BIODIVERSITY AND OXYGEN DYNAMICS

WITHIN SEAGRASS AND MACROALGAL CANOPIES IN THE BALTIC SEA

Master's thesis

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Coastal vegetated habitats such as seagrass and macroalgae canopies are generally associated with high biodiversity, but little is known about the oxygen dynamics within these habitats. This research aims to create a better understanding of the effect and duration of different oxygen conditions within these key coastal habitats of the Baltic Sea, as well as their potential impacts on the benthic fauna. In this study, a new system was developed to investigate the vertical oxygen distribution within the seagrass and macroalgal canopies. This data was combined with macrofauna community analyses to investigate the biodiversity associated with the canopies.

A combination of *in situ* instrumentation and biodiversity surveying was used to investigate the potential implications of oxygen dynamics for canopy-associated macrofauna. Six locations were selected for the study. Seagrass and macroalgal habitats were studied at sites with different wave exposure, i.e., sheltered and exposed. One site with bare sediments and one site with significant macroalgal detritus were sampled for comparison purposes. The duration of different oxygen conditions was studied using dissolved oxygen sensors placed at different heights of the canopy and left to sample for 3-5 days in one-minute intervals. The factors influencing oxygen dynamics were examined, such as flow velocity, irradiance, exposure, salinity, vegetation height, and shoot density. The potential effects of these factors on benthic macrofauna were studied by benthic biodiversity surveying.

Oxygen dynamics differed between the seagrass and macroalgal canopies and the sheltered and exposed locations. Waves oxygenated the exposed seagrass canopy, whereas the weaker current at the sheltered seagrass site did not penetrate well into the canopy, resulting in lower oxygen conditions within the canopy than above the canopy. The highest oxygen concentrations were measured at the sheltered macroalgal canopy. At most study sites, oxygen concentrations were high and likely did not affect the canopy-associated fauna. The order of decreasing gradient for the macrofauna biodiversity across the sites was macroalgae sheltered > seagrass exposed > seagrass sheltered > macroalgae exposed > detritus > bare sand. The site with bare sediment was well-oxygenated, yet the macrofauna biodiversity was low, indicating the importance of marine vegetation as a habitat foundation for species. The site with significant algal detritus showed temporary hypoxic and anoxic conditions and low macrofauna biodiversity, indicating a connection between oxygen availability and macrofauna survival.

This combination method is suitable when investigating oxygen dynamics close to the seabed (<1m) and benthic biodiversity *in situ*, and broader research with more replicates covering various seasons could provide knowledge on the duration of hypoxia in shallow coastal waters.

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Biodiversity, oxygen dynamics, macrofauna, Zostera marina, Fucus vesiculosus

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Tiivistelmä – Referat – Abstract

Rannikkoalueiden vedenalaiset luontotyypit, kuten meriajokas- ja rakkohaurupohjat, ovat biologisesti monimuotoisia elinympäristöjä, mutta niiden hapen dynamiikasta pohjan lähellä tiedetään vielä vähän. Tämän tutkimuksen tavoitteena on ymmärtää näiden Itämeren elinympäristöjen erilaisten happiolosuhteiden kestoa sekä niiden mahdollisia vaikutuksia pohjaeläimistöön. Tässä tutkimuksessa kokeiltiin uutta menetelmää meriajokas- ja makroleväpohjien vertikaalisen hapen jakautumisen tutkimiseksi. Tulokset yhdistettiin makrofaunayhteisöstä tehtyihin analyyseihin biologisen monimuotoisuuden tutkimiseksi.

Tutkimuksessa käytettiin *in situ* menetelmää, jossa yhdistettiin happiolosuhteiden vaihtelun mahdolliset vaikutukset pohjaeläinyhteisön biodiversiteettiin. Tutkimukseen valittiin kuusi kohdetta. Meriajokas- ja rakkohaurun elinympäristöjä tutkittiin suojaisilla ja avoimilla kohteilla. Lisäksi vertailuun valittiin yksi kohde paljaalla sedimenttipohjalla ja kohde, jossa kuollut rakkohaurumatto peitti pehmeän pohjan. Erilaisten happiolosuhteiden kestoa tutkittiin käyttäen happiantureita, jotka sijoitettiin kasvillisuuslaikun sisälle eri korkeuksille mittaamaan yhden minuutin välein 3–5 päivän ajan. Tutkimuksessa seurattiin hapen dynamiikkaan vaikuttavia tekijöitä, kuten virtausnopeutta, valon määrää, avoimuutta, suolapitoisuutta, kasvillisuuden korkeutta ja versojen tiheyttä sekä tutkittiin näiden tekijöiden mahdollisia vaikutuksia pohjaeliöstöön.

Happiolosuhteet erosivat meriajokas- ja rakkohaurupohjilla sekä suojaisten ja avointen kohteiden välillä. Aallot hapettivat avoimemman vyöhykkeen meriajokasniittyä, kun taas suojaisella niityllä vallinnut heikompi virtaus ei ulottunut kasvillisuuslaikun sisäosiin asti, mikä johti alhaisempiin happilukemiin laikun sisällä kuin sen yläpuolella. Tutkimuksen korkeimmat happipitoisuudet mitattiin suojaisassa rakkohauruyhteisössä. Useimmilla tutkimuskohteilla happipitoisuudet olivat hyvät eivätkä vaikuttaneet pohjaeläimistön esiintyvyyteen ja monimuotoisuuteen. Pohjaeläimistön monimuotoisuus oli suurimmasta pienempään suojaisa rakkohaurupohja > avoin meriajokaspohja > suojaisa meriajokaspohja > avoin rakkohaurupohja> levämatto > paljas hiekkapohja. Hiekkapohjalla happea oli runsaasti, mutta eläimistölle tärkeää kasvillisuus puuttui. Kohteella, jota peitti paksu levämatto, havaittiin useita hapettomia jaksoja sekä alhainen makrofaunan monimuotoisuus. Tulokset saattavat viitata yhteyteen hapen määrän ja pohjaeliöiden esiintymisen sekä selviytymisen välillä.

Tässä työssä testattua menetelmää voidaan käyttää elinympäristöjen happiolosuhteiden ja biodiversiteetin tutkimiseen pohjan välittömässä läheisyydessä selvittäessä laajemmin matalien rannikkoalueiden hapettomien jaksojen kestoa ja laajuutta.

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1 Introduction

1.1 Oxygen availability in coastal canopies

Some of the most important habitats in the Baltic Sea coastal areas are made of macrophyte species such as macroalgal canopies on rocky shores, and seagrass and limnic plants on soft sediments. These shallow habitats have high biodiversity and play a vital role in coastal ecosystem functioning (Attard et al. 2019a; Rodil et al. 2020).

Light conditions are high in shallow coastal areas (Gattuso et al. 2006). Seagrass and macroalgae form habitats with high photosynthetic biomass, and primary production and respiration are especially significant in these habitats (Mann 1973; Fourqurean et al. 2012). Oxygen is produced through photosynthesis during the day and consumed as respiration at night (Tyler et al. 2009). Respiration is synchronized with the decline in temperature at night, when photosynthesis stops. Chemical re-oxidation from anaerobic respiration pathways and aerobic respiration processes consume oxygen (Middelburg and Levin 2009).

Currents and waves provide oxygenated water to the coastal area through mixing and equilibration with the air above (Hansen and Reidenbach 2017). The dissolved oxygen values cycle between the canopy and the water layer above the canopy, and vertically within the canopy (Hansen and Reidenbach 2017) (Figure 1). Seagrass and macroalgae take nutrients from the water, and the needed nutrients must pass the canopy-water interface (Hansen and Reidenbach 2017). The flow intensity and the size of a canopy, i.e. height and shoot density, affects the canopy ventilation rate (Hansen and Reidenbach 2012).

1.2 Sheltered and exposed study sites

Flow velocities are lower in sheltered locations; hence less oxygenated water is brought into the canopy by the flow. Lower flow velocities result in less water mixing, and thermal stratification can occur, isolating the canopy from water exchange. Thus, oxygen conditions within the canopy may become different from those in the water layer above the canopy (Long et al. 2015; Camillini et al. 2021) or depleted during respiration (Rabalais et al. 2010). Consequently, the lack of oxygen may impact biodiversity (Vaquer-Sunyer and Duarte 2008).

Sheltered locations of seagrass canopies have lower shoot densities, hence potentially producing less oxygen. Lower below-ground biomass captures less sediment, and hence, potentially increases turbidity in the water. During low flow conditions, sediment accumulation can increase on the leaves, decreasing light capture (Long et al. 2015). Lower movement exposes fewer parts of the seagrass blades to the light, decreasing photosynthesis (Enriquez et al. 2002; Long et al. 2015) and oxygen production. Lower flow velocities may result in the accumulation of drift algae, reducing light and water exchange. The flow is more unstable in the sparse canopy than in dense canopy due to different interaction with the leaves, causing turbulence to increase between the top of the canopy and the water above the canopy. Turbulence is not as efficient as waves in transferring fluids within the canopy (Hansen and Reidenbach 2017), and ventilation rates within the sparse canopy remain low.

At exposed areas, waves induce oscillatory motions that can create the opening and closing movements of a seagrass canopy, thereby enhancing water and nutrient transport into the canopy (Koch and Gust 1999). Waves generated by winds enter deeper into the canopy than unidirectional currents (Hansen and Reidenbach 2017), which are more common at sheltered locations (Koch and Gust 1999). The drag created by the canopy does not influence at the exposed, wave-dominated areas as much as in sheltered areas (Hansen and Reidenbach 2017). Higher flow velocity also improves internal oxygen conditions inside the seagrass leaves (Binzer et al. 2005), potentially increasing growth (Peralta et al. 2006) and oxygen production.

1.3 Biodiversity and oxygen dynamics

1.3.1 Macroalgal canopies

Macroalgae are the most productive marine macrophytes (Smith 1981). Algae attached to a hard substrate with a holdfast can absorb nutrients from the water, thus having a high nutrient resource (Mann 1973). *Fucus vesiculosus*, Linnaeus 1753, is a large perennial macroalga that forms belts on rocky coastal areas (Rönnbäck et al. 2007). The habitat of *F. vesiculosus* has high biodiversity and is vital for invertebrates such as isopods and gastropods that live within those habitats. By grazing on the vegetation, invertebrates control epiphyte growth on macroalgae and filamentous algae on the rocky substrate (Rönnbäck et al. 2007).

Invertebrates are important food for fish (Lappalainen et al. 2001) and seabirds (Kautsky and Svensson 2003).

Macroalgal habitats also improve the biodiversity of non-vegetated areas. When macroalgae detach from a substrate, they can drift to unvegetated soft sediments. Under eutrophicated conditions, drifting algal mats can cause negative effects on the seafloor vegetation and associated macrofauna communities. However, under non-eutrophicated conditions, seasonal patchy occurrence of drift algae can have a positive short-term impact. Unvegetated soft-bottom sediments have lower biodiversity compared to vegetated areas (Rönnbäck et al. 2007; Rodil et al. 2020), hence drifting algal mats become an alternative habitat for benthic invertebrates, providing food and refuge from predators (Norkko and Bonsdorff 1996a; Norkko et al. 2000). Consequently, they also provide a food source for some fish species and zooplankton (Vetter 1994; Norkko et al. 2000).

Macroalgal canopies generate high biomass and therefore produce carbon in excess year-round (Attard et al. 2019a; b); therefore, they are currently considered potential carbon sinks (Krause-Jensen and Duarte 2016). Detached macroalgae can be highly mobile and drift seasonally with currents (Harrold et al. 1998). The gas vesicles of the *Fucus* genus improve their ability to drift further from the littoral than other macrophytes. Eventually, they sink, causing algae to sink into deeper habitats and provide food supply to adjacent food webs. Recently, it has been estimated that part of the produced organic macroalgal carbon, ~40%, is exported to adjacent habitats, and a smaller proportion of this (∼15 %) is sequestered in the deep sea (Duarte and Cebrián 1996; Krause-Jensen and Duarte 2016).

During the past recent decades, the depth distribution of *F. vesiculosus* has decreased on the shores of the Baltic Sea (Kautsky et al. 1986, Schramm 1999). Light availability correlates with the maximum growth depth of *F. vesiculosus* (Bäck and Ruuskanen 2000). Hence, increased turbidity, epiphytes and sediment dust on rocks worsens the growth conditions of *F. vesiculosus* (Eriksson and Johansson 2003; Torn et al. 2006).

1.3.2 Seagrass canopies

Seagrass *Zostera marina* (Linnaeus 1753) is the only fully submerged seed plant in the Baltic Sea (Lappalainen et al. 1977), and it differs from other vegetation with its robust leaf shape, creating a unique biotope with many niches for macroinvertebrates and fish (Boström et al. 2003). Seagrass meadows show high primary production and can entrap particles from the water and store them in sediments (Fourqurean et al. 2012). The below-ground biomass of seagrass canopies can withhold sediment, preventing erosion and reducing turbidity (Lappalainen et al. 1977), thereby enhancing light penetration (Rönnbäck et al. 2007).

Canopies have many positive effects on biodiversity but are known to dampen flow velocities. Significant above-ground biomass of a seagrass canopy can reduce water mixing and circulation within the canopy (Hansen and Reidenbach 2017.) A shear layer[1] above the canopy may develop, creating instabilities and turbulence between the water column and the canopy (Figure 1). Depending on how much oxygen is produced and consumed, reduced flow can worsen oxygen conditions within the canopy, causing an unknown effect on benthic fauna communities living there.

[1] A strong shear layer with a difference in flow velocities develops above the canopy, controlling the fluid exchange. In free water shear layers, flow vortices grow continually. Above a canopy, flow is forced to rotate around each leave; thus, vortices reach a fixed thickness and separate the canopy into layers. The thickness of a layer depends on flow intensity and the canopy area, density, and height (Nepf et al. 2007).

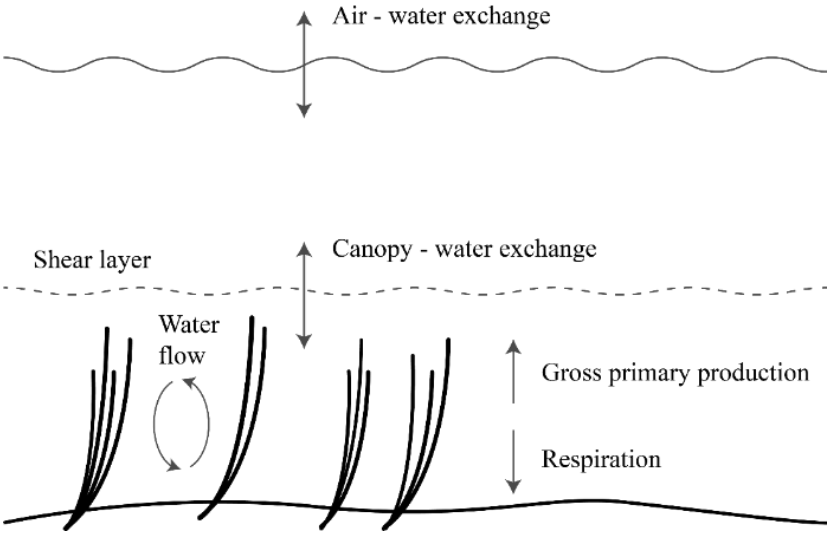


Figure 1. Canopy ventilation and water exchange with surrounding waters. Gross primary production produces oxygen, while respiration consumes oxygen. Illustration by Anna Lyssenko.

