the filter is classified as particulate organic carbon (POC), and the sum of DOC and POC constitutes total organic carbon (TOC). In marine systems, DOC represents one of Earth's largest organic carbon reservoirs, containing an amount of carbon comparable to the atmosphere and exceeding marine biomass carbon by over 200-fold (Hansell et al., 2009; Carlson & Hansell, 2015).

DOC is predominantly produced within the euphotic zone through autochthonous processes, including phytoplankton primary production, zooplankton grazing, and contributions from macroalgae, seagrasses, microbial activity, and the dissolution of organic particles (Carlson, 2002; Jiao et al., 2010). Additional inputs arise from terrestrial sources and hydrothermal vents (Carlson, 2002; Jiao et al., 2010). Prokaryotes, such as bacteria and archaea, contribute to the DOC pool by releasing capsular material, exopolymers, and hydrolytic enzymes, as well as through processes like viral-induced cell lysis (Azam & Malfatti, 2007; Weinbauer et al., 2011). Microbes are the primary consumers and decomposers of DOC, although highly recalcitrant DOC forms can persist for extended periods due to slow abiotic degradation (Hansell, 2013). Understanding the interactions between DOC and microbes is critical for elucidating the cycling and distribution of this dynamic carbon reservoir. DOC accounts for approximately 20% of all organic carbon on Earth and is integral to marine biogeochemical carbon cycles (Hedges, 1992; Hansell & Carlson, 2000). In the euphotic zone, 30–50% of net primary production is released as DOC, with around half comprising polysaccharides (Thornton, 2014; Myklestad, 2000). Surface ocean DOC is exported to deeper layers via water circulation and seasonal overturn, supporting diverse food webs throughout the water column (Carlson et al., 2011). This downward transport of carbon also represents a significant mechanism for blue carbon storage, sequestering organic carbon in the deep ocean for extended periods and contributing to long-term climate regulation (Duarte et al., 2005; Krause-Jensen & Duarte, 2016).

The vast pool of DOC found in the marine environment is highly heterogeneous, its origins and chemical composition represents an enormous number of biochemical and chemical processes. With advances in mass spectrometry (i.e., Fourier transform ion cyclotron resonance mass spectrometry) having now identified thousands of different molecular formulae (Lechtenfeld et al., 2013; Hansman et al., 2015; Zark and Dittmar, 2018). DOC therefore denotes a set of diverse and complex molecules ranging from labile (LDOC), semi-labile (SLDOC), semi-refractory (SRDOC), refractory (RDOC) and ultra-refractory (URDOC) relating to their lifetime and reactivity in the water column (Hansell, 2013; Jiao et al., 2010). It should be noted however, that whilst these classifications maybe useful when discussing the study or marine DOC, they are inherently arbitrary and are not linked to a given specific underlying physical property. As such, a given classification is dependent upon on the underlying ecosystem properties whereby one particular compound may be refractory in one system but readily degraded by microbes in another (Carlson and Hansell, 2015). Therefore, DOC reactivity should be viewed as a continuum with considerations made for the ecosystem properties present. Environmental conditions play a crucial role in determining how long different DOC molecules persist in marine systems. The degradation and transformation of DOC fractions depend on multiple factors, including water temperature, availability of nutrients, exposure to light, and the composition of microbial communities present. Additionally, the intrinsic properties of DOC molecules themselves, such as their chemical structure and abundance, influence their persistence in oceanic waters (Tranvik & Bertilsson, 2001; Carlson et al., 2004; Azam & Malfatti, 2007; Letscher et al., 2015; Shen & Benner, 2018).

The process by which DOC is incorporated into bacterial biomass from which it is then coupled with higher order trophic levels is termed the microbial loop (Azam et al., 1983; Pomeroy et al., 2007). Within the marine environment, it is microorganisms that dominate the processes controlling DOC and to a greater extent all dissolved organic matter (DOM) (Kirchmann, 2008). The great abundance of bacteria in the world's oceans, is estimated to contain on the order of 10^{29} cells, exceeding the combined biomass of all zooplankton and fish (Whitman et al., 1998; Arístegui et al., 2009). When unconstrained, heterotrophic bacteria exhibit exceptionally high metabolic rates. These rates are ultimately constrained by biomass (volume) with growth potential related to principles of surface-to-volume ratio with all products for biological function needing to traverse the cells surface (Fenchel & Finlay, 1983; Finkel et al., 2010). Therefore, metabolic rates are inversely proportional to the linear relationship between size and metabolism (Brown et al., 2004). Consequently, the small and vast abundance of microorganisms in the sea means they dominate the flux of energy biologically important elements in the marine system and explains why labile DOC is rapidly consumed upon entering the environment (Benner & Amon, 2015; Carlson & Hansell, 2015).

Mechanisms of Macroalgal DOC Release

The release of DOC by macroalgae has been demonstrated to have a strong effect on localized water column DOC concentrations. The large influence that seaweed communities can have on the local DOC pool is illustrated by Pfister et al., (2019) who found 47% more DOC within a *Nereocystis luetkeana* and *Macrocystis pyrifera* dominated kelp bed (1.50 mg C $\cdot$ L^{-1}) compared to the surrounding seawater (1.02 mg C $\cdot$ L^{-1}). Similar patterns have been observed in other kelp systems (Abdullah & Fredriksen, 2004; Wada et al., 2007). The mechanisms regulating DOC release in macroalgae are poorly understood but are largely believed to occur because of several physiological and physical processes (Paine et al., 2021; Mueller et al., 2016). The release mechanism, can in general, be defined as either a process of active release, termed 'exudation', or can be described as 'passive' in nature (Thornton et al., 2014; Paine et al., 2021). As it stands, no method exists to delineate between DOC released passively or as exudate once it has entered the marine environment. Additionally, little to no data exists regarding the composition of DOC in terms of its release as either a product associated with passive or active release (Carlson & Hansell, 2015; Barrón et al., 2014)

The passive release of DOC by algae has been observed to occur through several mechanisms including I) the diffusion of carbon molecules across the cell membrane, II) cell fragmentation, III) cell lysis and IV) release because of osmotic stress. The quantity of these release vectors is poorly studied with little to no information regarding the lability of this DOC source and its contribution to the marine carbon pool. Known processes of passive DOC release are described below.

I) **Diffusion across cell membranes:** This process involves the passive movement of small organic molecules, likely sugars, and amino acids, from areas of higher concentration within the algal cells to lower concentrations in the surrounding seawater (Paine et al., 2021; Thornton, 2014). Driven by concentration gradients, this type of DOC release does not require energy input from the algae. Factors influencing diffusion rates likely include the species of macroalgae, their metabolic activity, and environmental conditions such as light, temperature, and nutrient levels.

II) **Cell Fragmentation:** Cell fragmentation is another mechanism of passive DOC release in macroalgae. This process occurs when physical forces, such as wave action or grazing by herbivores, break down the structural integrity of algal blades, resulting in the release of cellular contents into the surrounding water (Krumhansl & Scheibling, 2011; Duggins et al., 1989; Weigel and Pfister 2020). For example, in *Saccharina latissima*, up to 40–50% of the carbon fixed through photosynthesis can be released as DOC due to distal decay of the blades (Johnston et al., 1977).

III) **Cell Lysis:** Induced by factors such as aging, viral infections, or physical damage, this process leads to the breakdown of cell walls and the subsequent release of DOC. As algal cells age or become infected by viruses, their structural integrity weakens, leading to the release of intracellular contents into the environment (Nagata 2000, Paine et al., 2021; Weigel & Pfister, 2020) This process is significant in senescent or diseased algae, which release larger amounts of DOC compared to healthy individuals (Garcia-Robledo et al., 2008; Leclerc et al., 2013).

IV) **Osmotic Stress:** Osmotic stress-induced DOC release occurs when macroalgae experience fluctuations in salinity or desiccation. These environmental changes disrupt the osmotic balance within algal cells, leading to the release of DOC as the cells attempt to restore equilibrium (Kirst 1996, Hurd et al., 2014). During osmotic stress, cells adjust their internal solute concentrations to maintain osmotic balance, resulting in the passive release of DOC across solute gradients (Kirst 1996, Hurd et al., 2014; Bennett et al., 2024). This mechanism is particularly relevant in intertidal zones, where macroalgae are regularly exposed to varying salinity and desiccation conditions.

Unlike passive leakage, active exudation is a deliberate cellular process facilitated by algae to manage various physiological and ecological functions. This mechanism is driven by five primary factors: V) maintaining cellular homeostasis, VI) deterring herbivores and competing organisms, VII) preventing desiccation, VIII) managing photorespiration by-products, and IX) investing in reproductive success. Each of these functions underscores the strategic importance of DOC exudation in enhancing macroalgae survival, optimizing metabolic processes, and influencing community interactions in their environment. Known processes of active DOC release are described below.

V) **Maintenance of Cellular Homeostasis:** Derived primarily from phytoplankton literature, the exudation of DOC by macroalgae is hypothesized to play a crucial role in maintaining cellular homeostasis, particularly under conditions of high photosynthetic activity (Fogg, 1984). This process, often referred to as the "overflow hypothesis," suggests that when the internal concentration of photosynthetic products, such as sugars and other organic compounds, exceeds the cellular storage capacity, macroalgae release excess carbon into the surrounding environment as DOC (Hatcher et al., 1977; Fogg 1984; Thornton, 2014; Iñiguez et al., 2016). This mechanism may prevent the detrimental accumulation of photosynthates within cells, thereby ensuring metabolic balance and stability (Hatcher et al., 1977; Fogg, 1984; Thornton, 2014; Iñiguez et al., 2016).

VI) **Deterring herbivores and competing organisms:** The exudation of DOC by macroalgae may also function as a protective mechanism, serving multiple ecological roles. One proposed role is as a feeding deterrent against herbivores, reducing the likelihood of grazing by releasing compounds that are unpalatable or toxic to potential consumers (Abdullah and Fredriksen, 2004; Steinberg & De Nys, 2002). Additionally, DOC release can act as a competitive strategy, inhibiting the growth of nearby seaweeds and corals, thereby securing space and resources in crowded marine environments (McCook et al., 2001; Gomez-Lemos & Diaz-Pulido, 2017). Furthermore, the exudation of specific organic compounds has been observed to deter fouling organisms, helping to maintain the integrity of the algal surface and reduce the risk of colonization by epiphytic species (Steinberg et al., 2001; Steinberg & De Nys, 2002).

VII) **Preventing desiccation:** The release of DOC by macroalgae may also aid in preventing desiccation, especially for intertidal species exposed to fluctuating environmental conditions. The exudation of mucilaginous compounds can form a protective layer on the algal surface, reducing water loss during periods of emersion and helping to maintain cellular hydration (Painter, 1983; Dring, 1992; Chapman, 1966; Wyatt et al., 2014). This mechanism is particularly advantageous for species inhabiting intertidal zones, where periodic exposure to air poses a significant risk of dehydration

VIII) **managing photorespiration by-products:** DOC release may help in managing the by-products of photorespiration. In species that rely solely on passive diffusion for dissolved inorganic carbon (DIC) uptake, RuBisCO's oxygenase activity can interfere with its carboxylase function, resulting in the production of glycolate and CO_2 (Raven et al., 2005; Gómez and Huovinen, 2012). While phytoplankton are known to release glycolate during photorespiration (Fogg, 1983; Stewart, 1974), the exact mechanism in macroalgae remains uncertain. Although the fate of glycolate in seaweeds remains unclear, it has been suggested that exudation might serve as a mechanism for disposing of this by-product, preventing its accumulation within cells (Iwamoto and Ikawa, 1997).

IX) **Investing in reproductive success:** macroalgae may utilize DOC as a form of parental investment to enhance reproductive success. For instance, fucoid sporophytes, such as those in the genera *Fucus* and *Pelvetia*, release gametes within a polysaccharide matrix, which is accompanied by the release of DOC (Brawley et al., 1999). This process is believed to offer multiple benefits, including providing a protective barrier against ultraviolet (UV) radiation and aiding in the aggregation of gametes to increase fertilization efficiency (Swanson and Druehl, 2002; Müller et al., 2009; Muhlin et al., 2011). Additionally, the polysaccharide matrix can help prevent polyspermy, thereby ensuring that only a single sperm fertilizes each egg, which is critical for successful development (Brawley et al., 1999).

Despite the recognized importance of DOC in marine ecosystems, the release and fate of DOC by macroalgae in the Baltic Sea remains poorly understood. Understanding this is particularly critical in the Baltic Sea due to its unique environmental conditions, such as low salinity, eutrophication pressures, and climate change-driven shifts in community composition, all of which can influence carbon cycling and overall ecosystem function. This thesis addresses key gaps in knowledge, including quantifying DOC release rates, determining the lability of macroalgal-derived DOC, and evaluating the ecological role macroalgae composition plays in coastal carbon dynamics. These gaps are critical for assessing whether released DOC enters the microbial loop, fuelling microbial activity, nutrient cycling, and supporting higher trophic levels, or is exported as blue carbon, contributing to long-term carbon sequestration.