1.4 The difference between the seagrass and macroalgal habitats

Seagrass and macroalgal habitats differ in many ways. Seagrass is rooted in soft sediments (Figure 2) and takes nutrients from the water into the sediment. It can store two-thirds of total organic carbon in its roots and rhizomes (Fourqueran et al. 2012). Hence carbon can be directly locked down from the leaves to the sediment. However, high amounts of carbon and oxygen are used for root metabolism. Seagrass canopies are often nutrient limited, indicating that part of their production is allocated to maintain the root biomass (Duarte et al. 1998). Therefore, by accumulating carbon, sediments also consume oxygen. As the significant below-ground biomass of seagrass is non-photosynthetic yet consumes oxygen, the balance between primary production and respiration may be different to macroalgae that lack a below-ground biomass.

Large perennial macroalgae normally grow on hard substrate (Figure 2) and take nutrients from the water column (Smith 1981). Carbon does not accumulate on a hard substrate; thus, macroalgal canopies potentially have lower oxygen consumption and potentially higher oxygen concentration values within the canopy.

Oxygen production within macroalgal habitats is high year-round (Attard et al. 2019b). Oxygen also accumulates inside the vesicles of *F. vesiculosus,* and it is potentially released at night or when exposed to darkness (Aleem 1969; Attard et al. 2019b), which may also increase oxygen concentration within the canopy, compared to seagrass.

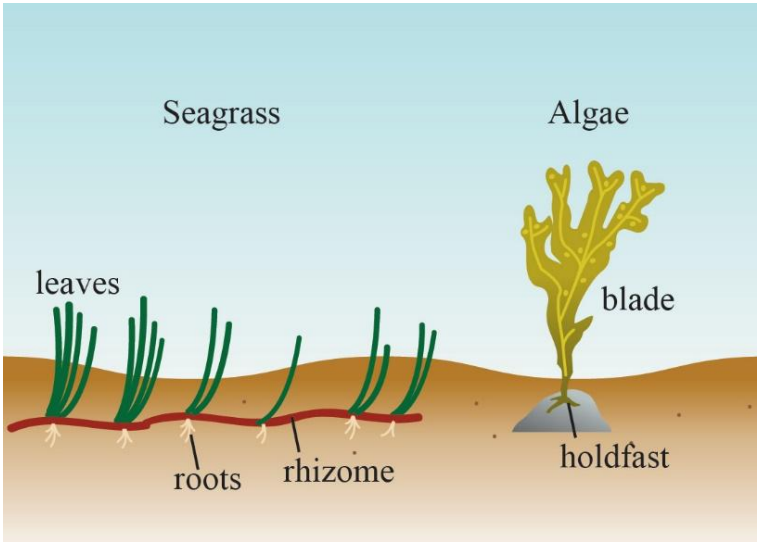


Figure 2. Seagrass attaches to the bottom sediment with roots and rhizomes, whereas algae attach with a holdfast and thus lack a below-ground biomass. The figure is a modification from Kruczynski and Fletcher (eds.) 2012.

1.5 Effects of increasing temperature on oxygen conditions within canopies

1.5.1 Oxygen solubility in water

Global warming affects the oxygen concentrations within the canopies. The solubility of oxygen in water is dependent on temperature, salinity, and pressure at the particular depth (Diaz and Rosenberg 1995). In coastal marine habitats, average oxygen concentrations are considered to range from 89.3 µmol L^{-1} to 357.3 – 446.6 µmol L^{-1}. In the atmosphere, the oxygen concentration is about 8932.2 µmol L^{-1} (Diaz and Rosenberg 1995). When the temperature increases, oxygen concentration decreases in the water column. For instance, waters of 9 °C at 6.0 ‰ can dissolve 347.5 µmol L^{-1} of oxygen, but if the temperature rises to 16 °C, only 297.2 µmol L^{-1} of oxygen is dissolved. Examples are derived from The Unisense Oxygen Solubility Table, which is found in Appendix A.

1.5.2 Increasing temperature within canopies

Primary productivity and respiration increase with temperature (Lee et al. 2007; Tait and Schiel 2013). Usually, these metabolic processes have a Q10 of 2, which means that they double when the temperature increases 10°C as the Q10 indicates the temperature increase of 10°C. This Q10 effect can vary between processes and may become mismatched (Tait and Schiel 2013) so that respiration increases with temperature faster than photosynthesis (Hancke and Glud 2004). Hence, more oxygen is consumed by organisms than produced via photosynthesis with increasing temperature.

1.5.3 Filamentous algae drifting into canopies

The epiphytic filamentous algae are short-lived seasonal species that increase with increasing temperature and nutrient enhancement (Norkko and Bonsdorff 1996b; Schramm 1999). Filamentous algae grow on hard substrate or as epiphytic on larger macroalgae. After detaching, filamentous algae can drift into the perennial macroalgae and seagrass canopies and may reduce water circulation and light availability. Drifting algae consume oxygen via heterotrophic activities and respiration, causing degeneration of canopies (Schramm 1999; Boström et al. 2003). High temperature conditions under the algal detritus may accelerate oxygen consumption (Norkko and Bonsdorf 1996b).

1.5.4 Hypoxia affecting animal groups

Anthropogenic activities make coastal habitats especially vulnerable to eutrophication (Doney 2010; Howarth et al. 2011), and low-oxygen events are predicted to increase with temperature (Díaz and Rosenberg 2008).

Hypoxia occurs when dissolved oxygen concentration is < 63 μmol L^{-1} (or 30% saturation) (Conley et al. 2009), and anoxic conditions occur when there is no oxygen in the water (Díaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008). Coastal hypoxia typically occurs during warm seasons and can last from some minutes to months. Hence, it may be diel-cycling, episodic, or seasonal (Tyler et al. 2009). Diel-cycling hypoxia occurs in shallow waters and is driven by oxygen production during the day and respiration at night. Temperature, mixing, and stratification affect the formation of episodic and seasonal hypoxia

(Tyler et al. 2009). Episodic hypoxia can be a precursor to seasonal hypoxia (Conley et al. 2011).

Oxygen is critical to marine invertebrates (Díaz and Rosenberg 1995), and they have different sensitivities to low oxygen levels (Vaquer-Sunyer and Duarte 2008). Some species can tolerate temporary hypoxia and anoxia and live in habitats where these events are common. Fauna can still experience mortality and symptoms like reduced growth, declines in reproduction, and physiologic stress at oxygen levels above 63 μmol L^{-1} (Díaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008). Severe or long-term hypoxia causes mass mortality of macrofauna communities (Díaz and Rosenberg 1995). Macrofauna inhabiting the coastal canopies are exposed to low-oxygen events of unknown duration and frequency.

1.6 The goals of this research

Shallow coastal areas are rich in biodiversity and ecologically important habitats for Baltic Sea ecosystem functioning (Rodil et al. 2020). These heterogenous habitats show intense oxygen production and consumption rates (Attard et al. 2019b) but the natural oxygen dynamics within the canopies are mainly unknown. Traditional coastal monitoring programs typically sample to within 1 m above the seafloor, largely excluding the benthic boundary layer. There is a need for more knowledge on the occurrence, duration, and frequency of different oxygen events within close proximity to the seafloor (i.e. 0-0.5 m) to better understand the variety of conditions that macrofauna experiences within the canopies.

The main goal of this master's thesis research was to investigate the oxygen dynamics in shallow vegetated coastal habitats of the Baltic Sea and their potential implications for canopy fauna using a novel combination of *in situ* instrumentation and biodiversity surveying. This study investigated how the dissolved oxygen varied vertically during the day and night periods and over several days across different key seafloor habitats. The oxygen dynamics and benthic macrofauna biodiversity surveys were performed at six different locations in the Tvärminne archipelago.

2 Material and methods

A novel combination of *in situ* instrumentation and benthic biodiversity surveying was used at all six study sites to investigate biodiversity and oxygen dynamics in locations of different exposure, i.e., sheltered and exposed. One habitat type was dominated by the seagrass *Z. marina* and showing a mix of limnic species, and another habitat type dominated by bladder-wrack *F. vesiculosus* and showing a mix of other algae species. Also, one location with significant macroalgal detritus and one bare sediment habitat were studied for comparison purposes.

2.1 Study sites

The study was conducted in the area of Tvärminne archipelago in SW Finland during May-June 2018. Six locations were selected for the study (Figure 3 and 4) consisting of one habitat with macroalgal detritus (Detritus, Figure 4a), two seagrass habitats (sheltered and exposed; SGsh and SGex, Figures 4b and 4c), two macroalgal habitats (sheltered and exposed; FUsh and FUex, Figures 4d and 4e), and one bare sediment site (Bare, Figure 4f). Two of the sites were located close to Spikarna archipelago, two sites at Ångbåtbryggan, one at Vindskären island and one in the area of Henriksberg (Figure 4). Biodiversity sampling within the study area was performed following the sampling protocol developed by Rodil et al. (2019). The detailed information of habitat descriptions, environmental conditions, locations, and sampling methods and periods are presented in Table 1.

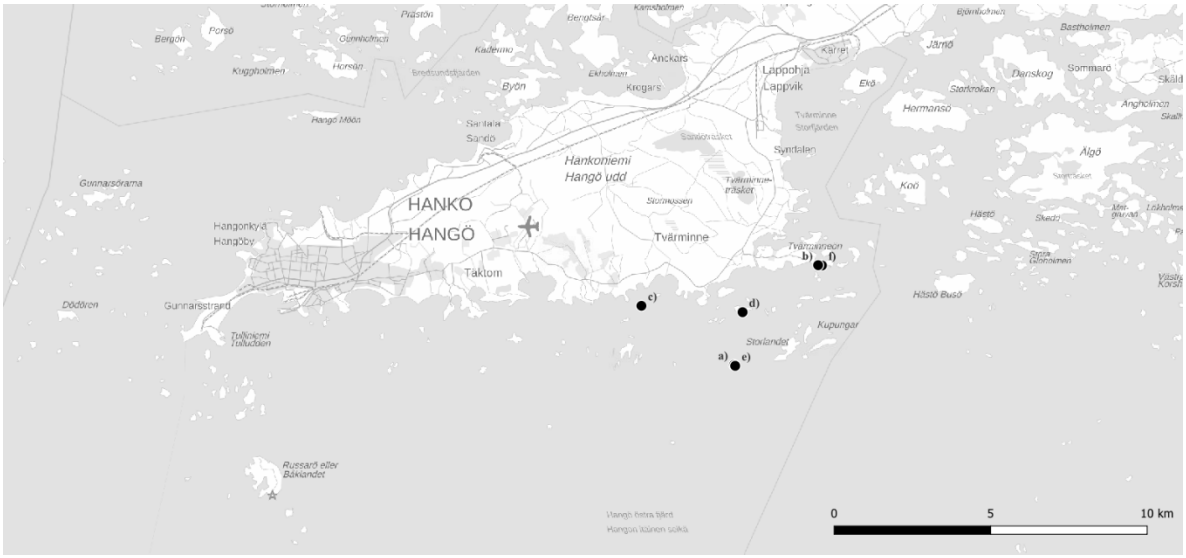


Figure 3. A map of the Hanko peninsula and six study sites. Base map © National Land Survey of Finland.

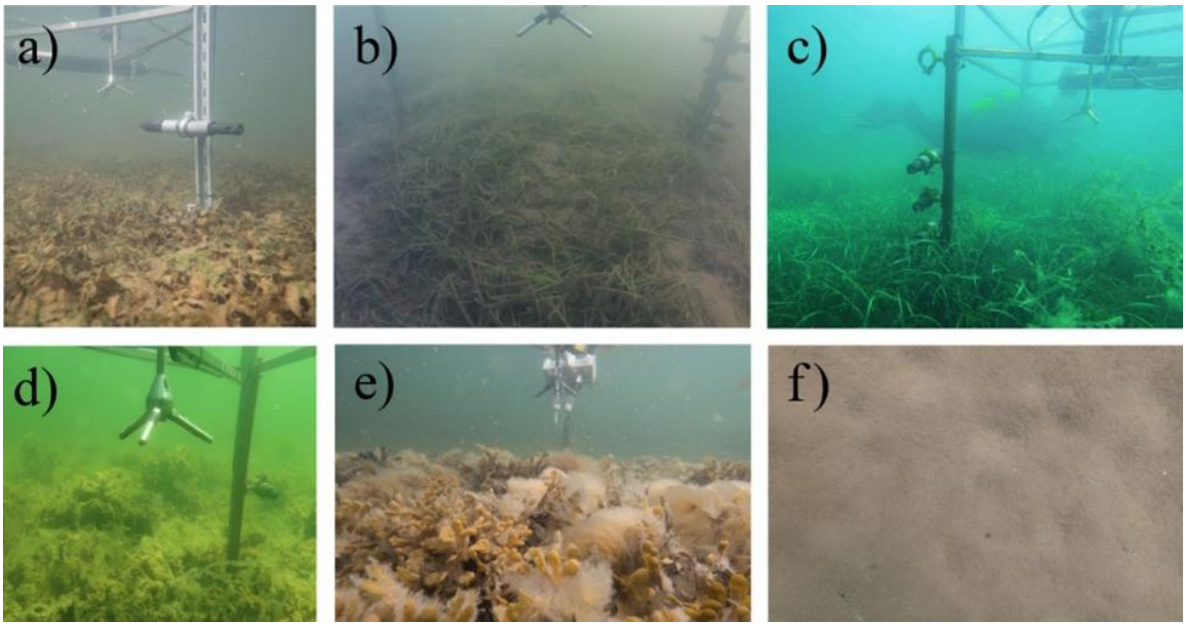


Figure 4. Six study sites used in research. a) A study site with significant macroalgal detritus covering seabed. b) Sheltered seagrass canopy c) Exposed seagrass canopy d) Sheltered macroalgal habitat e) Exposed macroalgal habitat. f) A habitat with a bare sediment bottom. Photo credits: Karl Attard

Table 1. Habitat descriptions and environmental conditions.

Name of the site	Habitat description	Bottom type	Biodiversity sampling method	Depth	Date of the biodiversity sampling	Location	The distance from the Tvärminne station	Date and the duration of the ODYSEA deployment	Height of the canopy	Salinity ppt	The average temperature of a sampling period	Maximum values of light (µmol m^{-2} s^{-1})
Bare	Bare bottom without vegetation	Sediment	Core for macroinfauna	3.7 m	24.5.2018	Ångbåtsbryggan 59°841532N 23°253370E	0.4 km N	20.-24.5.2018 96 h	_	5.3	11°C	269.2
SGsh	Seagrass habitat, sheltered	Sand	Core for macroinfauna, quadrat for vegetation and epifauna	4 m	31.5.2018	Ångbåtsbryggan 59°841551N 23°251203E	0.5 km N	27.-31.5.2018 87 h	13 cm	5.2	16°C	449.4
SGex	Seagrass habitat, exposed	Sand	Core for macroinfauna, quadrat for vegetation and epifauna	2.9 m	13.6.2018	Hendriksberg 59°827008N 23°151976E	7.6 km W	8.-13.6.2018 120 h	17 cm	_	10°C	1349.2
Detritus	Macroalgal detritus covering the whole study area	Sediment	Core for infauna and fine-mesh bags for detritus	3 m	6.6.2018	Spikarna 59°811613N 23°206624E	4.4 km SW	1.-6.6.2018 120 h	16 cm	_	12°C	_
FUex	*F. vesiculosus* habitat, exposed	Rock	Fucus-bag and Kautsky for epifauna	2 m	6.6.2018	Spikarna 59°811359N 23°207281E	4.4 km SW	1.-6.6.2018 116 h	27 cm	_	9°C	_
FUsh	*F. vesiculosus* habitat, sheltered	Rock and stones <60 cm	Fucus-bag and Kautsky for epifauna	2 m	13.6.2018	Vindskären 59°826856N 23°209721E	4 km SW	8.-13.6.2018 120 h	36 cm	_	10°C	_

2.2 Instrumentation and deployments

2.2.1 The ODYSEA

The ODYSEA (Oxygen DYnamics in SEAfloor habitats) is a new *in situ* instrumentation that we developed specifically to investigate oxygen dynamics in seafloor habitats (Figure 5). It consisted of three dissolved oxygen optodes with inbuilt temperature sensor (HOBO U26-001), a 6 MHz acoustic velocimeter (Vector, Nortek), a photosynthetic active radiation (PAR) sensor (RBRsolo with Licor PAR Quantum 192SA), and a saltwater conductivity sensor (HOBO U24-002-C). The equipment was mounted onto the 75 cm long stainless steel rail affixed to the tripod leg. Oxygen sensors were secured to the rail at various heights above the seabed using rail mount clamps. Two sensors were set inside the canopy; one sensor approximately 5 cm above the seafloor and one close to the top of the canopy. The third sensor was placed in the water above the canopy. The exact heights were noted at each site and are reported with the results.

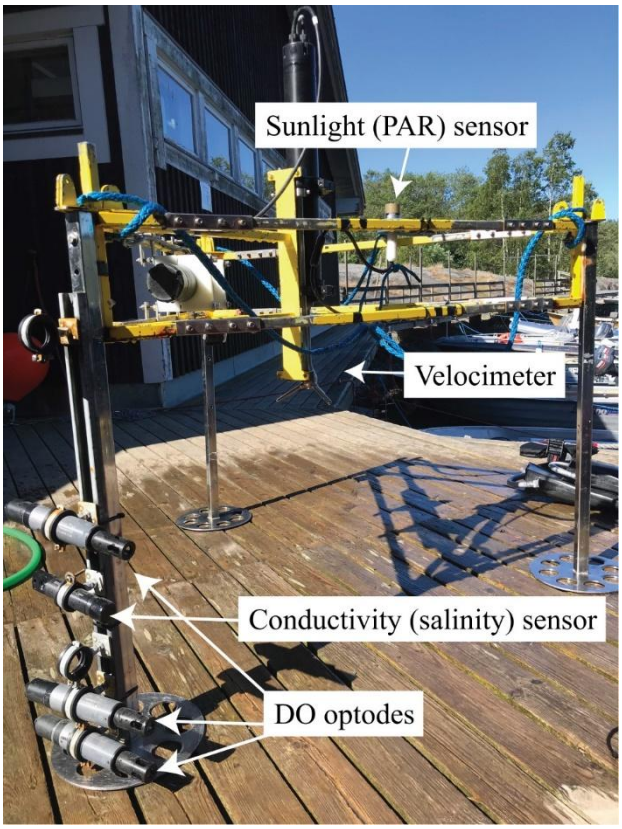


Figure 5. The ODYSEA instrumentation. Photo credit: Karl Attard.

The ODYSEA was deployed from a small boat and carried with a lift-bag to the study area by scuba diving. It was lowered at 2-4 m depth, adjusted to the height of the canopy, and left to sample for 3-5 days. The instrument had sufficient battery capacity for five days of continuous measurements, and this period was optimal to see changes in dissolved oxygen concentrations.

Flow velocity was studied using the acoustic velocimeter, which measured vertical and horizontal flow velocity in 8 Hz intervals (eight cycles per second). The velocimeter was mounted in the middle of the tripod frame and sampled ~15 cm above the seabed. At the sites with large canopies (FUsh and FUex), the velocimeter was lifted to sample in the water above the canopy ~ 35 cm above the seabed. (Figures 4 and 5).

2.2.2 Oxygen dynamics and sensor calibration

Dissolved oxygen sensors were set up using HOBOware software and a coupler (COUPLER-2-C). Optical sensors are factory calibrated and have a high accuracy of 0.2 mg L^{-1} and resolution of 0.02 mg L^{-1}. The values mean that the sensors are precise, and measure dissolved oxygen maintaining these values, but there may be small differences in the measurement offset. Consequently, it was essential to determine each sensors' offset in its measurement in relation to other sensors. A way to compensate for this offset was to determine each sensor's relative calibration in 100 % air-saturated and temperature-controlled fresh water.

Fresh water test

A tank with 30 L fresh water was placed in the temperature controlled cold room for 2 hours at 14 °C to stabilize the temperature. Water was oxygenated with an air stone and a pump to attain the 100 % air saturation point in the water. Sensors were attached to ensure them measuring from the same spot and placed in a tank filled with fresh water for 2 hours. Six sensors in total were calibrated and used for the test, with three sensors being deployed in the water at a time.

The sensors were set to measure at 1-minute intervals and removed from the freshwater tank after 2 hours. The data was read out using HOBOware program and uploaded to Excel for calculating each sensor's variation in measuring. Both temperature and dissolved oxygen were compared between sensors. At a salinity of 0 ‰ and temperature of 14°C the standard oxygen 100% solubility is 321,9 µmol L^{-1}. The sensors' result at this temperature should, therefore, be the same. The exact value of dissolved oxygen (DO) concentration was calculated for each sensor at each temperature.

Sensors' measurements were first converted from mg L^{-1} to µmol L^{-1} O_2, which can be written as:

$$O_2\ \mu mol\ L^{-1} = (X/Y) \times 1000$$

$$X = DO\ mg\ L^{-1}$$

$$Y = O_2\ (2 \times atomic\ mass\ of\ O_2\ 15.994\ g\ mol\ L^{-1})$$

The correction value was calculated by subtracting measured dissolved oxygen concentration from the standard value of 100% air saturated dissolved oxygen concentration at 14 °C. The standard values were implemented from the Oxygen Solubility Table (Appendix A). The most accurate sensor was selected to be the reference sensor for the whole study, and each sensor's dissolved oxygen concentration correction value was therefore adjusted to this reference sensor. Each sensors' correction values are represented in Appendix B.

Seawater test

After the fresh-water calibration, sensors were deployed in seawater at the station's dock at 2.5 m depth and left overnight. Five oxygen sensors and the conductivity sensor were attached to the ODYSEA frame at different heights for testing the oxygen concentration in different water layers. One sensor was set in open water at the top of the frame (80 cm from seabed), one in the middle of the frame (40 cm), and three sensors were attached close to the bottom (5-25 cm), as the oxygen concentration was expected to vary the most close to the bottom. After removing the sensors from water, data was uploaded using HOBOware.

Salinity was corrected by using values from the Oxygen Solubility Table, adjusted to 6 ‰ (Appendix A). As with the freshwater data, data was transferred to Excel, and corrections were counted using sensors' previous correction numbers.

2.3 Biodiversity sampling

2.3.1 Soft sediment habitats

Sheltered and exposed seagrass habitats

The seabed of the sheltered and exposed seagrass sites, SGsh and SGex, consisted of fine sand and silt. Representative macrovegetation samples were randomly collected around the instrumentation using four random quadrat replicates (20 x 20 cm). The seagrass within the quadrat was gently uprooted and transferred into a net-bag that was placed above the quadrat. Samples were rinsed at shore (or in the lab) through a 0.5 mm sieve to collect all the associated epifauna. Animals were stored in alcohol, and the seagrass was frozen in sealed bags for further processing. The seagrass samples were later thawed, and the length (cm) of each shoot was measured to determine the average length of the canopy. Individual shoots were counted to determine the canopy density and converted to m^2 to be comparable with other measurements.

Quadrat 20x 20 cm = 400 cm^2

400 cm^2 / 10000 cm = 0.04 m^2

X = X / 0.04 m^2

The root of each shoot was cut to distinguish and estimate the above and below-ground biomass. Leaves and roots of seagrass and other associated macrophytes and also the other drifting degrading material was dried at 60°C temperature for 48 hours for biomass calculations.

Six sediment core samples (ø 5 cm, 15 cm deep) were used at all four soft-sediment habitats (SGsh, SGex, Bare, Detritus) for sampling the sediment macroinfauna. The fauna was sieved through 0.5 mm sieve and stored in alcohol. The rest of the sediment in the sieve was frozen in sealed bags for later analysis under the microscope.

Algal detritus and bare sediment habitats

The detritus habitat showed a thick macroalgal detritus mat covering the seabed of the study area. For the detritus sampling, four core replicates (ø 19 cm) were taken and transferred into a fine mesh bag.

Detritus was rinsed in the laboratory through a 0.5 mm sieve to collect the associated epifauna, that was then stored in alcohol. Samples of algal detritus were dried at 60°C temperature for 48 hours, and (using the diameter of the core), the biomass was converted to dry weight m^2. Also, six core (ø 5 cm) samples were taken from sediments for macroinfauna.

The seabed at the bare sand habitat, Bare, consisted of fine sand and showed no vegetation. Therefore, we collected six random core samples for macroinfauna in this site.

2.3.2 Hard-bottom habitats

At the rocky substrate sites (FUsh and FUex) *F. vesiculosus* individuals (n = 4) were randomly collected around the ODYSEA instrumentation using mesh bags. A quadrat (1 m^2, n = 4) was used to quantify the number of individuals per m^2. *F. vesiculosus* individuals were rinsed at the station through a 0.5 mm sieve to collect the epifauna, which was then stored in alcohol. The height of the canopy was determined from average length of the sampled individuals. Both *F. vesiculosus* and epiphytes were dried separately at 60 °C.

Four Kautsky replicates (20 cm x 20 cm) were used at both rocky substrate sites for collecting macrofauna. The Kautsky sampler is a metal square with a sampling bag attached to the side. The epifauna was scraped from the rock into the bag using a spoon. In the laboratory, all the macrofauna from the Kautsky replicates were sieved through a 0.5 mm sieve and stored in alcohol.

2.3.3 Macrofauna handling, identification, and biomass calculation

After the sampling was completed, all the fauna from all the habitats was picked from sediments and sorted, identified into species, and counted. The wet weight was noted with 0.0001 g accuracy. The fauna from the Kautsky samples was divided into eight sectors on a

water-filled tray, and four sectors were chosen randomly to calculate the biomass. The length of gastropods and bivalves was measured from anterior to posterior axis using a Vernier calliper (an accuracy of 0.01 mm) for the later conversions to ash-free dry mass (AFDM). AFDM of bivalves and gastropods was calculated by first calculating their shell-free dry mass (SFDM) using a length-weight - relationship - formula for the animals of the Baltic Sea (Rumohr et al. 1987).

log-log-regression formula of length-weight-relationships:

*log (w) = b * log (l) + a, w = weight (SFDM), b = slope, l = length, a = y-axis intercept*

SFDM was then converted to ash-free dry mass (AFDM) by using the standard conversion factors for individual Baltic species listed in Rumohr et al. (1987). The wet weight (WW, grams) of shell-less fauna (Crustacea, Polychaeta, and Insecta) was converted to AFDM using average conversion factors:

weight - > weight (AFDM%WW)

The biomass and abundance of all individuals m^{-2} were then calculated.

2.4 The organic content

The sedimentary organic content was estimated from all the soft sediment sites (i.e. Bare, SGsh, SGex, and Detritus). Three syringe replicates were randomly collected within the study sites to collect the surface layer of the sediment. In the laboratory, the redundant part of the sediment in the syringe was emptied, retaining the first 2 cm of the surface layer of sediment. The top layer from each syringe was transferred into the crucible, and the weight was noted beforehand. The sample was dried at 60°C for 48 hours (Heraeus T 12). The dry weight was scaled, and samples were then placed in a muffle furnace at 500°C for 3 hours after which the burned weight was scaled. The organic content of the sediment was then calculated using the formula:

Organic content (%) = ((dry weight - burned weight)/dry weight) x 100

2.5 Data processing

2.5.1 ODYSEA measurement analyses

Velocimeter

After the ODYSEA was removed from the water, the velocimeter data was downloaded and processed using the Vector –program (Nortek) to convert the binary file to ASCII. Data handling and processing were performed in OriginPro 2018b (OriginLabs). The flow velocity magnitude units (*U,* in cm s^{-1}) were calculated by using Vector's horizontal (*X,* cm s^{-1}) and vertical (Y, cm s^{-1}) flow velocity measurements as:

$$U = \sqrt{(X^2 + Y^2)} /100$$

The flow velocity magnitude of eight cycles per second was bin-averaged to one cycle per minute to match with the oxygen sensors' sampling intervals.

Sensor data

The Oxygen sensor measurements were corrected according to the most accurate reference sensor number 6, following the method described in chapter 2.2.2. The corrected oxygen sensor values and bin-averaged flow velocity were then plotted as a time series in OriginPro. The interactions between the flow velocity and oxygen conditions within the canopy were studied from the time-series. An overall mean and standard deviation of oxygen concentration per site was calculated. Also, the difference between the lowest nighttime and the highest daytime dissolved oxygen value was computed. The duration and frequency of low oxygen events at the Detritus site were calculated and are represented in Appendix C. The temperature measured by the oxygen sensors was also studied through the time-series to identify any temperature gradients within the canopy.

Conductivity and sunlight PAR were measured at sites Bare, SGex, and SGsh in one-minute intervals using sensors attached to the ODYSEA frame (see details in 2.2.1). The data was read out in HOBOware and plotted as a time series in OriginPro, along with the oxygen and temperature measurements. Diel and day-to-day interactions between light availability and DO conditions within the canopy were studied from the time series.

2.5.2 Data analysis

The abundance (ind m^{-2}) and biomass (AFDM/SFDM g m^{-2}) of the invertebrates across sites were calculated. Primer (v.7 and PERMANOVA+) software was used to perform the nonmetric multidimentional scaling (nMDS) (with fourth-root-transformed data) to visualize macrofauna communities between locations. ANOSIM based on the Bray-Curtis similarity matrix was also performed in Primer (site as a fixed factor, 999 random sample permutations) to compare differences in macrofauna abundance and biomass between sites. Differences in macrophyte abundance and biomass across sites were compared using Two-Sample t-Test using OriginPro.

3 Results

3.1 Oxygen dynamics across sites

The study showed that dissolved oxygen (DO) concentrations increased during the day due to photosynthesis production and declined at night due to respiration (Table 2). Oxygen concentrations rose and dropped synchronically with the flow velocity with an hour delay at the exposed sites, where the flow was higher. The oxygen concentration within the canopy diverged from the values in the water column above the canopy by up to 200 μmol L^{-1} on average at all sites. The lowest and middle sensors measured DO concentration values that were close to each other. The common trend was that the exposed sites showed higher DO concentrations inside the canopy and sheltered sites showed higher DO concentrations in the water column above the canopy (Table 2).

Table 2. Oxygen sensors' values from different heights above seabed. The overall minimum and maximum O_2 concentrations (µmol L^{-1}), mean + SD, and the difference between the lowest and highest day- and nighttime value.