Objectives and Hypotheses

The primary aim of this thesis was to quantify the release of dissolved organic carbon (DOC) by various macroalgal species and evaluate its ecological role within coastal ecosystems, with a particular focus on its contribution to the microbial loop. By measuring DOC exudation rates and characterizing the biochemical properties of the released DOC, this study sought to elucidate the mechanisms by which macroalgae influence carbon cycling in marine environments, support microbial communities, and drive nutrient dynamics. Additionally, the research aimed to explore the physiological and environmental factors that regulate DOC release, advancing our understanding of the ecological functions and potential biogeochemical implications of macroalgal-derived DOC. An important aspect of this research was to investigate how changes in macroalgal community composition, driven by environmental or anthropogenic factors, may alter coastal DOC carbon flow and, consequently, impact local carbon cycling and ecosystem processes.

- It is hypothesized that macroalgal species exhibit significant differences in DOC exudation rates, driven by their distinct growth strategies, physiological traits, and adaptations to environmental conditions. Specifically, fast-growing opportunistic species are expected to release higher quantities of labile DOC compared to perennial habitat-forming species, which may prioritize structural maintenance and release less DOC overall. Conversely, slower-growing alga, may release smaller quantities of DOC with potentially higher proportions of recalcitrant compounds.
- It is hypothesized that the lability of DOC released by macroalgae varies significantly among species, shaped by their physiological traits and the environmental conditions under which DOC is exuded. Specifically, fast-growing species are expected to release more labile, easily degradable DOC, which supports rapid microbial uptake and activity. In contrast, species like slower growing groups may release DOC with a higher proportion of recalcitrant compounds, reflecting their slower growth rates and allocation of resources toward structural and defence mechanisms.
- It is hypothesized that a measurable fraction of the DOC released by macroalgae enters the microbial loop, supporting microbial community growth and enhancing nutrient cycling in the marine environment. The size of this fraction is expected to vary depending on the lability of the DOC, which is influenced by species-specific traits and the environmental conditions it was release under.
- It is hypothesized that environmental factors such as light intensity, temperature, pH, water motion, and DIC availability and form, modulate the rates at which macroalgae release DOC and influence the lability of the release DOC, influence subsequent utilization by microbial communities.
- It is hypothesized that changes in macroalgal community composition, particularly shifts toward opportunistic species, will measurably alter the flow of DOC through coastal ecosystems. Specifically, an increased dominance of opportunistic species is expected to alter the quantity and proportion labile DOC released, influencing microbial activity, and altering nutrient cycling dynamics. Conversely, declines in habitat-forming species such as *F. vesiculosus* are anticipated to reduce the availability of recalcitrant DOC, potentially diminishing carbon sequestration capacities.

METHODS

Rationale of the Approach

This study employs a multidisciplinary approach to address gaps in the understanding of macroalgal contributions to carbon cycling within coastal ecosystems. Coastal environments are inherently complex, driven by interactions between biological processes, environmental factors, and anthropogenic impacts. To better understand these dynamics, this research integrated controlled laboratory experiments with field-based observations, and long-term monitoring datasets to connect species-specific physiological processes with larger scale ecosystem carbon dynamics.

Laboratory experiments were designed to quantify dissolved organic carbon (DOC) release rates under varying environmental conditions, including light availability, water motion, and pH. These controlled settings allowed for the isolation and precise measurement of DOC production while minimizing confounding variables. Concurrently, bacterial growth assays were utilized to evaluate the bioavailability of the released DOC, elucidating its role within the microbial loop and its potential to support higher trophic levels or alternatively its relevance in for long-term carbon storage. Additionally, macroalgae carbon concentrating mechanisms (CCMs) were analysed through pH drift experiments and carbon isotope studies, offering insights into species-specific physiological adaptations to fluctuating environmental conditions. This was particularly relevant when predicting potential responses to climate-driven changes, such as ocean acidification.

To bridge experimental results with real-world ecological processes, the study utilized the extensive macrophytobenthos database from the Estonian Marine Institute, encompassing decades of data from the Estonian coastal area. This database provides valuable insights into historical and current macroalgal community composition, biomass distribution, and long-term ecological trends. By integrating this data, it is possible to capture the spatial and temporal variability of macroalgal standing stocks allowing for the assessment of their contributions to coastal DOC. Additionally, species distribution modelling complements this analysis, facilitating predictions of community shifts and their potential impacts on ecosystem function.

By integrating these methodological frameworks, the study seeks to provide a comprehensive examination of the mechanisms underpinning macroalgal DOC production, its ecological significance, and its sensitivity to environmental changes. These approaches ensure that the findings are not only experimentally rigorous but also ecologically meaningful, forming a robust basis for advancing our understanding of coastal carbon dynamics and informing future management strategies.

Study Area and Database

This research was conducted within the Estonian marine environment in the north-eastern Baltic Sea (Fig. 1), characterized by its complex coastal morphology formed during Holocene sea level changes (Snoeijs-Leijonmalm, 2017; Rosentau et al., 2011). The region encompasses diverse coastal features including sandy shores, rocky outcrops, and estuarine areas, with brackish conditions maintaining salinity typically below 8 PSU (Snoeijs-Leijonmalm, 2017; Martin et al., 2013). Environmental conditions are notably influenced by strong seasonal patterns, with winters leading to sea ice formation and summers affecting overall water temperature dynamics (Omstedt et al., 2004).

This study drew upon the extensive macrobenthos database maintained by the Estonian Marine Institute, University of Tartu. This comprehensive database, spanning from the 1950s, contains over 57,000 georeferenced benthic samples collected through various research initiatives, including basic scientific research, national marine monitoring, benthic habitat mapping, and environmental impact assessments (Martin et al., 2013; Kotta et al., 2000).

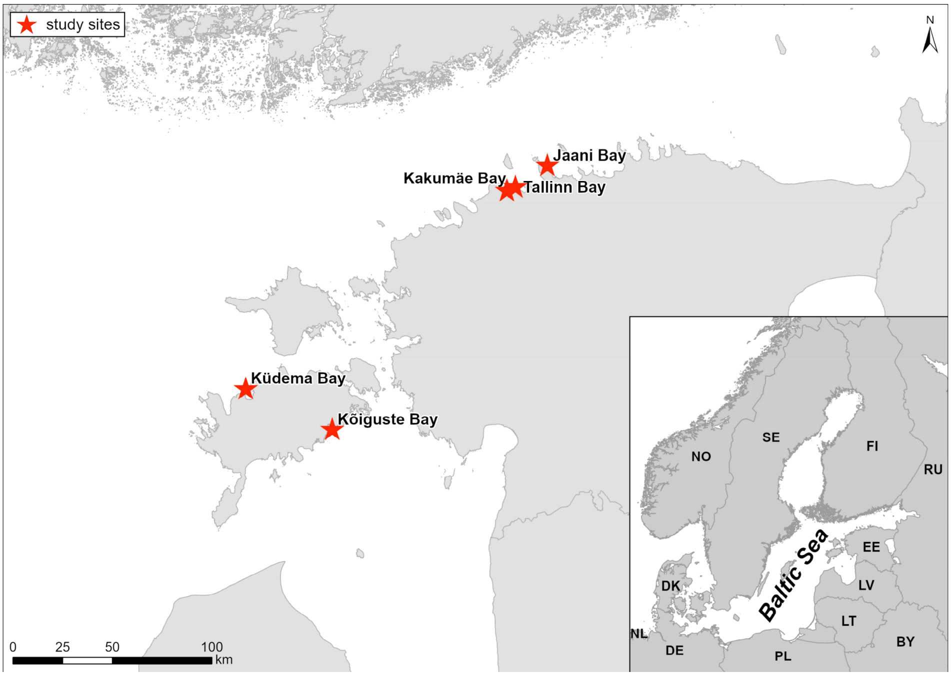

Figure 1. Map of the Estonian coastal area and NE Baltic Sea with marked locations for specimen collection sites.

The Estonian Marine Institute's macrophytobenthos database employs two distinct macrophytobenthos sampling approaches: diver-collected quantitative biomass samples and divers' visual coverage estimates. The quantitative biomass sampling protocol utilizes SCUBA divers that collect samples using 20 × 20 cm quadrats placed on the seabed. All macroscopic fauna and flora within these frames are collected and stored at –18 °C for subsequent analysis. In the laboratory, samples undergo microscopic identification, with dry weights measured after a two-week drying period at 60 °C. These measurements are then converted to biomass per square meter. Long-term monitoring data is collected from established phytobenthos transects following HELCOM COMBINE guidelines (HELCOM, 2015). Transects are positioned perpendicular to the shoreline, with observations conducted within 1 m depth intervals to the vegetation's deepest limit. Quantitative descriptions of phytobenthic communities are obtained through biomass samples collected from 5–7 depth intervals, typically ranging from 0.2 to 8 meters depth.

Study Species and Sample Collection

This study focused on key macroalgal species characteristic of the Northern Baltic Sea coastal ecosystem. The primary species investigated were *Fucus vesiculosus* (L.), *Ulva intestinalis* (L.), *Furcellaria lumbricalis* (Hudson), *Ectocarpus siliculosus* (Dillwyn) and *Cladophora glomerata* (L.) (Fig. 2). These species were selected based on their ecological significance and dominance within the Baltic Sea coastal system. (Torn et al., 2006; Martin et al., 2013; Kersen et al., 2011; Bučas, 2009; Paalme et al., 2002; Leskinen et al., 2004).

The studied algal species can be divided into two distinct ecological groups: habitat-forming perennial species and opportunistic fast-growing species. Among the habitat formers, *F. vesiculosus* (bladder wrack) is a dominant brown seaweed in rocky sublittoral zones that functions as a crucial ecosystem engineer, creating three-dimensional habitats and nursery grounds for numerous marine organisms (Torn et al., 2006; Kersen et al., 2011). The other habitat-forming species, *F. lumbricalis*, is a coarsely branched red alga that enhances benthic complexity providing habitat for a diverse range of epiphytic and invertebrate communities (Bučas, 2009). The fast-growing opportunistic species studied included *U. intestinalis*, a tubular green alga known for its rapid growth and high tolerance to fluctuating salinity (Leskinen et al., 2004); *E. siliculosus*, a fast-growing brown alga commonly found in the upper sublittoral zone, which responds quickly to environmental changes; and *C. glomerata*, a filamentous green alga that is a common opportunistic species that thrives in nutrient-rich conditions (Paalme et al., 2002; Martin et al., 2013).