Site	Sensor's height[1]	Min. DO conc.[2]	Max. DO conc.[2]	Mean DO conc.[2] + SD	Low DO events [3]	Lowest nigthttime DO conc.[2]	Highest daytime DO conc.[2]	Difference night- day [4]	Night time h [5]
Bare sediment	5	306.6	407.1	366.7 ± 18.6	0	324.1	407.1	83	22:00-06:00
Bare sediment	10	310.3	403.5	370.3 ± 15.8	0	336.6	403.5	66.9	22:00-06:00
Bare sediment	51	329.5	397.0	369.1 ± 12.5	0	329.5	397	67.5	22:00-06:00
Detritus	2	0.6	362.3	173.5 ± 114.6	27h 5 min.*	0.6	362.3	361.6	22:00-06:00
Detritus	10	158.5	420.6	312.7 ± 45.6	0	224.9	420.6	195.8	22:00-06:00
Detritus	35	229.7	429.2	329.6 ± 37.9	0	249.4	429.2	179.8	22:00-06:00
Sheltered seagrass	5	272.1	354.3	327.1 ± 14.4	0	272.1	354.3	81.8	22:00-06:00
Sheltered seagrass	12	302.4	351.8	330.0 ± 12.6	0	305.8	351.8	46	22:00-06:00
Sheltered seagrass	41	308.6	354.8	333.4 ± 13.1	0	312.8	354.8	42	22:00-06:00
Exposed seagrass	4	281.1	434.0	359.3 ± 30.0	0	281.1	434	152.9	22:00-06:00
Exposed seagrass	17	307.6	437.6	353.5 ± 26.3	0	307.6	437.6	130	22:00-06:00
Exposed seagrass	38	317.7	419.0	355.4 ± 20.3	0	317.7	419	101.2	22:00-06:00
Sheltered Fucus	6	255.7	466.7	352.7 ± 47.5	0	255.7	466.7	211	22:00-06:00
Sheltered Fucus	12	253.1	462.1	351.2 ± 41.2	0	253.1	462.1	208.9	22:00-06:00
Sheltered Fucus	38	270.9	489.2	351.0 ± 33.3	0	270.9	489.2	218.3	22:00-06:00
Exposed Fucus	5	294.0	427.0	348.6 ± 28.4	0	294	427	133	22:00-06:00
Exposed Fucus	11	286.7	407.6	336.7 ± 20.1	0	286.7	407.6	120.9	22:00-06:00
Exposed Fucus	40	295.1	424.5	347.1 ± 26.2	0	295.1	424.5	129.4	22:00-06:00

[1] cm above the seabed

[2] Dissolved oxygen conc. (µmol L^{-1})

[3] Duration and frequency of low DO events <63 µmol L^{-1} during the sampling period

[4] Difference between the lowest nighttime and the highest daytime DO conc. (µmol L^{-1})

[5] Night time PAR <20 (µmol m^{-2} s^{-1})

red = daytime DO value was lower than nighttime value

* = total time during nine low DO events (see Appendix C)

3.1.1 Sheltered and exposed seagrass canopies and bare sediment habitat

At the exposed seagrass site, DO concentrations increased up to 437 µmol L^{-1} during the day and decreased to 236 µmol L^{-1} at night (Figure 6, c1). The highest concentrations were measured in the evenings between 17:00-21:00 pm and the lowest values at 06:00 am (Figure 6, c1). The highest and the lowest DO concentrations were measured closest to the bottom for most of the days (Figure 6, c1). The DO concentration was generally higher within the canopy than in the water above the canopy (Figure 6, c 1).

In contrast to the exposed seagrass site, at sheltered seagrass site the highest DO concentrations were measured in the water column above the canopy. The lowest DO concentration was measured with the sensor that was placed closest to the seabed (5 cm) (Table 2). The middle sensor, which was placed at 12 cm above seabed, followed closely the dynamics of the sensor placed at 5 cm, but always measured higher DO concentrations (Figure 6, b1).

At the sheltered seagrass site, the oxygen concentrations ranged from 295-355 µmol L^{-1} during the day to 232-354 µmol L^{-1} during the night at all heights of the canopy (Figure 6, b1)**.** Unlike at the exposed seagrass site, the highest DO values were measured at night. Oxygen concentrations started to decrease after 4:00 am and continued to drop during the day, whereas at the exposed site DO levels started to increase after 6:00 am and decreased after 17:00 pm on average.

The exposed seagrass site showed 24-32 µmol L^{-1} higher oxygen concentrations within the canopy than the sheltered site (two lowest sensors). The highest daytime value within the canopy was on average 83 µmol L^{-1} higher at the exposed seagrass canopy than at the sheltered site. The temperature was commonly higher at the sheltered seagrass site (16 °C) than at the exposed site (10 °C) (Table 1; Figure 6, b4; c4), and average oxygen concentration above the sheltered canopy was 22 µmol lower than above the exposed canopy (Table 2).

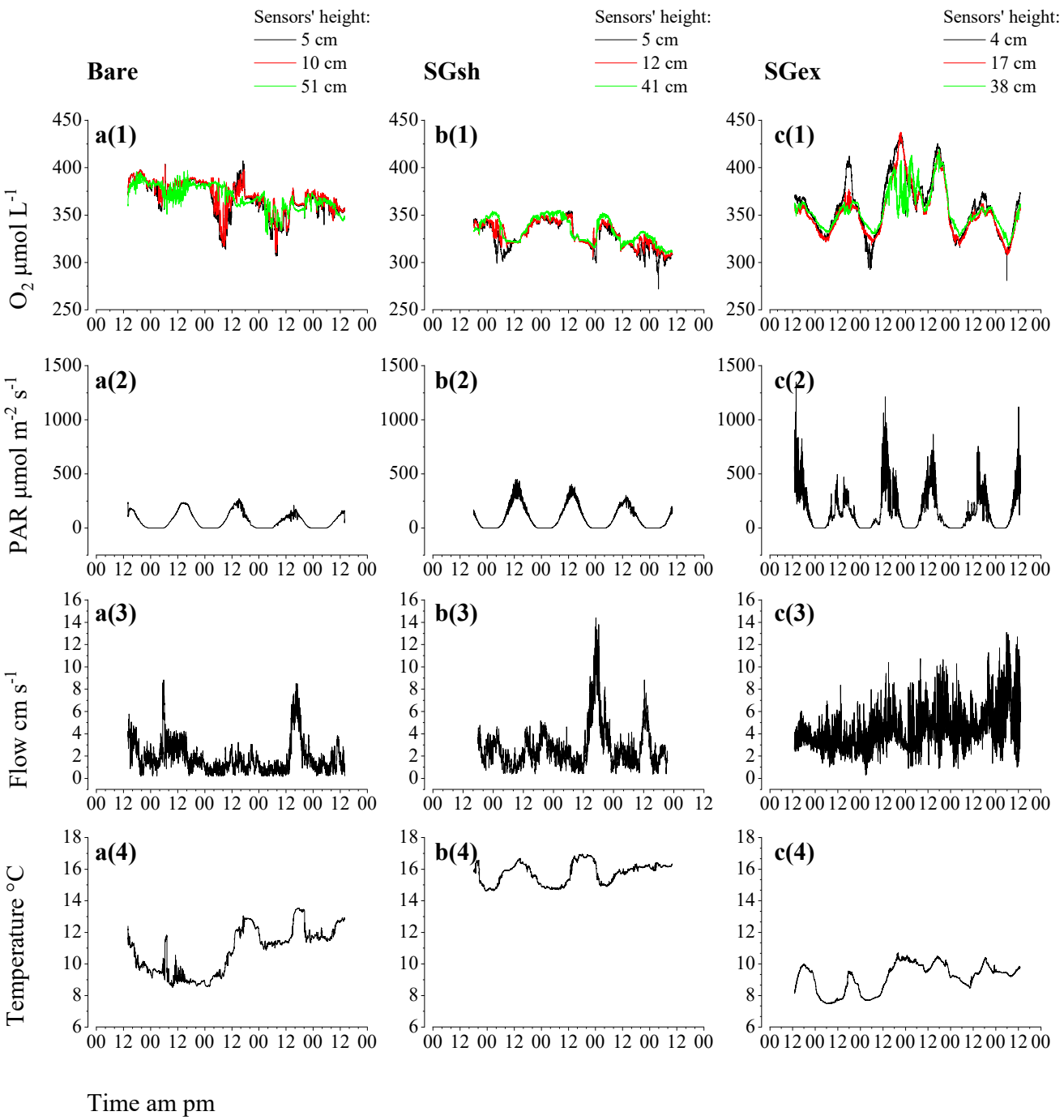


Figure 6. Oxygen dynamics measured by DO sensors at three different heights (cm) above seabed, sunlight PAR, flow velocity, temperature and salinity represented from three locations (a, b, and c) with different exposures (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy).

The flow velocity was higher at the exposed seagrass site than sheltered (Figures 6, c3; b3) cycling between 0.4 and 12 cm s^{-1}. At sheltered site, the flow velocity cycled mostly between 0.3 and 5 cm s^{-1} with a couple of higher peaks on windy days (Figure 7). On the third sampling day the flow remained low, 0.4-3 cm s^{-1}, until 12:00 pm and oxygen concentrations within the canopy continued to increase also during the day until 13:12 pm. When the flow picked up after 12:00 pm and increased to 14 cm s^{-1}, oxygen concentrations started to drop within and above the canopy. On the fourth sampling day, the flow increased only up to 9 cm s^{-1} and oxygen concentrations dropped within the canopy, while continued to increase above the canopy (Figure 7).

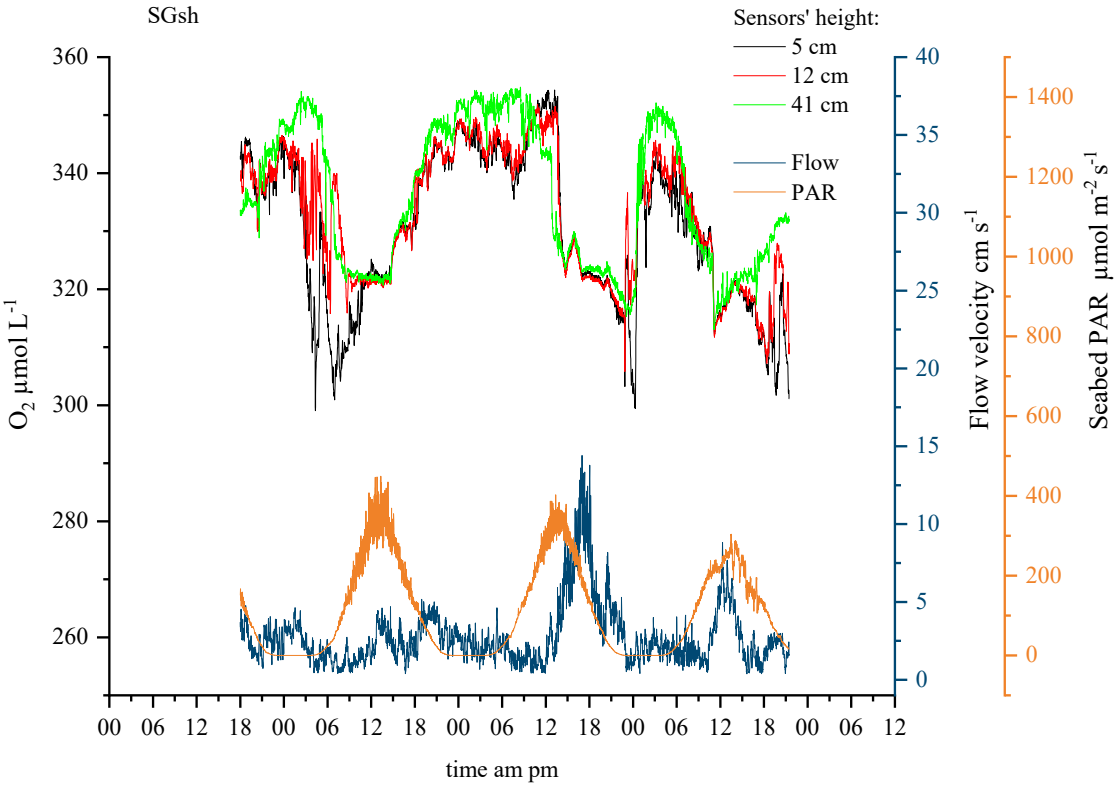


Figure 7. A closer look of a time series from the sheltered seagrass site (SGsh) representing DO dynamics, flow velocity, and seabed PAR. DO concentrations are measured by sensors placed in three different heights (cm) above seabed. Sensors at 5 and 12 cm are within the canopy, 41 cm is placed above the canopy.

At the bare sediment site, two sensors were set close to the bottom and one to the upper water layer. The sensor that was placed closest to the bottom, 5 cm, measured the highest and lowest oxygen concentration (Figure 8). Oxygen concentration increased up to 407 µmol L^{-1} during the day and declined to 324 µmol L^{-1} at night.

During the calm period at night, when the flow velocity was <2 cm s^{-1}, the DO concentration was the highest in the water at 51 cm above the seabed. Respiration activity of the sediment consumed oxygen, explaining the lower DO values closer to the seabed. When the flow velocity increased to >3 cm s^{-1}, DO concentration at 51 cm above seabed dropped within 10 minutes to the lowest concentration of all three sensors due to water mixing on all four sampling days (Figure 8).

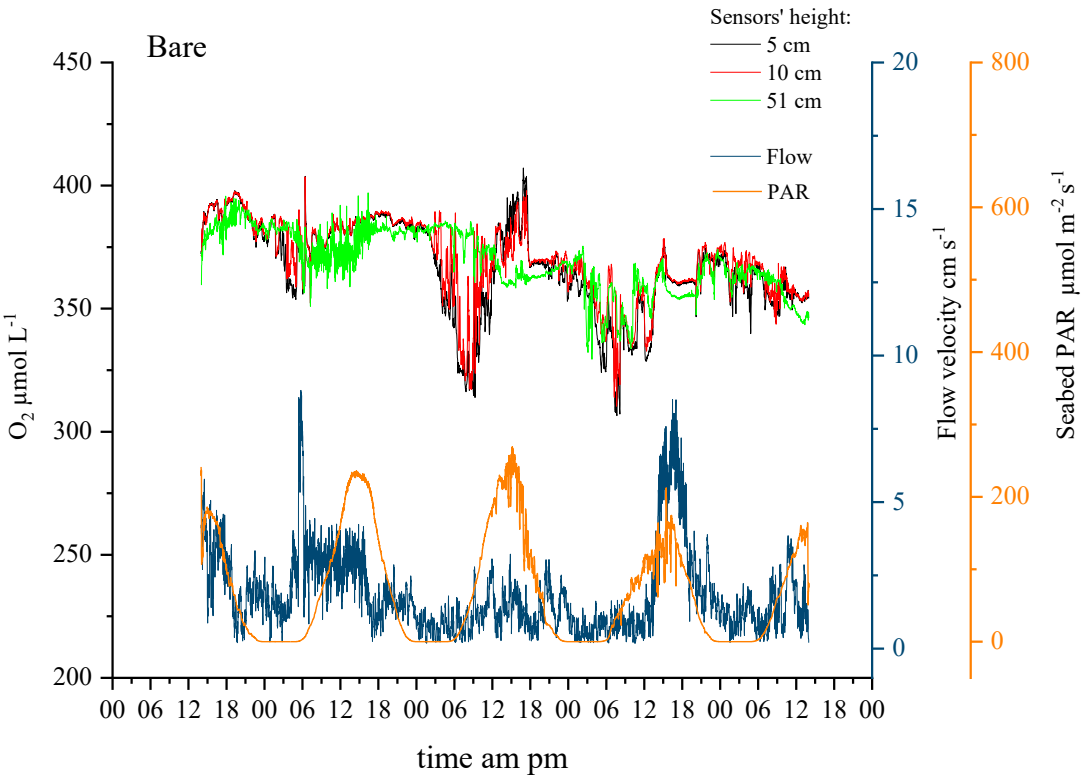


Figure 8. A timeline from the bare sediment site (Bare) representing DO dynamics at three different heights (cm) above seabed, flow velocity, and seabed PAR

Sunlight PAR measurements

PAR was measured at the site with bare sediment and the sheltered and exposed seagrass sites (Figure 6, a2; b2; c2). The daytime (when PAR > 20 µmol m^{-2} s^{-1}) started between 03:59 and 06:33 am and ended between 21:37 and 22:48 pm (PAR<20) depending on the weather conditions such as cloudiness and moonlight. At all sites, the daytime was considered to be from 6:00 am to 22:00 pm when PAR >20 µmol m^{-2} s^{-1}.

PAR was the lowest at the bare sediment site with no vegetation. However, more oxygen was produced above the seabed during the sunnier day. Figure 8 shows a substantial increase in DO levels of two bottom sensors relative to the highest sensor during the day when PAR was the highest.

PAR was highest at the exposed seagrass site (Figure 6, c2), and more oxygen was produced within the canopy during the days with higher radiation peaks (Figure 6, c1; c2), during which DO levels above the canopy stayed lower than within the canopy (Figure 6, c1). Flow velocity at the exposed site increased steadily from 3 to 13 cm s^{-1} during the sampling period (Figure 6, c3) while DO level peaks decreased with decreased radiation peaks (Figure 6, c1; c2).

At the sheltered seagrass site, increase in PAR also increased oxygen production within the canopy, and less DO was measured on cloudy days within the canopy (Figure 6, b2). However, higher peaks in flow velocity decreased DO levels within the canopy even in the presence of the highest radiation time of the day (Figure 7). On the first sampling day PAR was highest and the flow velocity remained low during the day, allowing oxygen production to continue within the canopy (Figure 7).

3.1.2 Sheltered and exposed *Fucus vesiculosus* canopies and habitat with algal detritus

Sheltered *F. vesiculosus* habitat showed the highest oxygen concentration levels of all sites, measured above the canopy (Table 2). Dissolved oxygen concentration was the same or higher within the canopy than in the water layer above the canopy during the day. At night, DO concentrations were always higher in the water above the canopy than within the canopy (Figure 9, b1). The lowest DO levels were measured by the sensor closest to the rocky seabed surface at 6 cm (Table 2).

At the exposed *F. vesiculosus* site, the sensor closest to the seabed measured the highest DO concentrations of all three sensors (Figure 9, a1). The lowest concentration was measured in the middle of the canopy (Table 2).

The detritus habitat showed the lowest DO concentrations of all sites (Table 2). It was found to be anoxic in the lowest part of the algal mat (2 cm above the seabed) for 3-6 h during the day and night (Figure 9, c1). The oxygenation of the bottom canopy started within 30-60 min after the flow picked up, depending on the flow velocity magnitude (Figure 9, c1;c2). A decrease in the flow velocity from 3 to 1 cm s^{-1} during 48 min led to a decline of DO from 270 to 100 µmol within three hours.

During the sampling period, the bottom was mostly hypoxic and anoxic 2 cm above seabed with short oxygen peaks coinciding with increases in flow velocity (Appendix C). When the flow started to increase from 0.5 to 7 cm s^{-1}, also DO at 2 cm increased continuously with the flow up until 300 µmol L^{-1} (Figure 9, c1). The oxygen concentration recorded at the two sensors located at 10 and 35 cm above seabed differed by ~100 µmol L^{-1} and varied at the same rate (Figure 9, c1). However, the sensor placed 35 cm above the algal detritus always measured higher DO concentration than the sensor that was placed in the middle of the detritus. Dissolved oxygen concentration dropped in the middle of the detritus during the calm periods when the flow was 0-3 cm s^{-1} (Figure 9, c1;c2). A closer look at the timeline from the site Detritus is represented in Appendix F.

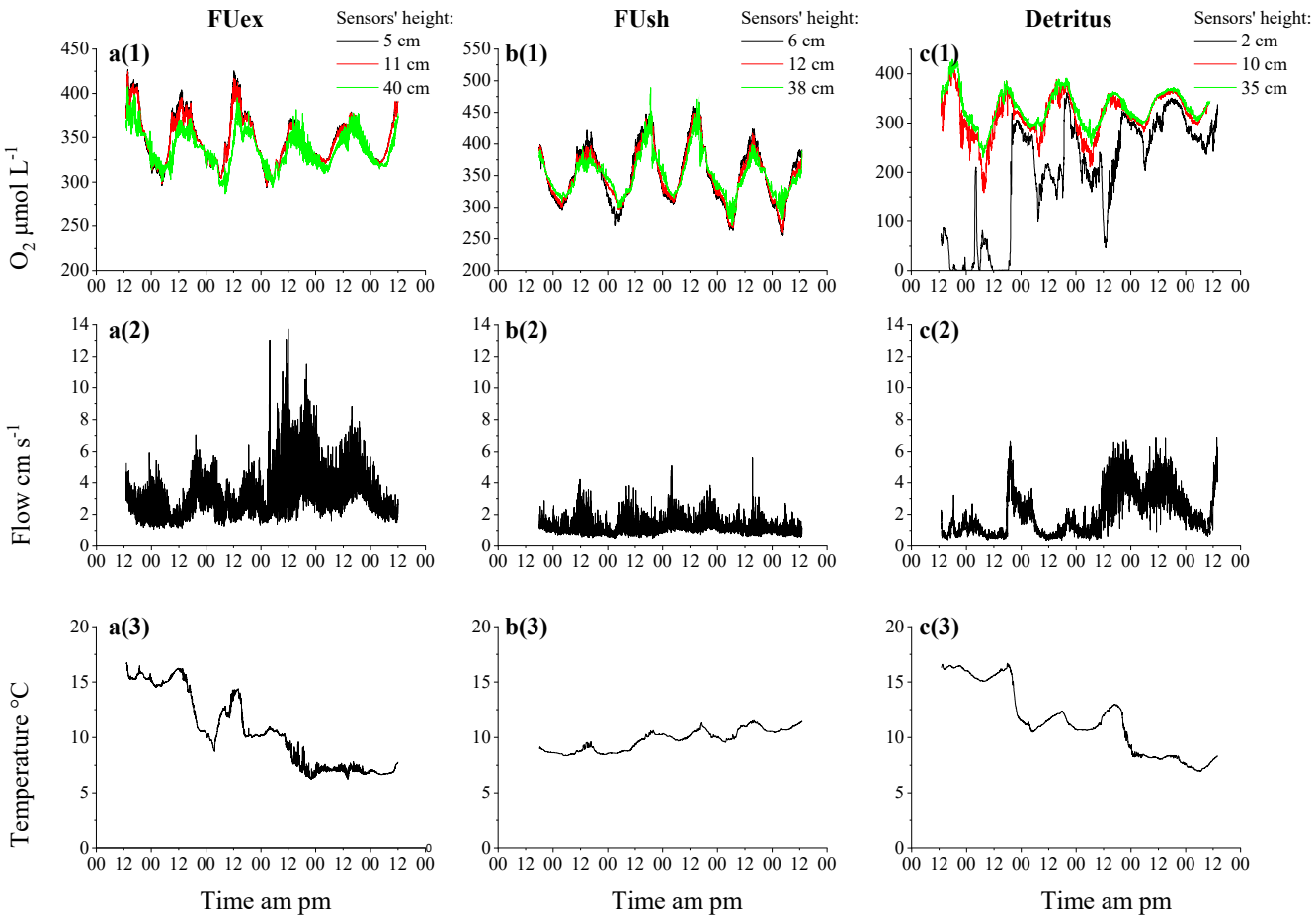


Figure 9. DO concentration, flow velocity, and temperature at sheltered and exposed *F. vesiculosus* sites and the site Detritus (Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy).

3.2 Biodiversity

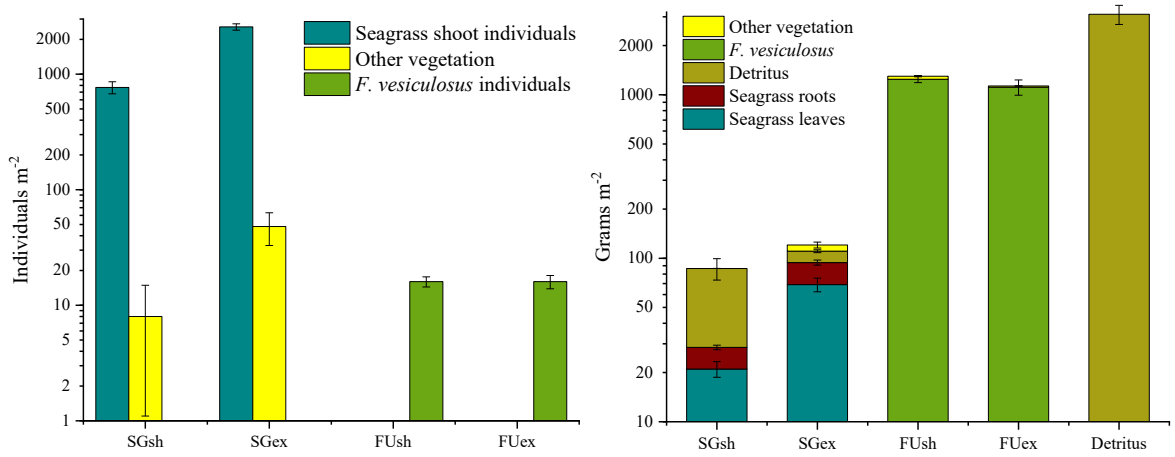
3.2.1 Macrovegetation species, abundance, and biomass

The sheltered *F. vesiculosus* site showed 17 different macroalgal species, of which nine were growing as epiphytes or attached to the substrate, and eight species were drifting filamentous algae. The exposed *F. vesiculosus* site showed ten species in total, of which six were attached to the substrate, and four species appeared only as drifting form. All the vegetation species that were found are listed in Appendix E.

Sheltered and exposed *F. vesiculosus* sites showed the same abundance of *F. vesiculosus* individuals (16 m^{-2}), and the biomass (g dry weight m^{-2}) did not differ significantly between sites (df = 6; $p = 0.835$). The *F. vesiculosus* sites showed the highest vegetation biomass of all sites (Table 3 and Figure 10, a; b).

Table 3. Mean (+SE) vegetation abundance, shoot length, biomass (dry weight) and the organic content of soft sediments (burned weight) (SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* conopy, FUsh: sheltered *F. vesiculosus* conopy, Bare: bare sediment bottom).

Site	Abundance Shoot ind. m^{-2}	Shoot length cm	Biomass leaves g m^{-2}	Biomass roots g m^{-2}	Biomass detritus g m^{-2}	Biomass other species g m^{-2}	Organic content of sediments % m^{-2}
SGsh	768 ± 92	13 ± 0.4	21 ± 2.3	7.5 ± 0.9	58 ± 13	0.1 ± 0.1	7.7
SGex	2565 ± 164	17 ± 0.8	69 ± 6.6	25.1 ± 3.4	16.4 ± 2.3	0.2 ± 0.2	5.6
Detritus	-	-	-	-	3108 ± 417	-	8.3
FUsh	16 ± 1.6	-	1244 ± 58	-	55 ± 11	-	-
FUex	16 ± 2.1	-	1112 ± 119	-	20 ± 1.6	-	-
Bare	-	-	-	-	-	-	0.7



a) b)

Figure 10. Vegetation mean (+SE) abundance and biomass (dry weight) at sampled sites where the vegetation material was observed. (SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy).

At seagrass sites, the sheltered site showed significantly (df = 5, p = 0.002) lower shoot density (768±92 m^{-2}) than the exposed site (2565±164 m^{-2}) (Table 3 and Figure 10a). The height of the seagrass canopy was higher at the exposed site (17±0.8 cm) than at the sheltered (13±0.4 cm) (Table 3). The exposed seagrass site showed higher above and below-ground macrophyte biomass than the sheltered seagrass site (Table 3 and Figure 10b). The sheltered seagrass site showed the highest amount of old drifting plant material of all vegetated sites (58±13 dry weight g m^{-2}) (Table 3 and Figure 10b) but the highest amount of detritus was observed at the Detritus site (3108±417 g m^{-2}) (Table 3 and Figure 10b).

The detritus habitat showed the highest organic matter content (8.3 %) whereas the site with the bare sediment showed the lowest (0.7 %). Organic content of the sheltered seagrass site was higher (7.7 %) than of the exposed seagrass site (5.6 %). (Table 3).

3.2.2 Macrofauna species number, abundance, and biomass

The nMDS analysis was performed from the species-specific abundance from all studied sites. Two of the points from the detritus site appeared far from other sites, as no fauna was found in these core samples. The sheltered *F. vesiculosus* habitat appeared as separate group, whereas the sheltered and exposed seagrass habitats clustered closer together (Figure 11).

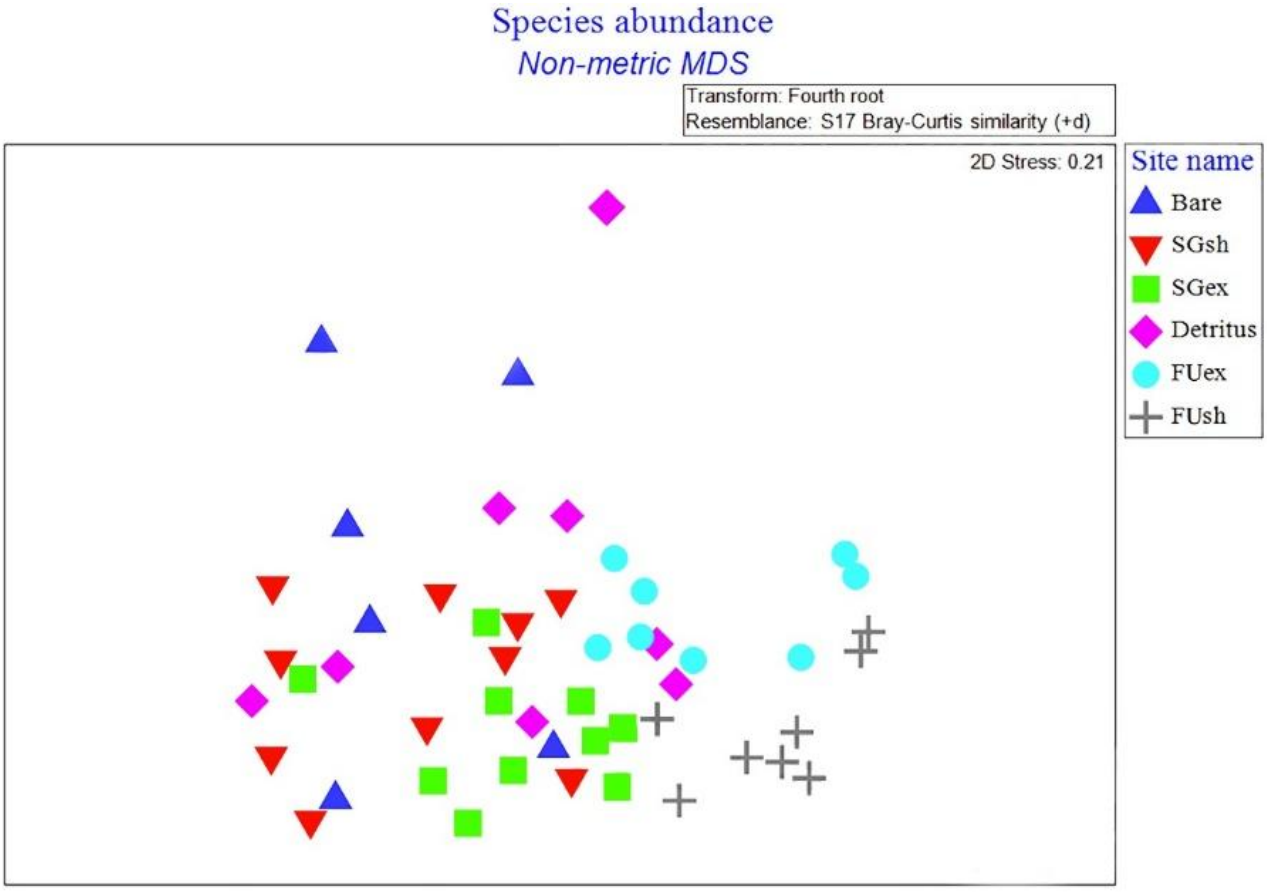


Figure 11. The nMDS analysis of macrofauna species abundance at studied sites. (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F.vesiculosus* canopy, FUsh: sheltered *F.vesiculosus* canopy).