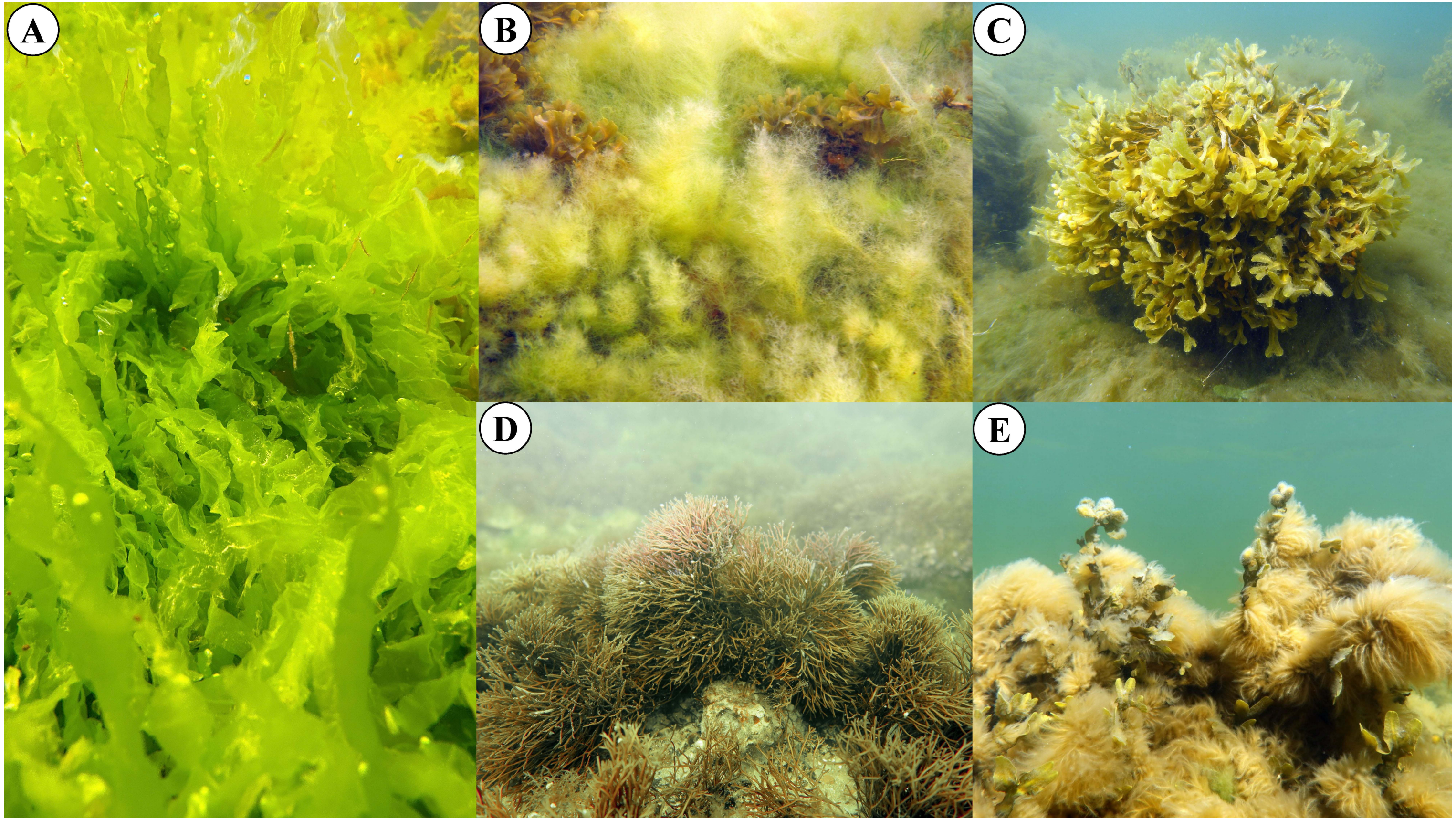

Figure 2. Studied macrophyte species in situ: A) *U. intestinalis*, B) *C. glomerata*, C) *F. vesiculosus*, D) *F. lumbricalis*, E) *E. siliculosus*) (Images sourced from the Estonian Marine Institute data base).

The studied algal species can be divided into two distinct ecological groups: habitat-forming perennial species and opportunistic fast-growing species. Among the habitat formers, *F. vesiculosus* (bladder wrack) is a dominant brown seaweed in rocky sublittoral zones that functions as a crucial ecosystem engineer, creating three-dimensional habitats and nursery grounds for numerous marine organisms (Torn et al., 2006; Kersen et al., 2011). The other habitat-forming species, *F. lumbricalis*, is a coarsely branched red alga that enhances benthic complexity providing habitat for a diverse range of epiphytic and invertebrate communities (Bučas, 2009). The fast-growing opportunistic species studied included *U. intestinalis*, a tubular green alga known for its rapid growth and high tolerance to fluctuating salinity (Leskinen et al., 2004); *E. siliculosus*, a fast-growing brown alga commonly found in the upper sublittoral zone, which responds quickly to environmental changes; and *C. glomerata*, a filamentous green alga that is a common opportunistic species that thrives in nutrient-rich conditions (Paalme et al., 2002; Martin et al., 2013).

Macroalgae specimens used for incubation experiments investigating DOC release dynamics were collected during the summer vegetative season to ensure optimal growth conditions (**I, II, III**). Collection sites were selected based on the presence of complex three-dimensional rock and boulder habitats with shallow degrees of relief and moderate wave exposure, typical of Northern Baltic temperate macroalgae dominated environments (Fig. 1). For *F. vesiculosus* and *U. intestinalis*, specimens were collected via snorkelling from locations in Kakumäe Bay (59.45931°N, 24.56750°E) and Tallinn Bay (59.45922°N, 24.58264°E) on the southern coast of the Gulf of Finland, Estonia (**I**). *F. lumbricalis* specimens were obtained through SCUBA diving from Kõiguste Bay (58.36092°N, 22.99033°E) on the southern coast of Saaremaa Island (**I**). *E. siliculosus* was collected from depths between 0.2 and 1.5m by wading in Jaani Bay (59.55019°N, 24.86928°E) (**II**). *C. glomerata* and *U. intestinalis* were collected by hand at a depth of 0.5m from Küdema Bay (58.536175°N, 22.235622°E) (**III**). Following collection, all specimens were immediately placed in 20-L clear plastic containers filled with site water. The containers were equipped with free-flowing air to provide aeration and maintain water motion during transport (**I, II, III**).

All specimens underwent a 24-hour acclimatization period in a climate-controlled laboratory setting, with temperature matched to ambient seawater conditions at the collection sites (**I, II, III**). Prior to experimental use, specimens were carefully cleaned to remove epiphytic algae and associated fauna, ensuring clean samples for subsequent analyses (**I, II, III**). Species identification was conducted using established morphological characteristics (**I, II, III**). However, for certain groups, particularly the '*Pylaiella-Ectocarpus*' group, species-level identification was challenging due to morphological similarities. In such cases, these species were treated as a combined group for analysis purposes (**II**). This approach was particularly relevant for monitoring data where in-situ visual distinguishing between similar species by divers was not feasible.

Laboratory Methods and Analysis

DOC production was quantified through incubation experiments conducted in acid-washed chambers (**I, II, III**). Each experimental setup consisted of ten replicates, with treatments divided equally between saturating light conditions and total darkness (**I, II**). Light levels were monitored using a Li-Cor light meter to maintain consistent photosynthetically active radiation (PAR) (**I, II, III**). The incubation medium consisted of either artificial seawater or filtered seawater processed through a sequential filtration system: initial filtration through 0.8-mm screens removed zooplankton, followed by 0.8-micron filters for phytoplankton removal, and final filtration through 0.22-micron filters eliminated the bacterioplankton fraction (**I, II, III**). DOC samples (50 ml) were collected at predetermined using sterile plastic lure lock-tipped syringes fitted with 0.45-micron G/F sterile syringe filters (**I, II, III**). Samples were immediately transferred to acid-washed glass bottles and frozen for subsequent analysis (**I, II, III**). DOC concentration was determined using high-temperature catalytic oxidation methodology, employing a Shimadzu total organic carbon analyser equipped with a platinum catalyst (**I, II, III**). Results were reported as micrograms of carbon per litre.

Carbon uptake mechanisms by macroalgae were investigated through multiple experimental approaches (**III**). pH drift experiments were conducted to assess species' affinity for bicarbonate (HCO_3^-) (**III**). These experiments utilized acetazolamide (AZ) as a photosynthetic inhibitor to study the role of carbonic anhydrase in DIC uptake (**III**). Experimental treatments included controls (filtered seawater), AZ addition (200 µM final concentration), and Tris buffer (15 mM final concentration) (**III**). Photosynthesis versus dissolved inorganic carbon (P vs. DIC) curves were generated using sealed chambers under controlled conditions (**III**). Light intensity was maintained at 500 µmol photons m^{-2} s^{-1}, with temperature regulated at 15 °C using a flowing water bath (**III**). Oxygen evolution was monitored using Ocean Optics NeoFox-TP oxygen probes, calibrated using a two-point method with nitrogen-bubbled and ambient air-bubbled seawater (**III**).

Carbon isotope (δ13C) analysis was performed to determine species' carbon uptake strategies. Samples were dried at 60 °C to constant weight and ground to a fine powder using a mortar and pestle. Approximately 1 mg of ground sample was analysed using an elemental analyser (FlashEA 1112 HT) coupled to an isotope ratio mass spectrometer (Delta V Plus) via a ConFlo IV dilutor. Results were expressed relative to the Vienna Pee Dee Belemnite (V-PDB) standard and standardized against international reference materials IAEA-CH-3 and IAEA-CH-6.

The microbial utilization of macroalgae-derived DOC was evaluated through microcosm experiments (**I, II**). Retained seawater from DOC production experiments was distributed into acid-washed glass vessels and inoculated with ambient bacteria (**I, II**). Microcosms were supplemented with nutrients ($NaNO_3$, KH_2PO_4,

NH_4Cl) to prevent limitation of bacterial growth (**I**). Bacterial biomass production was quantified through the incorporation of [^{3}H]-labelled leucine into bacterial cells, measured at 24-hour intervals over a 120-hour period (**I**). Bacterial biomass production was quantified using scintillation counting techniques (**I**). Samples were processed through centrifugation and washing steps before being immersed in liquid scintillation cocktail (**I**). Radioactivity was measured using a Tri-Carb® Liquid Scintillation Counter with quenching correction applied using the external standard ratio method (**I**). Results were converted from decompositions per minute to carbon biomass production rates.

Modelling and Analysis Methods

Environmental Variables

Environmental predictors were processed and standardized prior to model implementation to assess their influence on the distribution and abundance of macroalgal species. These predictors, including variables such as light availability, salinity, nutrient concentrations, depth, and seabed slope, were chosen because they represent critical environmental factors that directly or indirectly affect macroalgal growth, survival, and spatial distribution. Maintaining these variables as georeferenced raster layers in GeoTIFF format with consistent spatial resolution (50 m for most variables, 10 m for depth and seabed slope) ensured spatial accuracy and compatibility with species distribution models. These predictors were essential for identifying the environmental drivers of macroalgal distribution and understanding how these factors shape community composition in coastal ecosystems. The environmental variables were selected based on established ecological relationships and data availability, encompassing:

- Topographical variables (depth, slope of seabed)
- Hydrodynamic parameters (wave exposure, currents, ice conditions)
- Geological characteristics (seabed substrate)
- Physio-chemical parameters (temperature, salinity, nutrients)
- Biological indicators (water chlorophyll concentration)

Species Distribution Modelling Framework

Species distribution modelling (SDM) was implemented to generate seamless distribution estimations of macroalgal biomass across the Estonian marine waters (**II**). The primary objective was to assess the temporal and spatial changes in important algal groups, enabling distribution patterns to be connected with physical factors. The modelling framework employed boosted regression trees (BRT); a non-parametric machine learning method selected for its ability to handle complex, non-linear interactions between predictor variables (**II**). This approach combines the strengths of two algorithms: regression trees and boosting, providing robust predictive capabilities for ecological data.

The BRT model was developed using a systematic approach to ensure optimal performance (**II**). The model was trained using a learning rate of 0.005 and a maximum tree complexity of five, parameters selected based on established recommendations from ecological modelling literature (**II**). Training proceeded in a stepwise manner, with trees added iteratively until no further improvement in predictive accuracy was detected (**II**). Ten-fold cross-validation was applied at each iteration to test model performance and prevent overfitting (**II**). Response variables consisted of species biomass data (g m^{-2} dry weight) from selected sampling sites (n = 1,469), while predictor variables included 15 environmental parameters spanning physical, chemical, and biological factors. The final model was fitted using 100% of the available data after validation of model performance (**II**). Cross-validation based Pearson correlation coefficient (r) was used to report the prediction accuracy of the final BRT model (**II**). Spatial predictions were generated across the entire Estonian marine area to model the distribution and relative abundance of *Fucus* spp. using a prediction grid containing 4,249,989 points (**II**). The grid extended from the coastline to a depth of 20 meters, with deeper areas excluded based on known species depth limitations. Points were spaced at 50-meter intervals in a rectangular grid pattern, with environmental variable values available for each prediction point. This comprehensive spatial coverage enabled the generation of detailed distribution maps and the calculation of total standing stock biomass (**II**).

Statistical Analysis

Raw data from all experiments were initially processed using standardized procedures to ensure data quality and consistency (**I, II, III**). Where necessary, data transformations were applied to meet the assumptions of parametric statistical tests. Outliers were identified using standardized protocols and retained unless clear methodological errors were identified.

Changes in species DOC concentration and bacterial biomass production rates were assessed using repeated measures analysis of variance (ANOVA) to account for the temporal nature of the data (**I, II**). The assumption of sphericity was tested using Mauchly's sphericity test, and where violations occurred, the Greenhouse-Geisser correction was applied to adjust the degrees of freedom (**I, II**). This approach was particularly important for the analysis of DOC production data collected over 12-hour periods and bacterial production measurements spanning 120 hours. Long-term trends in species coverage and distribution were analysed using the Mann-Kendall test, a non-parametric approach for identifying monotonic trends in time series data (**II**). This test provided both statistical significance (p-values) and Kendall's tau coefficient (τ), where negative values indicated decreasing trends and positive values denoted increasing trends. This analysis was particularly relevant for the long-term monitoring data spanning multiple years.