ANOSIM based on Bray-Curtis for macrofauna species abundance showed a significance value of 0.001 and an R-value of 0.286 (Table 4). Soft-sediment sites showed the same species composition, whereas species at sheltered and exposed *F. vesiculosus* sites differed

between each other and from soft-sediment sites. All the macrofauna species found in the study are listed in Appendix D.

Table 4. The ANOSIM results on the pairwise species comparison between sites. Macrofauna species abundance m^{-2}

Sites			**R**	***p***	
Bare	vs	SGsh	0.037	0.328	*ns*
Bare	vs	SGex	0.28	0.019	*
Bare	vs	Detritus	0.07	0.23	*ns*
Bare	vs	FUex	0.677	0.001	***
Bare	vs	FUsh	0.763	0.001	***
SGsh	vs	SGex	0.081	0.124	*ns*
SGsh	vs	Detritus	-0.063	0.845	*ns*
SGsh	vs	FUex	0.478	0.001	***
SGsh	vs	FUsh	0.76	0.001	***
SGex	vs	Detritus	0.056	0.175	*ns*
SGex	vs	FUex	0.51	0.001	***
SGex	vs	FUsh	0.69	0.001	***
Detritus	vs	FUex	0.157	0.036	*
Detritus	vs	FUsh	0.285	0.002	**
FUex	vs	FUsh	0.358	0.005	*
Sample statistic (R):				0.286	
Significance level of sample statistic (*p*):				0.001	***

*$p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $0.10 < p < 0.05$ marginally significant ms, non significant ns*

The results from ANOSIM also showed that the total macrofauna (infauna and epifauna) abundance (ind. m^{-2}) between all sites varied significantly (R=0.371; $p < 0.001$) (Table 5). Similarly, the infauna abundance between soft- sediment sites (Bare, SGsh, SGex and Detritus) varied significantly (R= 0.253; $p < 0.001$) as well as the epifauna abundance between vegetated sites (SGsh, SGex, FUsh, FUex and Detritus) (R=0.216, $p < 0.05$) (Table 5).

Table 5. The difference in macrofauna individuals (m^{-2}) from the ANOSIM analysis between six studied sites (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy). The closer the R value is to 1, the greater the difference between sites. *p* tells the statistical significance for the R value.

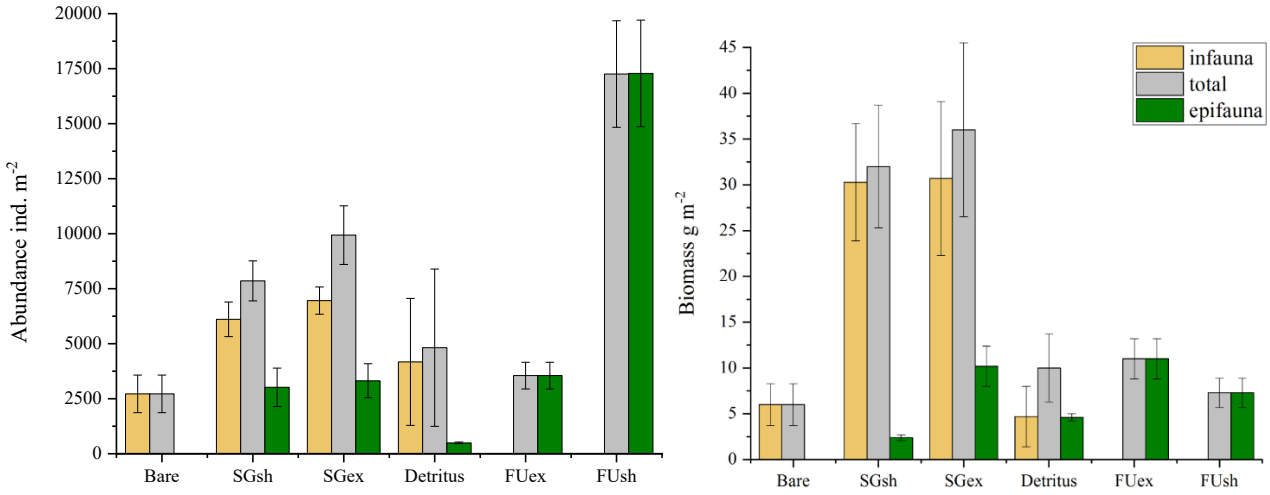
Total macrofauna abundance ind. m^{-2}					Epifauna abundance ind. m^{-2}					Infauna abundance ind. m^{-2}				
Sites			**R**	***p***	Sites			**R**	***p***	Sites			**R**	***p***
Bare	vs	SGsh	0.375	0.143 *ns*	SGsh	vs	SGex	-0.167	0.714 *ns*	Bare	vs	SGsh	0.269	0.028 *
Bare	vs	SGex	0.479	0.086 *ms*	SGsh	vs	Detritus	0.833	0.029 *	Bare	vs	SGex	0.38	0.011 *
Bare	vs	Detritus	-0.135	0.886 *ns*	SGsh	vs	FUex	0.085	0.216 *ns*	Bare	vs	Detritus	0.194	0.065 *ms*
Bare	vs	FUex	0.052	0.257 *ns*	SGsh	vs	FUsh	-0.059	0.568 *ns*	SGsh	vs	SGex	-0.037	0.45 *ns*
Bare	vs	FUsh	0.656	0.029 *	SGex	vs	Detritus	1.0	0.029 *	SGsh	vs	Detritus	0.356	0.006 **
SGsh	vs	SGex	-0.104	0.914 *ns*	SGex	vs	FUex	0.136	0.164 *ns*	SGex	vs	Detritus	0.444	0.002 **
SGsh	vs	Detritus	0.792	0.086 *ms*	SGex	vs	FUsh	-0.099	0.788 *ns*					
SGsh	vs	FUex	0.667	0.029 *	Detritus	vs	FUex	0.127	0.16 *ns*					
SGsh	vs	FUsh	0.25	0.029 *	Detritus	vs	FUsh	0.564	0.004 **					
SGex	vs	Detritus	0.875	0.114 *ns*	FUex	vs	FUsh	0.254	0.028 *					
SGex	vs	FUex	0.792	0.029 *										
SGex	vs	FUsh	0.125	0.114 *ns*										
Detritus	vs	FUex	0.333	0.057 *ms*										
Detritus	vs	FUsh	0.896	0.114 *ns*										
FUex	vs	FUsh	0.948	0.029 *										
Sample statistic (R):				0.371	Sample statistic (R):				0.216	Sample statistic (R):				0.253
Significance level of sample statistic (*p*):				0.001 ***	Significance level of sample statistic (*p*):				0.013 *	Significance level of sample statistic (*p*):				0.001 ***

*p < 0.001 ***, p < 0.01 **, p < 0.05 *, 0.10 < p < 0.05 marginally significant ms, non significant ns*

The sheltered *F. vesiculosus* site showed the highest number of species (23) and the highest total macrofauna abundance (17259±2421 ind. m^{-2}) of all sites (Table 6 and Figure 12). The exposed seagrass site showed 16 and the sheltered 18 macrofauna species (Table 6). The bare sediment site and the detritus site showed only six macrofauna species (Table 6). The detritus site showed the smallest amount of epifauna (493±37 ind. m^{-2}) from vegetated sites (Table 6), but the bare sediment site with no vegetation showed the lowest total macrofauna abundance (2719±854) (Table 6).

Table 6. Mean (+SE) macrofauna individuals and biomass (ash free dry weight) from the six studied sites (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy).

Site	Abundance Infauna ind. m^{-2}	Abundance Epifauna ind. m^{-2}	Abundance total fauna ind. m^{-2}	Biomass Infauna g m^{-2}	Biomass Epifauna g m^{-2}	Biomass total g m^{-2}	Number of species per site
Bare	2719 ± 854	-	2719 ± 854	6.0 ± 2.3	-	6.0 ± 2.3	6
SGsh	6110 ± 787	3020 ± 874	7857 ± 912	30.3 ± 6.4	2.4 ± 0.3	32 ± 6.7	18
SGex	6959 ± 620	3316 ± 772	9935 ± 1333	30.7 ± 8.4	10.2 ± 2.2	36 ± 9.5	16
Detritus	4175 ± 2885	493 ± 37	4821 ± 3574	4.7 ± 3.3	4.6 ± 0.4	10 ± 3.7	6
FUex	-	3551 ± 609	3551 ± 609	-	11 ± 2.2	11 ± 2.2	12
FUsh	-	17259 ± 2421	17259 ± 2421	-	7.3 ± 1.6	7.3 ± 1.6	23



a) b)

Figure 12. Mean (+SE) macrofauna individuals and biomass (ash free dry weight) from the six studied sites (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy).

The sheltered *F. vesiculosus* site differed from the exposed *F. vesiculosus* site ($p < 0.05$) in macrofauna abundance, but the biomass did not differ significantly ($p = 0.457$) (Table 7). The exposed seagrass habitat showed the highest infauna biomass (mean±SE; 30.7±8.4 g m^{-2}) of all soft-sediment sites (Table 7). The abundance of epifauna and infauna did not differ significantly between the sheltered and exposed seagrass habitat (Table 5). However, the biomass of the epifauna was significantly higher at the exposed seagrass site than at the sheltered site ($p < 0.05$) (Table 7).

Table 7. The difference in macrofauna biomass (ash free dry weight) from the ANOSIM analysis from six studied sites (Bare: bare sediment bottom, SGsh: sheltered seagrass canopy, SGex: exposed seagrass canopy, Detritus: macroalgal detritus covering the bare sediment bottom, FUex: exposed *F. vesiculosus* canopy, FUsh: sheltered *F. vesiculosus* canopy). The closer the R value is to 1, the greater the difference between sites. *p* tells the statistical significance for the R value.

Total macrofauna biomass g m^{-2}					Epifauna biomass g m^{-2}					Infauna biomass g m^{-2}				
Sites		**R**	***p***		Sites		**R**	***p***		Sites		**R**	***p***	
Bare vs SGsh		0.093	0.179	*ns*	SGsh vs SGex		-0.875	0.029	*	Bare vs SGsh		0.289	0.022	*
Bare vs SGex		0.198	0.131	*ns*	SGsh vs Detritus		0.781	0.029	*	Bare vs SGex		0.28	0.017	*
Bare vs Detritus		-0.091	0.681	*ns*	SGsh vs FUex		-0.101	0.691	*ns*	Bare vs Detritus		0.1	0.208	*ns*
Bare vs FUex		0.067	0.571	*ns*	SGsh vs FUsh		-0.029	0.453	*ns*	SGsh vs SGex		-0.1	0.74	*ns*
Bare vs FUsh		0.099	0.719	*ns*	SGex vs Detritus		0.333	0.086	*ms*	SGsh vs Detritus		0.375	0.006	**
SGsh vs SGex		-0.296	1	*ns*	SGex vs FUex		0.035	0.459	*ns*	SGex vs Detritus		0.336	0.015	*
SGsh vs Detritus		0.352	0.114	*ns*	SGex vs FUsh		-0.301	0.038	*					
SGsh vs FUex		0.167	0.2	*ns*	Detritus vs FUex		0.072	0.574	*ns*					
SGsh vs FUsh		0.519	0.086	*ms*	Detritus vs FUsh		0.092	0.695	*ns*					
SGex vs Detritus		0.444	0.086	*ms*	FUex vs FUsh		0.027	0.266	*ns*					
SGex vs FUex		0.315	0.114	*ns*										
SGex vs FUsh		0.704	0.057	*ms*										
Detritus vs FUex		-0.042	0.457	*ns*										
Detritus vs FUsh		-0.156	0.857	*ns*										
FUex vs FUsh		0.01	0.457	*ns*										
Sample statistic (R):			0.048		Sample statistic (R):			0.075		Sample statistic (R):			0.208	
Significance level of sample statistic (*p*):			0.262	*ns*	Significance level of sample statistic (*p*):			0.161	*ns*	Significance level of sample statistic (*p*):			0.005	*

*$p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $0.10 < p < 0.05$ marginally significant ms, non significant ns*

4 Discussion

This master's thesis research aimed to investigate the vegetation and benthic macrofauna biodiversity within key seafloor habitats of the Baltic Sea. This study also investigated how oxygen dynamics varied vertically in the water column at three different heights above the seabed over several days in these particular habitats. The frequency and duration of low oxygen events within the canopy were noted when they occurred. The further aim was to investigate the potential connections between low oxygen events and benthic fauna biodiversity.

4.1 Oxygen dynamics and biodiversity

4.1.1 Sheltered and exposed seagrass canopies and a habitat with bare sediment

Many studies have demonstrated that flow velocity, sunlight radiation, and shoot density influence canopy metabolism (Fonseca and Kenworthy 1987; Long et al. 2015; Hansen and Reidenbach 2017). At the exposed seagrass site of this study, the highest and the lowest oxygen concentration rates were measured within the canopy, indicating high daytime production and nighttime respiration rates of the canopy and seabed. Similar results were observed in the study by Long et al. (2015), where oxygen built up within the canopy during the day and decreased at night during low flow conditions.

Flow velocity is known to affect the water exchange between the canopy and the water column and vertical mixing within the canopy (Hansen and Reidenbach 2017). The shape of the flow at the exposed site was wave generated, whereas the sheltered seagrass site showed a weaker current (Figure 6, b3; c3). At the exposed seagrass site, DO decreased with a decrease in light and flow velocity. Wave-generated flow is known to penetrate deeper into the canopy than unidirectional currents, which are more common at sheltered locations (Koch and Gust 1999). At the exposed seagrass site of this study, an opening and closing movement of the canopy created by strong wave action likely oxygenated the canopy, and the DO levels within the canopy remained higher than in the water above the canopy (Figure 6, c1).

At the sheltered site, the DO levels above the canopy were mostly higher than within the canopy (Figure 6, b1), indicating that the flow did not oxygenate the canopy very effectively.

Unidirectional currents cause bending of seagrass blades in the direction of the current. Bending can compress the canopy and reduce flow penetration into the canopy by forming a layer between the canopy and the water above the canopy, resulting in water flowing over the canopy, termed 'skimming flows' (Koch and Gust 1999). Bending can also occur periodically at the exposed locations during the unidirectional currents, though it becomes disrupted when the top of the canopy undulates under wave movement (Koch and Gust 1999). The bending is also known to induce self-shading by overlapping leaves, which reduces light availability and oxygen production (Koch and Gust 1999). Bending of the seagrass blades was visually observed at the sheltered seagrass site of this study and can be seen in Figure 4b, whereas seagrass at the exposed site is growing more in an upright position (Figure 4c).

In a previous study by Hansen and Reidenbach (2012), unidirectional flow decreased by ~70% within the canopy, whereas wave-dominated currents decreased only by 20%. In the study by Long et al. (2015), increasing flow did not increase oxygen conditions within the canopies located in bays with lower flow velocities. In this study, at the sheltered seagrass site, where the flow was low, oxygen started to decrease within the canopy with the increasing flow with a ~15 min delay (Figure 7), suggesting that canopy dampened the flow velocity and a shear layer (Figure 1) between the canopy and the water layer above likely occurred. Also, within the sheltered canopy, more vertical variation in DO concentrations between the two sensors closest to the bottom was observed, indicating a low turbulence and mixing of water within the canopy. Turbulence is more common within canopies in sheltered locations, where unidirectional currents persist. Turbulence is not efficient in water mixing and transferring nutrients within the canopy (Hansen and Reidenbach 2017), as two layers can form; one above and another within the canopy (Fonseca and Kenworthy 1987).

At the exposed seagrass site, the average temperature was 6 °C lower (10 °C) than at the sheltered site (16 °C) (Table 1 and Figure 6, b4; c4) and had 22 μmol L^{-1} higher average DO concentration above the canopy. According to the Oxygen Solubility Table (Appendix A), a 6-degree difference in temperature can result in a 42 μmol L^{-1} difference in DO concentration. High flow velocities mix water bodies at exposed shores, whereas sheltered locations are more stratified and heated by sunlight. Since more oxygen is dissolved in the water at lower temperatures (appendix A), the water flow above the exposed canopy was more oxygenated

than the flow above the sheltered canopy. Although not statistically proven, sites with average lower temperatures (<11 °C) also appeared to have 15.2 - 36.9 µmol higher average DO concentrations (Table 2; Figures 6 and 9).

Respiration of the canopy may be facilitated by increased flow entrance by waves (Long et al. 2015) and reduced by unidirectional flows due to the bending of the leaves (Koch and Gust 1999). This can expose canopy-associated macrofauna to low oxygen conditions at both sheltered and exposed locations. During this study, oxygen did not deplete within the seagrass canopies, however, the sampling period of four days is not sufficient to cover the possible seasonal variations in light and flow intensities and canopy metabolism. Macrofauna abundance and species composition did not differ significantly between the sheltered and exposed seagrass sites (Tables 4 and 5). However, epifauna biomass was significantly higher at the exposed seagrass canopy (Tables 6 and 7), due to the presence of more grazer species, such as *Idotea* sp. (Fabricius 1798) and *Theodoxus fluviatilis* (Linnaeus 1758). The higher shoot density and height of the exposed canopy provide more food and shelter for the fauna.

The bare sediment site had no vegetation; thus, a large part of the oxygen was produced by microphytobenthos, and some was brought by the flow. Microphytobenthos live and photosynthesize on shallow unvegetated seafloor, at the sediment-water interface (MacIntyre et al. 1996). At the bare sediment site, the production of oxygen by microphytobenthos can be seen during quiescent flow periods, when the two sensors closest to the bottom show a clear diel cycle in DO concentration in relation to light. This diel cycle disappears when the flow picks up on the fourth sampling day and mixing occurs (Figure 8). The temperature also increased during the four-day sampling period from 9 °C to 13 °C (Figure 6, a4). The temperature increase reflected in a small, steady overall decrease in the DO concentrations at 51 cm above seabed during the sampling period of four days (Figure 6, a1), indicating that temperature causes some fluctuations in DO levels of the water column. Despite the highest mean DO values across all the soft sediment sites (Table 2), the bare sediment showed fewer macrofauna species (Table 6) and significantly lower infauna abundance than the seagrass sites (Tables 5 and 6), indicating the importance of vegetation as food and shelter for benthic invertebrates.

4.1.2 Light significance and oxygen conditions at the seagrass sites

PAR radiation was substantially higher at the exposed seagrass site than at the sheltered site; yet it improved the oxygen conditions within the canopy at both sites. The plots in Figures 6, b2 and c2 show a relationship between high PAR and high oxygen concentrations. In the research by Long et al. (2015), a relationship between photosynthesis and irradiance was observed at all seagrass sites.

Higher flow velocity reduces the boundary layer between the water column and the canopy, improving nutrient transport to the canopy (Hansen and Reidenbach 2017), which improves photosynthesis and oxygen production. Higher flow presumably penetrated deeper into the canopy at the exposed seagrass site, resulting in higher oxygen conditions and photosynthesis within the canopy.

The below-ground biomass of seagrass decreases turbidity by stabilizing sediment, enhancing light penetration (Lappalainen et al., 1977; Rönnbäck et al., 2007). The higher shoot density and below-ground biomass at the exposed site (Table 3 and Figure 10a) may retain more sediment, which could explain the higher irradiance and clearer water in the exposed site compared to the sheltered site. However, according to Long et al. (2015), canopies with higher shoot density have a high degree of self-shading and thus lower irradiance. At the exposed site the water was clearer, and the flow velocity was higher than at the sheltered site, which improved light conditions by preventing sediment from accumulating on the seagrass blades, even if shading occurred.

Movements of the blades with wave motion expose different parts of shoots to light, improving light penetration to the canopy (Enriquez et al. 2002) and oxygen conditions. Dense canopies capture light efficiently due to their wide surface area (Zimmerman 2003), hence producing more oxygen. In sheltered locations with lower flow velocities, the sediment accumulates on the blades, potentially decreasing light availability and photosynthesis (Long et al. 2015). In this study, sediment accumulation was also visibly observed at the sheltered site, showing that reduced flow may lead to the accumulation of organic matter. Sparse

canopies also have less root biomass and fewer shoots for stabilizing the sediment, thus increasing turbidity (Long et al. 2015).

The exposed seagrass canopy showed overall higher oxygen concentrations, shoot density, and biomass than the sheltered site (Table 3 and Figure 10b). The below-ground biomass of roots and rhizomes were higher at the exposed site. The below-ground biomass is non-photosynthetic and therefore consumes oxygen. Since both above- and below-ground biomass consume oxygen via respiration, it may be depleted within the canopy during low-flow conditions at night, also at exposed locations.

4.1.3 Sheltered and exposed *Fucus vesiculosus* canopies

Both *F. vesiculosus* sites showed the same amount of *Fucus* individuals m^{-2} and similar biomass (Table 3 and Figure 10), yet their day-to-day oxygen dynamics differed from each other. At the sheltered *F. vesiculosus* site, the flow velocity was low (<6 cm s^{-1}) though the maximum DO levels were the highest of all sites (Table 2). The high fluctuation in DO values (>200 µmol L^{-1}) between the daytime and nighttime (Table 2) indicates high oxygen production and respiration of the canopy.

At the exposed *F. vesiculosus* site, flow velocity was higher than at the sheltered site (Figure 9, a2; b2). When the flow was <7 cm s^{-1}, DO levels were higher within the canopy than above the canopy (Figure 9, a1). When the flow increased to 14 cm s^{-1}, DO concentration dropped within the canopy (Figures 9, a1 and a2). This suggests that the higher flow penetrated the canopy and mixed the water that was oxygenated by *F.vesiculosus*' oxygen production. As the biomass of *F. vesiculosus* did not differ significantly between the sites, we suggest that the flow at the exposed site resulted in the lower DO concentration above and within the exposed canopy.

The DO conditions were high at both *F. vesiculosus* sites, and compared to the seagrass sites, the higher biomass of *F. vesiculosus* (Table 3) presumably produced more oxygen (Attard et al. 2019a). During the night, when the flow was low at both sites, DO levels were higher in the water column than within the canopy (Figure 9, a1 and b1). This could be due to

respiration of the macrofauna inside the canopy consuming oxygen. Some oxygen may also be released in the canopy by the vesicles of *F. vesiculosus* during the night. This phenomenon was observed in previous studies by Aleem (1969) and Attard et al. (2019b). This could thus potentially reduce the drawdown of oxygen from the water column above the canopy, leaving the DO levels higher in the water column than within the canopy. Also, unlike seagrass, the algae do not have below-ground biomass that consumes oxygen, nor are there the same kind of microbial mineralization processes as in soft sediments, contributing to the overall higher oxygen conditions in the fucus canopies.

The macrofauna abundance and species biodiversity in the sheltered *F. vesiculosus* habitat were the highest of all sites (Table 6). The reason for high species richness might be the less exposed condition of the site and the wide variety of algal species in the form of epiphytes that can provide food for the macroinvertebrates, especially typical grazers such as amphipods and isopods (Appendix E). Jormalainen et al. (2001) studied the role of macroalgae and its epiphytes on the food consumption of *Idotea baltica* (Pallas) within the *F. vesiculosus* belts. *I. baltica* first preferred *F. vesiculosus*, even though it grew less than when feeding on filamentous algae, which contain more soluble sugars. *F. vesiculosus* is the only large perennial macroalgae in the northern Baltic Sea, providing a sheltered habitat for macrofauna; thus, specialization to other algae would be unprofitable. *I. baltica* also preferred the brown algae *Dictyosiphon foeniculaceus*, *Elachista fucicola*, and *Pylayella littoralis,* which contained suitable and metabolizable compounds. These seasonal algae were also found at the *F. vesiculosus* sites of this study (Appendix E). Epiphytes can attach and grow at a sheltered location, providing protection and food also for the less robust species, such as insect larvae Chironomidae, which were observed in high abundance at this site. In the study by Norkko et al. (2000), chironomids were the dominating species among drift algae, which provided food, oxygen, and cover from predators. *Chironomus* spp. has a short life cycle and can reproduce when drift algae are present (Norkko et al. 2000).

The exposed *F. vesiculosus* site showed a lower macrofauna abundance than the sheltered site, yet the fauna's biomass did not differ significantly (Table 7). This is explained by different species assemblages between the sheltered and the exposed sites (Table 4 and Figure

11). For instance, macrofauna species had to be more robust or sessile (e.g. blue mussels and barnacles) to resist wave motion at the more exposed site.

4.1.4 Detritus site

At the detritus site, algal detritus mostly originated from *F. vesiculosu*s and the biomass accumulated was the highest of all the studied sites (Table 3). Detached macroalgae can produce oxygen until they begin accumulating and slowly decomposing, and then mostly consume oxygen through respiration. Frontier et al. (2021) found that unattached kelp detritus can continue to photosynthesize and stay reproductively active for months after detaching from the substrate. Two upper sensors, placed at 10 and 35 cm in height, showed daily cycles in DO concentration (Figure 9; c1), suggesting that the upper parts of the detritus mat photosynthesized and produced oxygen in the sections exposed to light. In the lowest part of the mat (2 cm above the seabed), hypoxic and anoxic periods occurred and continued frequently during the measurement study period of six days (Appendix C and F). Flow velocity oxygenated periodically, even the lowest part, yet DO concentrations always remained lower at the bottom of the mat than further up (Figure 9; c1 and Appendix F). DO levels within the mat also dropped during the calm flow periods (0-3 cm s^{-1}), indicating that the DO conditions within the mat are dependent on the oxygen brought by the flow. A similar pattern was documented in a laboratory study by Norkko et al. (2000), where hypoxic or anoxic conditions were recorded under the algal mat, with fluctuating levels within the mat and high oxygen levels above the mat. In the study by Norkko and Bonsdorff (1996b) similar patterns were recorded in the field, and also significantly higher temperature under the algal mat than above the algal mat, which eventually leads to decreasing oxygen concentrations in the water.

The detritus site showed fewer epifauna individuals compared to vegetated habitats (Table 6). Finding epifauna within the detritus confirms that the detritus can serve as a temporary habitat for the fauna, providing food resource and refuge from predators. The fauna within the algae can consist of species that are escaping anoxic conditions under the algal mat and species that are colonizing the algae detritus (Norkko et al. 2000). Only six species were

found at the detritus site, suggesting the importance of good oxygen conditions for macrofauna.

Crustaceans are the most sensitive macroinvertebrate species to hypoxia (Vaquer-Sunyer and Duarte 2008), and only one crustacean species, the isopod *I. baltica,* was observed at the detritus site. *I. baltica* lives close to the surface among drift algae, where oxygen levels are high. Therefore, it is not well adapted to hypoxic and anoxic conditions and cannot regulate its oxygen consumption when DO concentration decreases in water (Vetter et al. 1999). At the detritus site of this study, *I. baltica* was potentially exposed to hypoxia and likely migrated to the upper layers of the detritus to avoid hypoxic conditions.

All other invertebrates observed at the detritus site were mollusks (Appendix D), the most hypoxia tolerant marine invertebrate group (Vaquer-Sunyer and Duarte 2008). This result indicates that there may not have been good enough oxygen conditions for other taxa in the sediment. The blue mussel *Mytilus trossulus x edulis* found within the core samples can survive 168-336 h of anoxia (Jørgensen 1980), although the survival of larvae stage depends on its developmental stage (Diaz and Rosenberg 1995). The mudsnail *Hydrobia ulvae* (Pennant 1777) found at this site can survive 168 h of anoxia (Jørgensen 1980) and was likely not affected by hypoxia in this study. *Hydrobia* spp. has a short life cycle and reproduces when the drift algae occur. It is also highly mobile and can migrate through the algal mat (Norkko et al., 2000). The bivalve *Macoma balthica* (Linnaeus 1758) is a hypoxia-tolerant infaunal species, which can survive 500 h of anoxia depending on its life stage (Norkko et al. 2000). However, bivalves have low mobility and thus are vulnerable to hypoxia. The study by Norkko et al. (2000) showed that *M. balthica* moved from the sediment onto the surface or only to the lowest layer of the algal mat during low oxygen conditions. Presumably it could not extend the siphons within the mat (Norkko and Bonsdorff, 1996a). It also could not move horizontally away from the algal mat (Norkko 1998). At the detritus site of this study, *M. balthica* was only observed within the sediment samples.

The occurrence of hypoxia-sensitive gastropod *Theodoxus fluviatilis* within the detritus indicates that hypoxia may not be permanent at that study site. *T. fluviatilis* consumes oxygen in proportion to the water's oxygen content, decreasing the consumption when DO

concentration decreases in the water, and is thus considered oxygen-dependent (Lumbye 1958). In the laboratory research by Norkko et al. (2000), low numbers of *T. fluviatilis* were found in those algal layers where DO concentrations were the highest. In this field study, detritus was not divided into layers, yet no *T. fluviatilis* individuals were found within the sediment samples. Vegetation is the natural living environment for grazers such as *T. fluviatilis*; therefore, it is possible that climbing through different algal layers in response to hypoxia also occurred in this study.

The sixth species observed at the detritus site was the gastropod *Lymnea* sp (Lamarck 1799). Gastropods have a lethal threshold of 0.89 O_2 mg L^{-1} or 29 µmol L^{-1}, and some of them respond to hypoxia by climbing to the upper layers of the mat to reach higher oxygen conditions (Vaquer-Sunyer and Duarte 2008). As the DO concentrations dropped below 29 µmol L^{-1} in the lowest part of the mat (Table 2, Appendix C; F), it is possible that the species was affected during hypoxia and anoxia.