The relationship between macroalgal species distribution, expressed as presence/absence and relative coverage or biomass, and environmental variables was examined using boosted regression trees (BRT), implemented with a learning rate of 0.005 and tree complexity of five (II). Model validation was performed using ten-fold cross-validation, with model performance assessed through cross-validation based Pearson correlation coefficients (**II**). The relative influence of each environmental predictor was quantified, providing insights into the key drivers of species distribution (**II**)

Differences between experimental treatments were analysed using a combination of parametric and non-parametric tests, the treatments compared included variations in light conditions (light vs. dark), pH levels (ambient vs. altered to simulate acidification), water motion (static vs. agitated), and CO_2 concentrations (ambient vs. elevated) (**I, II, III**). For pairwise comparisons, Student's t-tests with Bonferroni correction were employed to control for multiple comparisons (**I, II, III**). Where multiple factors were involved, factorial ANOVA was used to examine main effects and interactions (**III**). For non-parametric data, Kruskal-Wallis tests were employed, followed by Dunn's test for post-hoc comparisons (**I, III**)

Analysis of carbon isotope data (δ13C) was conducted using standardized procedures to assess the carbon acquisition strategies of macroalgae and determine the sources of carbon contributing to their growth. By analysing δ13C, the study evaluated the relative reliance of macroalgae on different forms of dissolved inorganic carbon (DIC), such as CO_2 and bicarbonate (HCO_3^-), as well as the efficiency of carbon concentrating mechanisms (CCMs) employed by these species under diverse environmental conditions (**III**). These analyses provide insights into how macroalgae adapt their carbon utilization strategies in response to environmental changes, particularly fluctuations in pH and CO_2 availability (**III**). The results were expressed relative to the Vienna Peedee Belemnite standard (**III**). Precision and accuracy of measurements were maintained within ±0.1‰. The Michaelis-Menten model was applied to photosynthesis versus DIC concentration data, optimizing parameters for maximum photosynthetic rate (Pmax) and half-saturation constant (k0.5) using maximum likelihood estimation within non-linear mixed effects models (**III**).

RESULTS

Dissolved Organic Carbon Production and Consumption

DOC Release Under Light and Dark Conditions

F. vesiculosus exhibited the highest DOC production under light conditions, releasing 3.26 mg C per gram of dry weight material during the 12-hour incubation period, achieving a maximum production rate of 0.27 mg C · g DW^{-1} · h^{-1} (**I**) (Table 1). In contrast, under dark conditions, *F. vesiculosus* showed no significant change in DOC concentration throughout the time course, indicating photosynthesis-dependent release (**I**) (Table 1).

U. intestinalis demonstrated significant DOC release under both light and dark treatments, with concentrations increasing significantly from baseline after 3 hours in light conditions and 6 hours in dark conditions (**I**) (Table 1). Total release reached 2.64 mg C · g DW^{-1} under light and 1.01 mg C · g DW^{-1} under dark conditions over the 12-hour period, achieving maximum release rates of 0.22 mg C · g DW^{-1}· h^{-1} and 0.13 mg C · g DW^{-1}· h^{-1} respectively (**I**) (Table 1).

E. siliculosus released DOC under both light and dark conditions, with light treatment achieving 1.14 mg C per gram of dry weight material (production rate 0.095 mg C · g DW^{-1}· h^{-1}), while dark treatment yielded 0.84 mg C · g DW^{-1} (production rate 0.070 mg C · g DW^{-1}· h^{-1}) (**II**) (Table 1). The light treatment demonstrated a 30.3% higher release rate compared to dark conditions (**II**) (Table 1).

F. lumbricalis showed minimal DOC release under light conditions, with no significant change in concentration observed (**I**) (Table 1). Under dark conditions, a small but statistically significant decrease of 0.19 mg C per gram dry weight was observed after 9 hours (**I**).

Table 1. The taxonomic group, species, general morphology, site of specimens collected, DOC release (specific values reported as: mg C · g DW^{-1} · h^{-1}), DOC consumption (reported as the percentage of DOC consumed when exposed to natural marine microbial communities at the conclusion of 120 hours), major experimental conditions, and the papers its was examined in.

Taxanomic Group	Species	Morphology	Site	DOC Release	DOC consumption	Conditions	Paper
Phaeophyta	*F. vesiculosus* L.	Leathery, Branching fronds	Kukumäe Bay	0.27	20.7%	Light	I
Phaeophyta	*F. vesiculosus* L.	Leathery, Branching fronds	Kukumäe Bay	No release	No conusmption	Dark	I
Phaeophyta	*E. siliculosus* (Dillwyn) Lyngbye	Filamentous	Jaani Bay	0.095	28.7%	Light	II
Phaeophyta	*E. siliculosus* (Dillwyn) Lyngbye	Filamentous	Jaani Bay	0.070	18.6%	Dark	II
Chlorophyta	*U. intestinalis* L.	Tubular	Kukumäe Bay	0.22	13.1%	Light	I
Chlorophyta	*U. intestinalis* L.	Tubular	Kukumäe Bay	0.13	9.1%	Dark	I
Chlorophyta	*U. intestinalis* L.	Tubular	Küdema Bay	No release	–	Light, 7.6 pH, water motion	III
Chlorophyta	*U. intestinalis* L.	Tubular	Küdema Bay	No release	–	Light, 7.6 pH, no water motion	III
Chlorophyta	*U. intestinalis* L.	Tubular	Küdema Bay	Release	–	Light 8.2 pH, water motion	III
Chlorophyta	*U. intestinalis* L.	Tubular	Küdema Bay	No relase	–	Light 8.2 pH, no water motion	III
Chlorophyta	*C. glomerata* (L.) Kützing	Filamentous	Küdema Bay	No release	–	Light, 7.6 pH water motion	III
Chlorophyta	*C. glomerata* (L.) Kützing	Filamentous	Küdema Bay	Release	–	Light, 7.6 pH, no water motion	III
Chlorophyta	*C. glomerata* (L.) Kützing	Filamentous	Küdema Bay	Release	–	Light 8.2 pH, water motion	III
Chlorophyta	*C. glomerata* (L.) Kützing	Filamentous	Küdema Bay	No release	–	Light 8.2 pH, no water motion	III
Rhodophyta	*F. lumbricalis* (Hudson) J.V.Lamouroux	Cylindrical branching fronds	Kõiguste Bay	No release	No consumption	Light	I
Rhodophyta	*F. lumbricalis* (Hudson) J.V.Lamouroux	Cylindrical branching fronds	Kõiguste Bay	No release	No consumption	Dark	I

Environmental Effects on DOC Release

Water motion and pH significantly influenced DOC release patterns among species (**III**) (Table1). For *U. intestinalis*, significantly higher DOC release was observed with water motion compared to no water motion at pH 8.2 ($p < 0.05$), but no significant difference was found at pH 7.6 (**III**) (Table 1). *C. glomerata* exhibited significant differences in DOC release between water motion and no water motion conditions at both pH 8.2 and pH 7.6 ($p < 0.05$) (**III**) (Table 1).

Bacterial Consumption of Released DOC

The lability of released DOC varied between species and treatments (**I, II**) (Table 1). DOC produced by *F. vesiculosus* under light conditions decreased by 20.7% after 120 hours, from 8.07 mg $C \cdot L^{-1}$ to 6.40 mg $C \cdot L^{-1}$ (**I**). No significant consumption was observed for DOC produced under dark conditions (**I**). *U. intestinalis* derived DOC showed consumption under both conditions, with light treatment DOC decreasing by 13.1% (7.93 to 6.89 mg $C \cdot L^{-1}$) and dark treatment by 9.1% (7.34 to 6.67 mg $C \cdot L^{-1}$) over 120 hours (**I**). *F. lumbricalis* showed no significant changes in DOC concentration after the 120-hour bacterial consumption period in either light or dark treatments (**I**). *E. siliculosus* derived DOC demonstrated varying consumption patterns between treatments (**II**). Light treatment DOC decreased by 28.7% (8.42 to 6.00 mg $C \cdot L^{-1}$), while dark treatment showed an 18.6% reduction (7.2 to 5.86 mg $C \cdot L^{-1}$) (**II**).

Bacterial Biomass Production

Bacterial biomass production (BBP) rates varied based on DOC source and treatment (**I**). *F. vesiculosus* light-derived DOC supported maximum BBP rates of 219 µg $C \cdot L^{-1} \cdot D^{-1}$ at 24 hours, 47.18% higher than dark-derived DOC, which peaked at 135.4 µg $C \cdot L^{-1} \cdot D^{-1}$ at 48 hours (**I**). *U. intestinalis* derived DOC produced similar patterns, with light treatment supporting maximum BBP of 214 µg $C \cdot L^{-1} \cdot D^{-1}$ at 48 hours, while dark treatment achieved 152.8 µg $C \cdot L^{-1} \cdot D^{-1}$ after 24 hours, representing a 28.6% decrease (**I**). Control seawater showed minimal changes, with light treatment decreasing by 8.8% (6.36 to 5.8 mg $C \cdot L^{-1}$) and no significant change observed in dark treatment, indicating the background DOC was largely refractory (**I**).

Species Distribution, Community Trends and Standing Stock Estimation

Analysis of the macrophytobenthos time series (1995–2021) revealed distinct patterns in species distribution and abundance across different monitoring transects (**II**). Opportunistic algae demonstrated statistically significant upward trends in three monitoring locations: Eru, Liu, and Tallinn transects ($p < 0.05$) (**II**). The '*Pylaiella-Ectocarpus*' group showed divergent patterns, with a significant increase observed in the Eru transect but a contrasting decrease in the Kõiguste transect (**II**). No statistically significant trends were identified in the Küdema transect (**II**). Notably, *Fucus* spp. displayed no discernible trends across any of the monitored transects, suggesting population stability under current environmental conditions (**II**).

The distribution of *Fucus* spp. biomass was modelled using BRT, incorporating 15 environmental predictor variables including topographical, hydrodynamic, geological, physio-chemical, and biological parameters (**II**). The model demonstrated good predictive performance with a cross-validation based Pearson correlation value of 0.61. The analysis utilized data from 1,469 sampling sites collected between 2005–2021, providing comprehensive spatial coverage of the Estonian marine area (**II**).

Based on the spatial prediction of biomass distribution, the total standing stock of *Fucus* spp. within Estonian marine waters was estimated at approximately 150,000 tonnes (dry weight) (**II**). This estimation was generated using a prediction grid containing 4,249,989 points, extending from the coastline to a depth of 20 meters, with points spaced at 50-meter intervals. The prediction grid was constrained to areas above 15 meters depth, as *Fucus* spp. never occurs deeper in these waters.

Inorganic Carbon Uptake and Carbon Concentrating Mechanisms

The pH drift experiments revealed distinct patterns of inorganic carbon acquisition between species (**III**). *U. intestinalis* demonstrated significant ability to modify seawater pH, increasing it from 8.7 to 10.60 ± 0.2 (± SE) within 24 hours under control conditions (**III**). When treated with acetazolamide (AZ), a marked decrease to 7.79 ± 0.54 (± SE) was observed within three hours, indicating strong reliance on carbonic anhydrase for carbon acquisition (**III**). In contrast, *C. glomerata* maintained high pH values across all treatments (control: 10.54 ± 0.04; AZ: 10.40 ± 0.11; Tris: 10.32 ± 0.11), with no significant differences between treatments ($p > 0.05$), suggesting different carbon acquisition strategies (**III**). Stable carbon isotope analysis supported these findings, with both species showing intermediate $\delta 13C$ values (*U. intestinalis*: –22.21 ± 0.28‰; *C. glomerata*: –21.03 ± 0.42‰), indicating the presence of carbon concentrating mechanisms (CCMs) and versatile carbon acquisition strategies (**III**). These values, falling between –30 and –10‰, suggest that both species employ a mix of carbon uptake mechanisms rather than relying solely on CO_2 diffusion or bicarbonate uptake (**III**).

Photosynthetic performance under varying dissolved inorganic carbon (DIC) concentrations demonstrated species-specific responses to both pH and water motion (**III**). *U. intestinalis* consistently exhibited higher maximum photosynthetic rates (Pmax) across all treatments, with the highest values observed at pH 8.2 with water motion (330.16 ± 7.28 µmol O_2 h^{-1} g DW^{-1}) (**III**). *C. glomerata* showed lower overall Pmax values but maintained significant photosynthetic capacity, particularly at pH 8.2 with water motion (260.28 ± 9.41 µmol O_2 h^{-1} g DW^{-1}) (**III**). The half-saturation constants (K0.5) revealed that *U. intestinalis* demonstrated more efficient DIC uptake at pH 8.2 compared to pH 7.6, with K0.5 values significantly lower under current pH conditions (0.48 ± 0.13 mM DIC with water motion at pH 8.2 versus 0.90 ± 0.21 at pH 7.6) (**III**).

Water motion significantly enhanced photosynthetic performance in both species, particularly at pH 8.2 (**III**). For *C. glomerata*, Pmax values under water motion at pH 8.2 were significantly higher than at pH 7.6 ($t = 6.7$, $p < 0.001$) (**III**). Similarly, *U. intestinalis* showed significant enhancement in photosynthetic performance with water motion at current pH levels (**III**).

DISCUSSION

This research provides significant insights into the dynamics of carbon acquisition, dissolved organic carbon release, and macroalgal community shifts within the Baltic Sea ecosystem (**I, II, III**). The findings reveal complex interactions between species-specific physiological responses, environmental conditions, and broader ecological implications, particularly in the context of changing marine environments.

Species-Specific Patterns of DOC Release

The observed patterns of DOC release demonstrate significant variability among species and environmental conditions supporting our first hypothesis regarding species-specific differences in DOC exudation. *F. vesiculosus* exhibited the highest rates of DOC release under photosynthetic conditions, while showing minimal release in darkness, supporting the stoichiometric 'overflow' hypothesis (**I**). The consistent release of DOC by *U. intestinalis* under both light and dark conditions suggests a combination of passive diffusion and photosynthetically driven release mechanisms (**I**). This steady baseline release may reflect a strategy to maintain carbon balance under varying environmental conditions. *F. lumbricalis* displayed a markedly different pattern, showing negligible DOC release under light and dark conditions (**I**). This minimal release pattern suggests fundamentally different physiological functions compared to the other studied species, possibly related to its deeper water habitat, where light limitation may require more conservative carbon use, or lack of adaptations to manage DOC build-up under high photosynthetic conditions (**I**). *E. siliculosus* demonstrated significant DOC release in both light and dark conditions, with an increased release rate under light, suggesting that photosynthesis enhances exudation. Like *U. intestinalis*, *E. siliculosus* maintains a baseline level of passive release (**II**), consistent with its opportunistic life strategy and high surface-to-volume ratio, characteristic of filamentous algae, which may favour both passive diffusion and active exudation. Regarding *C. glomerata*, the species showed significant differences in DOC release between water motion and no water motion conditions at both pH 8.2 and pH 7.6 indicating that environmental factors, particularly water movement, strongly modulate carbon release patterns. (**III**).

The diversity in release patterns among these species has important implications for coastal carbon cycling and microbial loop dynamics, particularly when considering ecosystem-wide carbon budgets. These differences would appear to align with species' life strategies and habitat preferences, consistent with theoretical frameworks of functional form characteristics in macroalgae (Littler & Littler, 1980; Steneck & Dethier, 1994). Perennial species like *F. vesiculosus*, with its more regulated, photosynthesis-dependent release, may require more precise internal carbon regulation in relation to their slower growth, similar to patterns observed in other Fucoids (Pregnall, 1983; Wada et al., 2007). This controlled release strategy aligns with findings by Abdullah & Fredriksen (2004), who demonstrated a strong link between DOC release and high metabolic activity at both seasonal and diurnal levels in the perennial brown alga *Laminaria hyperborea*. Additionally, the observations align with studies on DOC release by phaeophyceae, including *Eklonia cava*, *Macrocystis pyrifera*, *Nereocystis luetkeana* as well as *F. vesiculosus*, which have demonstrated marked increases in DOC release under daytime conditions compared to nighttime (Wada et al., 2007; Abdullah & Fredriksen, 2004, 2004; Reed et al., 2015; Weigel & Pfister, 2021). Sieburth (1969) suggested that as much as 30%–40% of *F. vesiculosus*' total fixed carbon is released back as dissolved organic matter.

In contrast to slow growing species, opportunistic species like *U. intestinalis* and *E. siliculosus* demonstrated more consistent DOC release, likely linked to their rapid growth rates and high surface-to-volume ratios (Paine et al., 2021). Fast-growing macroalgae rapidly assimilate and store photosynthetic products (Raven & Hurd, 2012). Provided they are not nutrient-limited, these species are likely less dependent upon active exudation processes to protect internal cell structures, as their growth rates facilitate the effective management of photosynthetic outputs through storage and utilization of said products (Mueller et al., 2016). As such, it is likely this rapid growth that enables them to better capitalize on environments with high light and nutrient availability whilst maintaining internal cellular integrity without the need for active protective mechanisms. Regarding the absence of observed DOC release by *F. lumbricalis*, this may be consistent with its adaptation to deeper, light-limited environments, thus not requiring adaptations to the rapid build-up of photosynthetic products. These physiological patterns appear to be closely linked to each species' ecological role and life history strategy, supporting theoretical frameworks that connect form, function, and carbon release in marine macroalgae (Paine et al., 2021; Hurd et al., 2014).

Overall, the variability in DOC release patterns observed in this study provides valuable insights into how different macroalgal species contribute to coastal carbon cycling and microbial loop dynamics. These findings complement previous work on species-specific carbon allocation strategies (Krause-Jensen & Duarte, 2016) and their implications for marine carbon budgets (Duarte & Cebrián, 1996; Krause-Jensen et al., 2018). The observed patterns highlight the potential for species-specific strategies to shape ecosystem-scale carbon fluxes in marine environments, contributing to our understanding of coastal carbon dynamics (Wada & Hama, 2013; Abdullah & Fredriksen, 2004) (**I, II, III**).

Environmental Controls on DOC Release and Carbon Acquisition

Water motion emerged as a critical factor influencing both carbon acquisition and DOC release (**III**). Enhanced photosynthetic rates observed under water motion conditions, particularly at the current pH level (8.2), underscore the role of physical dynamics in mediating macroalgal physiological responses (**III**). Insufficient water movement can lead to nutrient concentration gradients at the seaweed surface, restricting nutrient uptake. Conversely, appropriate water flow enhances nutrient availability and gas exchange, facilitating optimal metabolic activity (Hurd, 2014). These findings suggest that water motion benefits both species by reducing boundary layer effects and improving carbon delivery to the thallus surface (**III**). However, the magnitude of these benefits varies between species and across pH conditions, reflecting differing physiological capacities (**III**), similar to species-specific responses observed in other studies (Hurd, 2014; Comeau & Cornwall, 2016; Noisette & Hurd, 2018). The species-specific responses to water motion and pH further highlight their variable adaptability to environmental changes, suggesting that shifts in these physical and chemical factors under future climate scenarios could reshape macroalgal community composition (Pedersen & Borum, 1997; Stewart & Carpenter, 2003; Gao & Zheng, 2010).

The investigation of carbon acquisition mechanisms reveals distinct strategies between the studied species (**III**) adding to a growing understanding of CCM diversity in marine macroalgae (Pajusalu et al., 2016; Zhang et al., 2024). The pH drift experiments, and carbon isotope analyses demonstrate that both *U. intestinalis* and *C. glomerata* possess effective carbon concentrating mechanisms (CCMs), though with notable differences in their operation (**III**). *U. intestinalis* showed strong sensitivity to carbonic anhydrase inhibition, while *C. glomerata* maintained high pH levels under similar conditions, suggesting different evolutionary adaptations to carbon limitation (**III**). These differences in carbon acquisition strategies may influence species' competitive abilities under future climate scenarios, particularly considering predicted changes in ocean pH and carbon availability (Raven & Beardall, 2014; Koch et al., 2013). More specifically, differential responses of species to varying pH conditions provide insights into potential future ecosystem changes (Koch et al., 2013). The more efficient carbon acquisition by *U. intestinalis* at current pH levels, combined with its flexibility in DOC release mechanisms, suggests potential resilience to future conditions (**III**), supporting previous predictions about opportunistic species' adaptability (Wang et al., 2021; Gubelit, 2022). However, the improved performance of *C. glomerata* under elevated CO_2 conditions indicates possible shifts in competitive dynamics under future climate scenarios (**III**), consistent with observations in other freshwater-tolerant chlorophytes (Olischläger et al., 2013; Young & Gobler, 2016).

DOC Lability and Microbial Loop Dynamics

The bacterial consumption experiments reveal that the lability of released DOC varies significantly between species and conditions (**I, II**), confirming our hypothesis regarding species specific DOC lability and aligns with the limited number of previous studies which have explored the matter (Wada et al., 2007; Paine et al., 2021). The higher consumption rates of *F. vesiculosus* derived DOC under light conditions compared to other species suggests that changes in macroalgal community composition could significantly affect carbon transfer through the microbial loop (**I**). *U. intestinalis* demonstrated intermediate levels of DOC lability, with bacterial consumption reducing DOC concentrations by 13.1% under light conditions and 9.1% under dark conditions. This differential consumption between light and dark-derived DOC suggests that photosynthetically produced DOC may contain more bioavailable compounds (**I**), and as such may be linked to diel variations in DOC composition (Hulatt et al., 2009). These findings align with our hypothesis regarding the variable nature of DOC lability among species and its dependence on production conditions and suggests that DOC released during photosynthesis may be more readily available to bacterial communities than DOC released through passive mechanisms (**I, II**).

The bacterial biomass production (BBP) measurements provided key insights into the dynamics of the microbial loop (**I**). DOC released by *F. vesiculosus* under light conditions supported higher BBP compared to DOC released in darkness, with peak production occurring earlier in the light treatment (**I**). A similar trend was observed in *U. intestinalis*, where light-derived DOC also supported greater and earlier BBP compared to dark-derived DOC (**I**). The timing of peak bacterial production rates offers additional insights into DOC quality, with the earlier peak in bacterial production under light conditions suggesting that photosynthetically produced DOC contains more readily metabolizable compounds, facilitating rapid microbial utilization (**I**). This temporal pattern highlights not only species-specific differences in DOC quality but also how the physiological conditions under which DOC is produced influence its biochemical composition and subsequent microbial uptake (**I**). These findings illustrate that DOC is not only consumed but is efficiently converted into bacterial biomass, providing strong support for our hypothesis regarding the integral role of macroalgal DOC in sustaining the microbial loop (**I**). Additionally, timing of peak bacterial production rates aligns with previous observations of bacterial responses to fresh photosynthate (Obernosterer & Herndl, 1995; Amon & Benner, 1996), suggesting that photosynthetically produced DOC contains more readily metabolizable compounds (**I**). The relationship between DOC release conditions and subsequent bacterial consumption sheds light on the mechanisms driving carbon transfer in coastal ecosystems (**I, II**). The enhanced bacterial response to photosynthetically produced DOC indicates that diel patterns in macroalgal metabolism may introduce temporal fluctuations in carbon availability to microbial communities. This temporal coupling between primary producers and bacterial consumers likely plays a critical role in sustaining efficient carbon cycling in coastal ecosystems, emphasizing the need for further investigation.

The observed patterns of DOC lability and bacterial utilisation carry important implications for coastal carbon cycling. The higher lability of *F. vesiculosus*-derived DOC suggests that its historical decline in the Baltic Sea, which has been documented by Vogt & Schraam (1991) and Rohde et al. (2008), may have already altered carbon flow through the microbial loop. Furthermore, the species-specific differences in DOC release and lability indicate that future changes in macroalgal community composition could have cascading effects on microbial food web dynamics and overall ecosystem productivity, as suggested by similar studies in other coastal systems (Wada et al., 2007; Zhang et al., 2022).

Community Shifts and Implications for Coastal Carbon Cycling

Analysis of the macrophytobenthos time series (1995–2021) reveals distinct trends in species distribution and community composition across Estonian coastal waters (**II**). The historical decline in *F. vesiculosus* populations appears to have stabilized, likely reflecting the positive effects of nutrient reduction measures (Nilsson et al., 2004) (**II**). Since 1995, nitrogen inputs have decreased by approximately 30%, while phosphorus inputs initially declined before stabilizing (Kuss et al., 2020). However, the persistent impacts of eutrophication continue to shape coastal ecosystems (Gustafsson et al., 2012; HELCOM, 2018). Opportunistic algae showed significant upward trends in three monitored locations (Eru, Liu, and Tallinn transects) aligning with broader Baltic Sea trends documented by Korpinen et al. (2007) and Worm et al. (1999), while the 'Pylaiella-Ectocarpus' group displayed divergent patterns, increasing in Eru but declining in Kõiguste (**II**). *F. vesiculosus* exhibited no discernible trends across transects, suggesting population stability under current conditions (**II**). These shifts in community structure have important implications for carbon cycling, given species-specific differences in DOC release and microbial consumption observed in this study (**I, II, III**).

Our modelling of the biomass distribution of *F. vesiculosus* builds upon previous efforts to understand environmental drivers of macroalgal distribution in the Baltic Sea (Rinne & Salovius-Laurén, 2020; Nyström Sandman et al., 2013) (**II**). The total standing stock of *F. vesiculosus* in Estonian marine waters was estimated at approximately 150,000 tonnes (dry weight), representing a substantial carbon pool with an annual potential DOC release of 7,391 tonnes under optimal conditions (**II**). The shift from *F. vesiculosus*-dominated habitats to filamentous and opportunistic algal species may significantly impact coastal carbon cycling. *F. vesiculosus*, with its high DOC release and bacterial consumption efficiency, plays a critical role in carbon transfer through the microbial loop (**I**), similar to the role of other perennial brown algae in coastal systems (Abdullah & Fredriksen, 2004; Wada et al., 2007). In contrast, opportunistic species release less labile DOC, potentially reducing microbial loop efficiency and altering ecosystem productivity (**I, II**). Temporal stability of DOC release also varies between perennial and opportunistic species, suggesting that community shifts influence both the quantity and timing of carbon availability to microbial communities.

Community shifts carry broader implications as documented in other coastal systems experiencing similar changes (Mineur et al., 2015; Jiménez-Ramos et al., 2022). Reduced efficiency in carbon transfer through the microbial loop in filamentous algae-dominated systems could affect food web dynamics and productivity. Differences in DOC composition may also influence bacterial communities, potentially creating feedback loops that alter ecosystem processes. These findings emphasize the importance of incorporating macroalgal community composition into coastal carbon cycling models and management strategies. While the stabilization of *F. vesiculosus* populations suggests that nutrient reduction measures are effective, continued monitoring is critical to track the effects of ongoing environmental changes on community composition and associated carbon dynamics. This research provides essential baseline data for predicting how future changes in macroalgal communities may influence coastal carbon cycling and ecosystem function in the Baltic Sea and similar systems worldwide, contributing to our broader understanding of coastal ecosystem dynamics under environmental change (Duarte et al., 2013).

FUTURE DIRECTIONS AND MANAGEMENT IMPLICATIONS

While this research has provided valuable insights into the dynamics of macroalgal DOC production and its ecological implications, the short-term nature of the experiments conducted may not fully capture the complexity of seasonal or long-term carbon dynamics. Natural systems are influenced by multifaceted environmental interactions, which may lead to outcomes different from those observed under controlled laboratory conditions. To address these limitations and build upon the foundation established in this work, several key areas of future research merit attention.

First, long-term and seasonal studies of macroalgal DOC release patterns are essential for understanding variability over time. Seasonal changes in light availability, temperature, and nutrient levels could significantly influence the rates and composition of DOC release. For instance, the role of macroalgae in carbon cycling may be more pronounced during peak growth seasons, while their contributions may differ during senescence or dormancy phases. Such studies would provide a more nuanced understanding of the temporal dynamics of DOC contributions.

Second, future research should explore the interactive effects of multiple environmental stressors on macroalgal DOC release and its subsequent consumption by microbial communities. Variables such as temperature, nutrient loading, ocean acidification, and water motion do not act independently in natural systems, and their combined effects could produce emergent properties not predictable from single-factor experiments. Understanding these interactions is crucial for predicting the resilience or vulnerability of coastal ecosystems under changing environmental conditions.

Third, the detailed characterization of DOC compounds is a critical next step. The ecological significance of DOC depends not only on the quantity released but also on its chemical composition and bioavailability. Advances in analytical techniques such as mass spectrometry could allow for a more precise identification of DOC compounds and their roles in microbial food webs. This would enable the linking of specific macroalgal contributions to microbial activity and higher trophic levels.

Fourth, an improved understanding of the mechanisms of carbon acquisition under fluctuating environmental conditions is necessary. Species-specific variations in carbon concentrating mechanisms (CCMs) and their effectiveness under different pH and CO_2 scenarios could influence competitive dynamics among macroalgal species. This, in turn, could affect community composition and the broader ecological role of macroalgae in carbon cycling.

Finally, there is a need to develop comprehensive models that integrate physiological responses with ecosystem-level processes. Such models should account for carbon flow pathways, including DOC release, microbial processing, and transfer to higher trophic levels. Incorporating these elements into predictive frameworks would provide valuable tools for understanding how coastal ecosystems might respond to both natural variability and anthropogenic stressors.

Management Implications

The findings of this research carry important implications for the management of coastal ecosystems. The stabilization of Baltic Sea *Fucus* spp. populations in some regions suggests that nutrient reduction measures may be yielding positive outcomes. However, ongoing monitoring remains essential to ensure these populations continue to recover and remain resilient. Such monitoring programs should go beyond traditional biomass assessments to include evaluations of dissolved organic carbon (DOC) release and its broader ecological impacts, as these factors are integral to the functioning and productivity of coastal ecosystems.

Maintaining diverse macroalgal communities is crucial for fostering ecosystem resilience. Habitat-forming species like *F. vesiculosus* play a pivotal role in maintaining microbial loop function and nutrient cycling, while fast-growing opportunistic species often dominate in degraded environments, potentially destabilizing ecosystem dynamics. Management strategies must therefore prioritize the protection and restoration of diverse macroalgal habitats, recognizing their dual role as critical carbon processors and ecosystem engineers. Moreover, management plans must account for the potential impacts of climate change on macroalgal communities. Rising CO_2 levels, ocean acidification, and warming waters are expected to alter species distributions and DOC dynamics, potentially exacerbating ecosystem degradation. Adaptive strategies that address these challenges are essential. These should include measures to mitigate eutrophication, conserve biodiversity, and enhance ecosystem resilience in the face of environmental change.

By addressing both direct anthropogenic pressures and climate-driven changes, management strategies can safeguard the essential ecological functions provided by macroalgal communities. This integrated approach is vital for maintaining the health of Baltic Sea ecosystems as well as coastal ecosystems globally, ensuring their continued role as critical buffers in the global carbon cycle. Such efforts are not merely essential for preserving local biodiversity and sustaining ecosystem productivity but are also fundamental for broader climate regulation and the long-term stability of marine ecosystems worldwide.

CONCLUSIONS

Dissolved Organic Carbon Dynamics

- Macroalgal species show distinct patterns of DOC release, with *F. vesiculosus* exhibiting the highest rates under photosynthetic conditions.
- DOC release appears to be driven by both passive diffusion and active photosynthetic processes, with species-specific variations in the relative importance of each mechanism.
- The lability of released DOC varies significantly between species and environmental conditions, with bacterial consumption ranging from 13.1% to 28.7% over 120 hours.

Community Structure and Species Distribution

- Historical decline of *F. vesiculosus* in the Estonian coastal waters appears to have stabilized under current eutrophic conditions, suggesting potential effectiveness of nutrient reduction measures.
- A clear shift from *F. vesiculosus* dominated habitats to those characterized by filamentous and opportunistic algal species has occurred, with significant increases in opportunistic algae observed in multiple monitoring locations.
- The estimated standing stock of approximately 150,000 tonnes (dry weight) of *F. vesiculosus* within the Estonian marine area represents a significant carbon pool in the coastal ecosystem.

Carbon Acquisition Mechanisms

- *U. intestinalis* and *C. glomerata* demonstrate distinct carbon concentrating mechanisms (CCMs), evidenced by their δ13C values (–22.21‰ and –21.03‰ respectively) and pH drift responses.
- Species exhibit different sensitivities to carbon acquisition inhibitors, with *U. intestinalis* showing strong dependence on carbonic anhydrase, while *C. glomerata* maintains carbon uptake efficiency even under inhibition.
- Water motion significantly enhances photosynthetic performance and carbon acquisition, particularly under current pH conditions (8.2), though the magnitude of this effect varies between species.

Environmental Responses and Future Implications

- Species demonstrate varying abilities to adapt to different pH levels and water motion conditions, suggesting potential shifts in competitive dynamics under future climate scenarios.
- The transition from *F. vesiculosus* to filamentous algae-dominated systems has likely altered carbon flow patterns in coastal ecosystems, potentially affecting microbial loop dynamics and overall ecosystem function.
- Current pH conditions (8.2) appear optimal for most studied species, though responses to predicted future pH decreases vary among species

SUMMARY

This thesis explores the critical role of macroalgae-derived dissolved organic carbon (DOC) in marine carbon cycling, focusing on its production, consumption, and ecological impact for coastal ecosystem function. Macroalgae, commonly known as seaweeds, are significant primary producers in marine ecosystems, contributing substantially to the global carbon cycle. Unlike phytoplankton, which dominate open ocean systems, macroalgae thrive in coastal zones, creating structurally complex habitats and producing both particulate and dissolved organic matter. Dissolved organic carbon, released during photosynthesis and cellular processes, represents a dynamic component of the carbon cycle, serving as a substrate for microbial activity and influencing nutrient fluxes within marine ecosystems. However, the variability in DOC release among macroalgal species and its lability, the extent to which it is consumed by marine microbes, remains underexplored, particularly in the context of Baltic Sea.

Through controlled laboratory experiments, this work quantified DOC release rates under both light and dark conditions, finding that release patterns varied significantly between species and were influenced by photosynthetic activity. *F. vesiculosus* exhibited the highest DOC production under light conditions while showing minimal release in darkness, supporting the stoichiometric overflow hypothesis. *U. intestinalis* demonstrated consistent DOC release under both conditions, suggesting a combination of passive diffusion and photosynthetically driven release mechanisms. In contrast, *F. lumbricalis* showed negligible DOC release, indicating this process is not a universal trait among macroalgae. Additionally, this research investigated the bioavailability of the released DOC through bacterial consumption experiments. DOC produced under light conditions was generally more readily assimilated into bacterial biomass compared to that released in darkness, suggesting photosynthesis may influence DOC lability. *F. vesiculosus*, *U. intestinalis* and *E. siliculosus* all released DOC that supported significant bacterial production implicating it as an important carbon source for coastal sea microbes.

Integration of experimental results with long-term monitoring data revealed broader ecological implications. Analysis of phytobenthos time series (1995–2021) indicated a stabilization in the historical decline of *F. vesiculosus* populations, concurrent with increases in opportunistic filamentous algae across multiple monitoring locations. Species distribution modelling estimated the current *F. vesiculosus* standing stock in Estonian waters at approximately 150,000 tonnes dry weight. This biomass, under optimal conditions, could contribute up to 7,391 tonnes of DOC annually to coastal waters, though actual release rates are likely modulated by environmental variables including light availability, temperature, and water motion. The observed shift from *F. vesiculosus* to filamentous algae-dominated communities likely has major implications for coastal carbon cycling. The higher rates of DOC release and bacterial consumption associated with *F. vesiculosus* suggest that its displacement by species with different carbon

exudation characteristics, such as *E. siliculosus*, may alter carbon flow through the microbial loop. This finding is particularly relevant given the role of bacterial biomass production in transferring dissolved organic matter to higher trophic levels.

Environmental parameters, particularly water motion and pH, were found to be significant factors influencing both carbon acquisition and DOC release. The enhanced photosynthetic rates observed under water motion conditions, especially at current pH levels (8.2), underscore the importance of physical factors in mediating physiological responses. Species-specific responses to these variables suggest varying abilities to adapt to changing environmental conditions, which could influence future community composition and subsequently carbon dynamics under climate change scenarios. Additionally, the research also provided insights into carbon concentrating mechanisms (CCMs). pH drift experiments and carbon isotope analyses demonstrated that both *U. intestinalis* and *C. glomerata* possess effective CCMs, though with notable differences in their operation. These variations in carbon acquisition strategies may influence species' competitive abilities under future climate scenarios, particularly considering predicted changes in ocean pH and carbon availability.

This thesis advances our understanding of coastal carbon cycling while raising important questions about ecosystem responses to environmental change. The findings demonstrate that macroalgal community shifts can potentially significantly affect carbon flow patterns and emphasize the need to consider DOC dynamics in coastal ecosystem management. Future research directions should focus on characterizing DOC compound composition, understanding environmental controls on release rates, and evaluating longer-term bacterial consumption patterns. Additionally, investigation of seasonal variation in DOC release and the effects of multiple stressors will be crucial for predicting ecosystem responses to climate change.

The work provides essential baseline data for understanding coastal carbon dynamics while highlighting the complex interactions between macroalgal physiology, bacterial metabolism, and ecosystem function. These insights are particularly valuable for predicting and managing coastal ecosystem responses to environmental change in the Baltic Sea and similar systems globally.

SUMMARY IN ESTONIAN

Läänemere makrovetikate lahustunud orgaanilise süsiniku dünaamika: tootmine, biojuurdepääsetavus ja ökosüsteemi mõju.

Doktoritöös uuriti Läänemere makrovetikatest pärineva lahustunud orgaanilise süsiniku (DOC) tootmist, biosaadavust ja ökoloogilisi mõjusid. Rannikuökosüsteemide alustalana annavad makrovetikad olulise panuse primaarproduktsiooni ja süsinikuringesse, samas on DOC eraldumise mehhanismid ja selle laiem ökoloogiline roll endiselt ebapiisavalt uuritud. Doktoritöö eesmärk oli need lüngad täita, kirjeldades protsesse, mille käigus võtmetähtsusega makrovetikaliigid eraldavad DOC-i ja süsiniku liikumist mikroobide ja rannikuökosüsteemide kaudu. Uuringu tulemused annavad uusi teadmisi makrovetikate, mikroobikoosluste ja keskkonnategurite keerulisest koosmõjust merekeskkonnas, mis on väga vastuvõtlik inimtegevusele ja kliimamuutustele.

Uurimistöö keskendus peamiselt viiele olulisele Läänemere makrovetikaliigile: *Fucus vesiculosus*, *Furcellaria lumbricalis*, *Ulva intestinalis*, *Ectocarpus siliculosus* ja *Cladophora glomerata*. Nimetatud liigid esindavad erinevaid ökoloogilisi strateegiaid – alates mitmeaastasest, elupaiku moodustavast pruunvetika liigist *F. vesiculosus* kuni kiirekasvuliste ja oportunistlike rohevetikaliikideni *U. intestinalis* ja *C. glomerata*. Läbiviidud laborikatsetes ilmnesid selged erinevused makrovetikate DOC eraldamise kiirustes. Nii *F. vesiculosus* kui ka *U. intestinalis* eraldasid valguse tingimustes märkimisväärses koguses DOC-i, kusjuures protsess oli tihedalt seotud fotosünteesi aktiivsusega. Vastupidi, *F. lumbricalis* eraldas tühiselt vähe DOC-i nii valguse kui ka pimeduse tingimustes. Tulemused viitavad sellele, et DOC eraldumise mehhanismid ei ole ühtsed, vaid kujunevad vastavalt iga liigi füsioloogilistele omadustele. Tulemused toetavad kahte peamist hüpoteesi: stöhhiomeetrilise ülejäägi hüpoteesi, mis eeldab, et kõrge metaboolse aktiivsuse ajal väljutatakse liigseid fotosünteesi produkte, ning passiivse difusiooni mudelit, kus DOC lekib läbi rakumembraanide. Nende mehhanismide vastastikmõju sõltub tõenäoliselt keskkonnatingimustest ja liigispetsiifilistest omadustest.

Töö peamine eesmärk oli hinnata makrovetikatest pärineva DOC biosaadavust heterotroofsetele bakteritele. Bakterid mängivad olulist rolli süsinikuringes, muutes DOC-i biomassiks, mis võib toetada kõrgemaid troofilisi tasemeid. Saadud tulemused näitavad, et DOC lagundatavus varieerub oluliselt eri liikide vahel ja erinevate keskkonnatingimuste juures. Näiteks pruunvetikast *F. vesiculosus* eraldunud DOC oli kergemini lagundatav, toetades kiiret bakteriaalset kasvu, samas kui rohevetikast *U. intestinalis* pärinev DOC oli vähem biosaadav ja aitas vähemal määral kaasa bakteriaalse biomassi tootmisele. DOC lagundatavuse varieeruvus mõjutab süsinikuringet laiemalt, määrates, kui palju süsinikku säilib ökosüsteemis ja kui palju eksporditakse või seotakse pikaks ajaks. Kergesti lagundatav DOC toetab mikroobide hingamist ja taaskasutatakse sageli kiiresti, samas kui vähem lagundatavad vormid võivad veesambas kauem püsida või aidata kaasa pikaajalisele süsiniku ladestumisele. Seega võivad muutused makrovetikakoosluste koosseisus ja biomassis muuta tasakaalu lühiajalise energiavoo ja pikaajalise süsiniku sidumise vahel, millega kaasnevad ahelreaktsioonid mõjutavad ökosüsteemi funktsioone ja kliimaregulatsiooni.

Üks doktoritöö laiematest ökoloogilistest järeldustest on see, kuidas muutused makrovetikakoosluste struktuuris on mõjutanud süsinikuringet Läänemere rannikualadel. Eksperimentaalsete tulemuste ja pikaajaliste seireandmete integreerimine paljastas olulisi trende ja tagajärgi ökosüsteemi dünaamikale. Fütobentose aegridade analüüs (1995–2021) näitas, et *F. vesiculosus* populatsioonide ajalooline langus on stabiliseerunud, samal ajal kui oportunistlike niitjate vetikate osakaal on mitmes seirekohas märkimisväärselt suurenenud. Liikide leviku modelleerimine hindas *F. vesiculosus* varu praeguseks suuruseks Eesti vetes umbes 150 000 tonni kuivkaalus. Optimaalsetes tingimustes on selle biomassi potentsiaalne panus rannikuveekogude DOC-i kuni 7 391 tonni aastas. Kuid tegelikud DOC eraldumise määrad sõltuvad keskkonnateguritest, nagu valguse kättesaadavus, temperatuur ja vee liikumine, mis protsessi mõjutavad. Uuringust selgus, et *F. vesiculosus* vähenemine Läänemeres eutrofeerumise ja teiste inimtekkeliste mõjurite tõttu ning selle asendumine niitjate vetikaliikidega, nagu *E. siliculosus*, võib häirida süsiniku dünaamikat. *F. vesiculosus* eraldab märkimisväärses koguses biosaadavat DOC-i, mis toetab mikroobide aktiivsust, samas kui niitjad vetikad eraldavad väiksemaid koguseid vähem lagundatavat DOC-i. Selline muutus võib vähendada *microbial loop* aktiivsust, vähendades ökosüsteemi produktiivsust ja vastupidavust. Sellised muutused võivad potentsiaalselt destabiliseerida toiduvõrgustikke ja häirida toitainete ringlust. Tulemused rõhutavad pruunvetikale *F. vesiculosus* sarnaste, elupaiku moodustavate liikide kriitilist rolli rannikuökosüsteemide ökoloogilise terviklikkuse säilitamisel ja vajadust nende liikide kaitsmiseks, et tagada olulised ökosüsteemi funktsioonid.

Oluline uurimissuund oli ka väliste keskkonnategurite mõju uurimine makrovetikate füsioloogiale ning sellele, kuidas need mõjutavad DOC tootmist ja saatust. Rannikuökosüsteemid on olemuslikult dünaamilised ja muutujad nagu veeliikumine, pH ja süsinikdioksiidi tase võivad oluliselt mõjutada nii DOC eraldumist kui ka selle omastamist, komplitseerides veelgi süsinikuringe protsessi. Minu katsed näitasid, et kõrgendatud CO_2 kontsentratsioonid ja vähenenud veeliikumine võivad otseselt mõjutada fotosünteetilist efektiivsust ja muuta makrovetikate DOC eraldumise mustreid. Suurenenud fotosünteesi kiirused vee liikumise tingimustes, eriti praegustel pH tasemetel (8,2), rõhutavad füüsikaliste tegurite kriitilist rolli füsioloogiliste reaktsioonide reguleerimisel. Liigispetsiifilised reaktsioonid nendele muutujatele viitavad erinevale kohanemisvõimele muutuvate keskkonnatingimustega, mis võivad mõjutada tulevasi koosluse koosseise ja süsinikuringet kliimamuutuste tingimustes. Lisaks andis uuring uusi teadmisi makrovetikate süsiniku kontsentreerimise mehhanismidest (CCM-idest). pH-drifti katsete ja süsiniku isotoopanalüüside tulemused näitasid, et nii *U. intestinalis* kui ka *C. glomerata* omavad väga tõhusaid CCM-e, kuid nende toimimine erineb oluliselt kahe liigi vahel. Need erinevused süsiniku omandamise strateegiates võivad mängida olulist rolli nende konkurentsivõimes tulevaste kliimatingimuste tingimustes, eriti arvestades prognoositud muutusi ookeanide pH-s ja süsinikusaadavuses. Sidudes liigispetsiifilised DOC eraldumismäärad ja füsioloogilised mehhanismid nende keskkonnamõjuritega, pakub minu uurimus raamistiku mõistmaks, kuidas kliimamuutustest põhjustatud muutused ookeani keemias ja füüsikalistes tingimustes võivad fundamentaalselt ümber kujundada süsinikuringet ja ökosüsteemi funktsionaalsust ranniku piirkondades.

Nende leidude tähtsus ulatub kaugemale Läänemerest, andes teadmisi rannikuökosüsteemide kohta kogu maailmas. Rannikualasid peetakse üha enam kriitilisteks tsoonideks süsinikuringes ja süsiniku sidumises, mida sageli nimetatakse "sinise süsiniku" süsteemideks. Makrovetikad aitavad neisse süsteemidesse kaasa mitte ainult otsese süsiniku sidumise, vaid ka lahustunud orgaanilise aine pakkumise kaudu, mis toetab mikroobseid ja troofilisi protsesse. Käesolev uurimus rõhutab vajadust arvestada DOC eraldumist ranniku süsinikubilansi hindamisel ja keskkonnamuutuste mõjude prognoosimudelites. Liikidevaheline DOC lagundatavuse varieeruvus rõhutab liigirikkuse ja koosluse struktuuri tähtsust ökosüsteemi funktsionaalsuse säilitamisel.

Uurimistöö rõhutab ka rannikuökosüsteemide haavatavust inimtekkeliste mõjurite, näiteks eutrofeerumise, saastumise ja kliimamuutuste suhtes. Oluliste liikide, nagu *F. vesiculosus*, vähenemine ja niitjate vetikate tõus illustreerivad, kuidas inimtegevus võib põhimõtteliselt muuta ökosüsteemi dünaamikat. Need muutused ei mõjuta ainult kohalikku bioloogilist mitmekesisust, vaid avaldavad ka ahelmõjusid süsinikuringele, toitainete dünaamikale ja toiduvõrgustiku stabiilsusele. Makrovetikate mitmekesiste koosluste kaitsmine ja taastamine on seetõttu kriitilise tähtsusega rannikuökosüsteemide ökoloogilise terviklikkuse ja süsiniku sidumise potentsiaali säilitamiseks.

Tulevikku vaadates osutavad minu tulemused mitmele kriitilisele uurimisvaldkonnale. Vajalikud on pikaajalised uuringud, et jälgida DOC eraldumise hooajalist ja aastate vahelist varieeruvust ning selle seost keskkonnamuutustega. Uuringu laiendamine täiendavatele makrovetikaliikidele ja nende panusele süsinikuringesse võiks anda terviklikuma arusaama nendest protsessidest. Lisaks aitaks DOC dünaamika integreerimine toiduvõrgustiku uuringutega paremini mõista, kuidas lahustunud orgaaniline aine toetab kõrgemaid troofilisi tasemeid ja säilitab ranniku produktiivsust ning oleks aluseks tõhusate kaitse- ja majandamisstrateegiate väljatöötamiseks, mis käsitleksid rannikuökosüsteemide ees seisvaid mitmetahulisi väljakutseid.

Kokkuvõttes on doktoritöö edendanud meie arusaama makrovetikate DOC dünaamikast ja nende ökoloogilisest tähendusest, eriti Läänemere kontekstis. Selgitades DOC eraldumise mehhanisme, hinnates selle biosaadavust ning uurides keskkonna ja koosluste muutuste mõju, pakub uurimistöö väärtuslikke teadmisi makrovetikate rollist ranniku süsinikuringes. Tulemused rõhutavad mitmekesiste ja vastupidavate makrovetikakoosluste kaitsmise tähtsust, et säilitada rannikuökosüsteemide ökoloogilised ja süsiniku sidumise funktsioonid kiiresti muutuvas maailmas.

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PUBLICATIONS

CURRICULUM VITAE

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RESEARCH INTERESTS

My research focuses on coastal ecosystem dynamics, with a particular emphasis on the cycling, storage, and remineralization of organic and inorganic carbon in marine systems. I investigate how diverse organic matter sources, such as macroalgal derived carbon, influence food webs, the microbial loop, and broader ecosystem functioning. This work includes examining the roles of microbial communities in nutrient cycling and their implications for carbon sequestration in coastal habitats. In addition to this, I am experienced in sustainable aquaculture, specializing in seaweed cultivation for integrated multi-trophic aquaculture systems, aiming to minimize environmental impacts and optimize resource use. Beyond research, I am passionate about science communication, striving to connect scientific research with both students and the public.

EDUCATION

01.09.2019 –	Ph.D. Zoology and Hydrobiology, University of Tartu Estonia. “Mechanisms and Ecological Significance of Macroalgal-Derived DOC in Coastal Food Webs” Supervisors: Georg Martin (University of Tartu, Estonia), Christopher D. Hepburn (University of Otago, New Zealand, Federico Baltar (University of Vienna, Austria).
24.02.2016– 01.08.2018	M.Sc. in Marine Science (*with distinction*), University of Otago, New Zealand. Thesis title “Heterotrophic Bacterial Biofilms of Macroalgae” Supervisors: Christopher D. Hepburn & Federico Baltar (University of Otago).
24.02.2013 – 08.11.2015	B.Sc. in Aquaculture and Fisheries Science, University of Otago, New Zealand

SCIENTIFIC EMPLOYMENT

01.09.2019– Current	Junior Research Fellow – Estonian Marine Institute, University of Tartu. *Scientific Projects:* Restoration and sustainable management of bladderwrack (*Fucus vesiculosus*) in the Gulf of Riga, (01.10.2024 – 30.11.2027) Role: Researcher & Comms. Manager Baltic Protect WP4 (2023–2028) Role: Researcher Offshore Low-trophic Aquaculture in Multi-Use Scenario Realization WP1, OLAMUR, (2023–2026) Role: Researcher Demonstration of Innovative Functional Food Production Systems Based on a Sustainable Value Chain of Marine and Freshwater Raw Materials for Conscientious European Consumers, (01.05.23–30.04.26) Role: Researcher EIA study on benthic communities and habitats of offshore wind park in Gulf of Riga, (27.03.23–26.01.24) Role: Scientific Diver Studies in Support to the Implementation of the Mission: Lot 1 – ‘Marine Biodiversity Monitoring Harmonisation’, (14.12.23–13.12.24) Role: Researcher Land-based cultivation technology of green algae Ulva intestinalis in the fresh and brackish waters, (01.09.20–31.12.22) Role: Researcher Treatment of fish farm effluent through macroalgae cultivation, (2017–2021). Role: Researcher
01.08.2018– 01.09.2019	Scientific Observer – Falkland Islands Fisheries Department, Falkland Islands (UK) *Research Cruises:* Routine fisheries surveys – 14–35 days Skate/Ray mesh survey – 14 days Juvenile Toothfish recruitment survey – 17 days Joint FIFD/Argentina Calamar research study – 14 days
2017–2018	Research Assistant – Tipping Points (National Science Challenge), University of Otago
2016–2018	Lab Demonstrator – University of Otago
2016–2018	Scientific Diver – University of Otago

INTERNATIONAL COLLABORATIONS

2024	Research collaboration with Dr. Stina Kolodzey & Dr. Gauthier Schaal, European Marine Institute (LEMAR), Université de Bretagne Occidentale, Brest, France. Tracking the Fate of Carbon During the Degradation of Macroalgae (Reasearcher) – 4 weeks. Funded by French Institute of Estonia & Erasmus
2024	COST Action SeaWheat (CA20106) Training School: "Emissions, Capture, Utilisation: Methodologies and Challenges for Ulva", Estonia (Host, Trainer) – 4 days
2024	COST Action SeaWheat (CA20106) Conference: "Emissions, Capture, and Utilisation: Principles and Frameworks", Estonia (Organiser) – 3 days
2024	Research collaboration with 3 visiting M.Sc. students from the University of Otago. "The Long-Term Consumption of Fucus DOC by Bacteria"
2023, 2024	Estonian Coastal Carbon Workshop with Invited Guest Researchers, Kõiguste Field Station, Estonian Marine Institute, (Host) – 9 days

INTERNATIONAL COFERENCE PRESENTATIONS

Hall, J.R., Martin, G., et al., (2024). Macrophytobenthos Monitoring and the Need for Long-Term Ecological Monitoring. American Academy of Underwater Science (AAUS) Diving for Science Symposium. Fort Pierce, Florida, USA; April 14–20, 2024. Oral Presentation.

Albert, G., Hall J.R., Twigg I.M., Wenley, J., Pajusalu, L., Martin, G. (2023). Seaweed in a Changing Sea: Assessing the Role of Water Motion and Elevated CO_2 On the Availability of Dissolved Inorganic Carbon to Macroalgae. 12th Nordic Seaweed, Grenaa, Denmark; October 11–12, 2023. Poster Presentation.

Hall, J.R., Baltar, F., Twigg, I.M., Hepburn, C.D., Martin, G. (2023). Marine Dark Matter: Shifts in Macroalgae Composition Alter Carbon Flow in Coastal Ecosystems. The 24th International Seaweed Symposium (ISS), Hobart, Tasmania, Australia; February 19–24, 2023. Poster Presentation.

Hall, J.R. (2022) Marine Dark Matter. Estonian Marine Institute 30th Anniversary Conference, Tallinn, Estonia, October 14, 2022. Oral Presentation.

Hall, J.R., Baltar, F., Twigg, I.M., Hepburn, C.D., Martin, G. (2022). The Release of Dissolved Organic Carbon by Macroalgae and its Consumption by Bacteria: Implications for Coastal Ecosystems. Joint Aquatic Sciences Meeting (JASM, PSA), Grand Rapids, Michigan, USA; May 14–20, 2022. Oral Presentation.

Hall, J.R., Martin, G. (2021). Filtering Fish farm Wastewater Using a Macroalgae Biofilter. YOUMARES 12 Conference for Young Marine Researchers, Hamburg, Germany, October 5–7, 2021. Oral Presentation.

Hall, J.R., Baltar, F., Hepburn, C.D. (2018). Heterotrophic Bacterial Biofilms of Macroalgae. Joint meeting Phycological Society of America (PSA) and the International Society of Protistologists (ISOP), University of British Columbia, Vancouver, BC, Canada; July 29–August 2, 2018. Oral Presentation.

PUBLICATIONS

Albert, G., **Hall, J.R.**, Pajusalu, L., Twigg, I.M., Wenley, J., & Martin, G. (2025). The effect of water motion and elevated carbon on two green algae *Ulva intestinalis* and *Cladophora glomerata* DIC acquisition and DOC release in the brackish Baltic Sea. *European Journal of Phycology*, 1–10.

Hall, J.R., Herkül, K., Baltar, F., Hepburn, C.D., & Martin, G. (2024). Shifts in macroalgae composition alters carbon flow in Coastal Baltic Sea ecosystems: implications for dissolved organic carbon bioavailability and flux. *Frontiers in Marine Science*, *11*, 1384165.

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*, 934229.

Hall, J.R., & Martin, G. (2021). Filtration of dissolved organic nutrients from fish farm wastewater using a macroalgae biofilter. *WIT Trans Ecol Environ*, *250*, 73–80.

Twigg, I. M., Baltar, F., **Hall, J.R.**, & Hepburn, C.D. (2020). Revealing hydrogen peroxide as an external stressor in macrophyte-dominated coastal ecosystems. *Oecologia*, *193*, 583–591.

ELULOOKIRJELDUS

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TEADUSTEGEVUSE HUVIVALDKONNAD

Minu uurimistöö keskendub rannikuökosüsteemide dünaamikale, pöörates erilist tähelepanu orgaanilise ja anorgaanilise süsiniku ringlusele, ladustamisele ja remineraliseerimisele mereökosüsteemides. Uurin, kuidas mitmesugused orgaanilise aine allikad, nagu makrovetikatest pärinev süsinik, mõjutavad toiduvõrgustikke, mikroobide ahelat ja laiemat ökosüsteemi toimimist. See hõlmab ka mikroobikoosluste rollide uurimist toitainete ringluses ja nende mõju süsiniku sidumisele rannikualadel. Lisaks olen kogenud jätkusuutliku vesiviljeluse alal, spetsialiseerudes vetikate kasvatamisele integreeritud mitme troofilise taseme vesiviljelussüsteemides, mille eesmärk on minimeerida keskkonnamõjusid ja optimeerida ressursside kasutamist. Lisaks uurimistööle olen kirglik teaduskommunikatsiooni valdkonnas, püüdes siduda teadusuuringuid nii õpilaste kui ka avalikkusega.

HARIDUS

01.09.2019 –	Ph.D. zooloogias ja hüdrobioloogias, Tartu Ülikool, Eesti. “Makrovetikatest pärineva lahustunud orgaanilise süsiniku mehhanismid ja ökoloogiline tähtsus rannikutoiduvõrgustikes.” Juhendajad: Georg Martin (Tartu Ülikool, Eesti), Christopher D. Hepburn (Otago Ülikool, Uus-Meremaa), Federico Baltar (Viini Ülikool, Austria).
24.02.2016– 01.08.2018	M.Sc. merebioloogias (cum laude), Otago Ülikool, Uus-Meremaa. Lõputöö pealkiri: “Makrovetikate heterotroofsete bakteriaalsete biofilmide uurimine.” Juhendajad: Christopher D. Hepburn ja Federico Baltar (Otago Ülikool).
24.02.2013 – 08.11.2015	B.Sc. vesiviljeluse ja kalandusteaduse alal, Otago Ülikool, Uus-Meremaa.

TEADUSLIK TÖÖKOGEMUS

01.09.2019–praegu	Nooremteadur – Eesti Mereinstituut, Tartu Ülikool. *Teadusprojektid:* Restoration and sustainable management of bladderwrack (*Fucus vesiculosus*) in the Gulf of Riga, (01.10.2024 – 30.11.2027) Role: Researcher & Comms. Manager Baltic Protect WP4 (2023–2028) Role: Researcher Offshore Low-trophic Aquaculture in Multi-Use Scenario Realization WP1, OLAMUR, (2023–2026) Role: Researcher Demonstration of Innovative Functional Food Production Systems Based on a Sustainable Value Chain of Marine and Freshwater Raw Materials for Conscientious European Consumers, (01.05.23–30.04.26) Role: Researcher EIA study on benthic communities and habitats of offshore wind park in Gulf of Riga, (27.03.23–26.01.24) Role: Scientific Diver Studies in Support to the Implementation of the Mission: Lot 1 – 'Marine Biodiversity Monitoring Harmonisation', (14.12.23–13.12.24) Role: Researcher Land-based cultivation technology of green algae Ulva intestinalis in the fresh and brackish waters, (01.09.20–31.12.22) Role: Researcher Treatment of fish farm effluent through macroalgae cultivation, (2017 – 2021). Role: Researcher
01.08.2018–01.09.2019	Teadusvaatleja – Falklandi Saarte Kalanduse osakond, Falklandi saared (Ühendkuningriik). *Teadusreisid:* Routine fisheries surveys – 14–35 days Skate/Ray mesh survey – 14 days Juvenile Toothfish recruitment survey – 17 days Joint FIFD/Argentina Calamar research study – 14 days
2017–2018	Teadusassistent – Tipping Points projekt (National Science Challenge), Otago Ülikool.
2016–2018	Labori juhendaja – Otago Ülikool.
2016–2018	Teadussukelduja – Otago Ülikool.

RAHVUSVAHELISED KOOSTÖÖD

2024	Teaduskoostöö dr. Stina Kolodzey ja dr. Gauthier Schaaliga, Euroopa Mereinstituut (LEMAR), Bretagne'i Lääne-Ülikool, Brest, Prantsusmaa. Makrovetikate lagunemise süsiniku jälgimine. Roll: Teadlane – 4 nädalat. Rahastatud Prantsuse Instituudi poolt Eestis ja Erasmuse kaudu.
2024	COST Action SeaWheat (CA20106) koolitus: "Emissioonid, sidumine ja kasutamine: meetodid ja väljakutsed Ulva puhul," Eesti (võõrustaja, koolitaja) – 4 päeva.
2024	COST Action SeaWheat (CA20106) konverents: "Emissioonid, sidumine ja kasutamine: põhimõtted ja raamistikud," Eesti (korraldaja) – 3 päeva.
2024	Koostöö kolme Otago Ülikooli magistrandiga: "Pikaajaline bakterite tarbimine Fucus'e lahustunud orgaanilisel süsinikul."
2023, 2024	Eesti ranniku süsinikuteemaline töötuba koos külalisuurijatega, Kõiguste Välijaam, Eesti Mereinstituut (võõrustaja) – 9 päeva.

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PUBLIKATSIOONID

Albert, G., **Hall, J.R.**, Pajusalu, L., Twigg, I.M., Wenley, J., & Martin, G. (2025). The effect of water motion and elevated carbon on two green algae *Ulva intestinalis* and *Cladophora glomerata* DIC acquisition and DOC release in the brackish Baltic Sea. *European Journal of Phycology*, 1–10.

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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*, 934229.

Hall, J.R., & Martin, G. (2021). Filtration of dissolved organic nutrients from fish farm wastewater using a macroalgae biofilter. *WIT Trans Ecol Environ*, *250*, 73–80.

Twigg, I. M., Baltar, F., **Hall, J.R.**, & Hepburn, C.D. (2020). Revealing hydrogen peroxide as an external stressor in macrophyte-dominated coastal ecosystems. *Oecologia*, *193*, 583–591.

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