Vaquer-Sunyer and Duarte (2008) studied lethal thresholds of hypoxia for organisms and reported that the conventional definition of 2 mg L^{-1} is below empirical thresholds for many species. Different taxa have different vulnerabilities and thresholds to hypoxia, and many organisms experience stress at higher oxygen concentrations. Moreover, oxygen demand can be even higher when experiencing simultaneous stresses in the environment, such as eutrophication and an increase in temperature.

The infauna abundance at the detritus site was significantly lower than at the seagrass sites. Compared to the well-oxygenated site with bare sediment, the infauna abundance in the detritus site was only marginally significant (Table 5). However, the variability of the fauna abundance within the sediment samples from the detritus site was high (Table 6). Many of the core samples were empty, demonstrating patchy occurrence and potential mortality of the fauna. Also, some species typical of that habitat, such as Polychaeta and Gammarus spp., were missing and found in the other soft sediment habitats of this study. The study by Norkko et. al (2000) suggests that low fauna abundance under algae mat could partly be explained by the fauna moving up into the mat and not only indicate the mortality.

When avoiding hypoxic waters mobile taxa become more vulnerable to predation; crustaceans can move to shallower waters, and fish swim to near-surface water. Benthic fauna may have to leave tubes and burrows when escaping hypoxia. Fauna can also reduce activity and metabolism (Vaquer-Sunyer and Duarte, 2008). In this study also sulfide traces were observed on the sediment; hence, it is likely that anoxic periods are common at that site and can cause toxicity. Increasing hypoxic and anoxic conditions in shallow waters in the Baltic Sea and globally can lead to a shift in benthic species composition from bivalves and other long-lived species to opportunistic species with shorter life cycles, such as chironomids (Norkko et al. 2000), thus impacting biodiversity in the future.

5 Conclusions

Oxygen dynamics within the canopies differed between the sheltered and exposed locations. Waves oxygenated the exposed seagrass canopy, whereas the weaker current at the sheltered seagrass site seemed not to penetrate well into the canopy, resulting in lower oxygen conditions and higher vertical variation in oxygen levels within the canopy. In contrast to the exposed seagrass canopy, at the exposed *F. vesiculosus* canopy, waves seemed to mix some of the oxygen produced by the canopy with the surrounding waters. The sheltered *F. vesiculosus* canopy was the most oxygenated site. The difference in oxygen levels between seagrass and macroalgal canopies can in part be explained by the root structure and the sedimentary conditions of the seagrass meadow, which also consumes oxygen. At all the study sites except for the detritus site, oxygen concentrations were high and likely did not affect the canopy-associated fauna. The fauna biodiversity was the highest at the sheltered *F. vesiculosus* site. The site with bare sediment was well-oxygenated, yet the macrofauna biodiversity was low, indicating the importance of marine vegetation as a habitat foundation for species. The site with significant algal detritus showed temporary hypoxic and anoxic conditions and low macrofauna abundance and biodiversity, indicating a connection between oxygen availability and macrofauna survival. Most of the species found at the detritus site were mollusks, the most tolerant group to hypoxia. Both bare sand and detritus sites showed low macrofauna biodiversity, yet for different reasons: bare sand was limited by the availability of suitable habitats, and the detritus site affected by temporary hypoxic and anoxic conditions.

This was an *in situ* study on oxygen dynamics and biodiversity across different coastal habitats, including both vegetated and unvegetated sites. This study provides insight into day-to-day oxygen dynamics within key seafloor habitats of the Baltic Sea. Coastal monitoring programs measure oxygen concentrations 1 m above seabed. To better understand coastal oxygen conditions and periodic hypoxia that ecosystems are exposed to under anthropogenic pressures, broader *in situ* measurements covering seasonal variations and different environmental conditions could be performed. Additionally, further studies on the vulnerability of macrofauna to hypoxia, as well as the identification of fauna's different size classes, life stages, and sex ratios, could enhance the accuracy of results in comparison to previous studies conducted under laboratory conditions. A treatment in the laboratory could exclude other environmental factors, different from oxygen, to confirm the links between oxygen availability and macrofauna biodiversity.

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References

Aleem A. A. 1969. Zonation, vesicle pressure and gas composition in Fucus vesiculosus and Ascophyllum nodosum at Kristineberg (west coast of Sweden). Marine Biology 4:36

Attard K.M., Rodil I.F., Glud R.N., Berg P., Norkko J., and Norkko A. 2019a. Seasonal ecosystem metabolism across shallow benthic habitats measured by aquatic eddy covariance. Limnology and Oceanography Letters 4(3):79-86

Attard K. M., Rodil I.F., Berg P, Norkko J., Norkko A. and Glud R. N. 2019b. Seasonal metabolism and carbon export potential of a key coastal habitat: The perennial canopy-forming macroalga *Fucus vesiculosus*. Limnology and Oceanography 64(1):149-164

Binzer T., Borum J., Pedersen O. 2005. Flow velocity affects internal oxygen conditions in the seagrass Cymodocea nodosa. Aquatic Botany 83:239–247

Boström, C., Baden S. P. and Krause-Jensen D. 2003. The seagrasses of Scandinavia and the Baltic Sea, p. 27–37. In E. P. Green and F. T. Short [eds.], *World atlas of seagrasses*. University of California Press

Bäck S., Ruuskanen, A., 2000. Distribution and maximum growth depth of *Fucus vesiculosus* along the Gulf of Finland. Marine Biology 136:303–307

Camillini N, Attard K.M, Eyre B.D, Glud R.N 2021. Resolving community metabolism of eelgrass *Zostera marina* meadows by benthic flume-chambers and eddy covariance in dynamic coastal environments. Marine Ecology Progress Series 661:97-114

Conley DJ., Bjorck S, Bonsdorff E, Carstensen J., and others 2009. Hypoxia-related processes in the Baltic Sea. Environmental science & technology 43:3412-3420

Conley DJ., Carstensen J., Aigars J., Axe P., and others 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. Environmental science & technology 45:6777–6783

Diaz RJ., Rosenberg R. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanography and Marine Biology - an Annual Review 33:245-303

Diaz RJ., Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. Science 321:926-929

Doney S.C. 2010. The growing human footprint on coastal and open-ocean biogeochemistry. Science 328:1512-1516

Duarte C. M. and J. Cebrián. 1996. The fate of marine autotrophic production. Limnology and Oceanography 41: 1758–1766

Duarte C.M., Merino M., Agawin N.S.R., Uri J., Fortes M.D., Gallegos M.E., Marbá N, and Hemminga M. 1998. Rootproduction and belowground seagrass biomass, Marine ecology. Progress series 171:97–108

Enriquez S., Merino M., Iglesias-Prieto R. 2002. Variations in the photosynthetic performance along the leaves of the tropical seagrass *Thalassia testudinum*. Marine Biology 140: 891−900

Eriksson, B.K., Johansson, G., 2003. Sedimentation reduces recruitment success of *F. vesiculosus* (Phaeophyta) in the Baltic Sea. European Journal of Phycology 38: 217–222.

Fourqurean, J. W. and others 2012. Seagrass ecosystems as a globally significant carbon stock. Nature geoscience 5:505–509

Fonseca MS, Kenworthy WJ 1987. Effects of current on photosynthesis and distribution of seagrasses. Aquatic Botany 27:59−78

Frontier N., de Bettignies F., Foggo A., Davoult D. 2021. Sustained productivity and respiration of degrading kelp detritus in the shallow benthos: Detached or broken, but not dead. Marine Environmental Research, Volume 166

Gattuso J.P., Gentili B., Duarte C.M., Kleypas J.A., Middelburg J.J., and Antoine D. 2006. Light availability in the coastal ocean: Impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. Biogeosciences 3:489–513

Hancke K., Glud R.N. 2004. Temperature effects on respiration and photosynthesis in three diatom-dominated benthic communities. Aquatic Microbial Ecology 37:265-281

Hansen, J. C. R., Reidenbach, M. A. 2012. Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. Marine Ecology Progress Series, 448:271–287.

Hansen, J.C.R., Reidenbach M.A. 2017. Turbulent mixing and fluid transport within Florida Bay seagrass meadows. Advances in Water Resources 108:205–215

Harrold C., Light K., and Lisin S. 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. Limnology and Oceanography 43:669–678

Howarth R, Chan F, Conley DJ, Garnier J, Doney SC, Marino R, Billen G. 2011. Coupled biogeochemical cycles: Eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. Frontiers in Ecology and the Environment 9:18-26

Jormalainen V, Honkanen T, Heikkilä N. 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Marine Ecology Progress Series 220: 219-230

Jørgensen, B. B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. Oikos 34:68-76

Kautsky, N., H. Kautsky, U. Kautsky, and M. Waern. 1986. Decreased depth penetration of *Fucus vesiculosus* (L) since the 1940s indicates eutrophication of the Baltic Sea. Marine ecology. Progress series. 28:1–8

Kautsky L, Svensson S. 2003. Understanding, protecting and managing the environment in the Baltic Sea Region / In: Lars Rydén, Pawel Migula and Magnus Andersson [ed] Environmental Science. Baltic University Press, Uppsala, p. 148-181

Koch EW, Gust G. 1999. Water flow in tide- and wave dominated beds of the seagrass *Thalassia testudinum.* Marine ecology. Progress series 184:63−72

Krause-Jensen, D. and Duarte C. M. 2016. Substantial role of macroalgae in marine carbon sequestration. Nature Geoscience 9:737–742

Kruczynski, W.L. and P.J. Fletcher (eds.). 2012. Tropical Connections: South Florida's marine environment. IAN Press, University of Maryland Center for Environmental Science, Cambridge, Maryland. 492 pp.

Lappalainen A., Hällfors, G. and Kangas, P. 1977. Littoral benthos of the northern Baltic Sea. IV. Pattern and dynamics of macrobenthos in a sandy-bottom *Zostera marina* community in Tvärminne. Internationale Revue der gesamten Hydrobiologie und Hydrographie 62:465-503

Lappalainen A., Rask M., Koponen H. and Vesala S. 2001. Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea in 1975 and 1997: Responses to eutrophication? Boreal Environment Research 6:107–118

Lee K-S, Park SR, Kim YK 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. Journal of Experimental Marine Biology and Ecology 350:144-175

Long MH, Berg P, McGlathery KJ, Zieman JC 2015. Sub-tropical seagrass ecosystem metabolism measured by eddy covariance. Marine Ecology Progress Series 529:75-90

MacIntyre H.L., Geider R.J., & Miller D.C. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19: 186–201

Mann, K. H. 1973. Seaweeds—their productivity and strategy for growth. Science 182: 975–981

Middelburg JJ, Levin LA 2009. Coastal hypoxia and sediment biogeochemistry. Biogeosciences 6:1273-1293

Nepf, H.M., Ghisalberti, M., White, B., Murphy, E., 2007. Retention time and dispersion associated with submerged aquatic canopies. Water Resources Resesrch 43, W04422

Norkko A., Bonsdorff E. 1996a. Population responses of coastal zoobenthos to stress induced by drifting algal mats. Marine Ecology Progress Series 140:141-151

Norkko A, Bonsdorff E 1996b. Rapid zoobenthic community responses to accumulations of drifting algae. Marine Ecology Progress Series 131:143-157

Norkko, A. 1998. The impact of loose-lying algal mats and predation by the brown shrimp *Crangon crangon* (L.) on infaunal prey dispersal and survival. Journal of Experimental Marine Biology and Ecology, 221(1):99-116

Norkko J, Bonsdorff E, Norkko A 2000. Drifting algal mats as an alternative habitats for benthic invertabrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology 248:79-104

Peralta, G., Brun, F.G., Pérez-Lloréns, J.L., Bouma, T.J., 2006. Direct effects of current velocity on the growth, morphometry and architecture of seagrasses: a case study on *Zostera noltii.* Marine Ecology Progress Series 327:135-142

Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J 2010. Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences 7:585-619

Ramsing N., Gundersen, J. 2000. Seawater and Gases. Tabulated physical parameters of interest to people working with microsensors in marine systems. Edited by Unisense. Denmark.

Reynolds P.L, 2018. Seagrass and seagrass beds, Smithsonian NMNH, accessed 30 June 2024, https://ocean.si.edu/ocean-life/plants-algae/seagrass-and-seagrass-beds

Rodil, I. F., Attard K. M., Norkko J., Glud R. N. and Norkko A. 2019. Towards a sampling design for characterizing habitat-specific benthic biodiversity related to oxygen flux dynamics using aquatic eddy covariance. PLoS One 14: e0211673

Rodil, I.F., Attard, K.M., Norkko, J. Glud R.N, Norkko A. 2020. Estimating Respiration Rates and Secondary Production of Macrobenthic Communities Across Coastal Habitats with Contrasting Structural Biodiversity. Ecosystems 23:630–647.

Rumohr H., Brey T., Ahkar S. 1987. A Compilation of Biometric Conversion Factors for Benthic Invertebrates of the Baltic Sea. THE BALTIC MARINE BIOLOGISTS No. 9

Rönnbäck P, Kautsky N, Pihl L, Troell M, Söderqvist T, Wennhage H 2007. Ecosystem Goods and Services from Swedish Coastal Habitats: Identification, Valuation, and Implications of Ecosystem Shifts. A Journal of the Human Environment 36(7):534-544

Schramm W. 1999. Factors influencing seaweed responses to eutrophication Some results from EU-project EUMAC. Journal of Applied Phycology 11:69–78.

Smith, S. V. 1981. Marine macrophytes as a global carbon sink. Science 211:838–840

Tait LW, Schiel DR. 2013. Impacts of Temperature on Primary Productivity and Respiration in Naturally Structured Macroalgal Assemblages. PLoS ONE 8(9):74413

Torn, K., Krause-Jensen D, and Martin G. 2006. Present and past depth distribution of bladder wrack (*Fucus vesiculosus*) in the Baltic Sea. Aquatic botany 84:53 –62

Tyler RM, Brady DC, Targett TE 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. Estuaries and Coasts 32:123-145

Vetter EW. 1994. Hotspots of benthic production. Nature 372:47-47

Vetter RAH, Franke HD, Buchholz F. 1999. Habitat-related differences in the response to oxygen deficiencies in *Idotea baltica* and *Idotea emarginata* (Isopoda, Crustacea). Journal of Experimental Marine Biology and Ecology 239(2):259-272

Vaquer-Sunyer R, Duarte CM 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences 105:15452-15457

Zimmerman RC 2003. A biooptical model of irradiance distribution and photosynthesis in seagrass canopies. Limnology and Oceanography 48:568−585

Appendix A. The Unisense Oxygen Solubility Table that was used for brackish water dissolved oxygen conversions (Ramsing and Gundersen 2000).

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by Niels Ramsing & Jens Gundersen

Oxygen solubility at different temperatures and salinities of seawater

Units: µmol/l

Salinity	Temperature (°C)																				
(‰)	0.0	1.0	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0
0.0	456.6	444.0	431.9	420.4	409.4	398.9	388.8	379.2	369.9	361.1	352.6	344.4	336.6	329.1	321.9	314.9	308.3	301.8	295.6	289.7	283.9
1.0	453.5	441.0	429.0	417.6	406.7	396.3	386.3	376.7	367.6	358.8	350.4	342.3	334.5	327.1	319.9	313.0	306.4	300.0	293.9	287.9	282.2
2.0	450.4	438.0	426.1	414.8	404.0	393.6	383.7	374.3	365.2	356.5	348.1	340.1	332.4	325.0	317.9	311.1	304.5	298.2	292.1	286.2	280.6
3.0	447.3	435.0	423.2	412.0	401.3	391.0	381.2	371.8	362.8	354.2	345.9	338.0	330.4	323.0	316.0	309.2	302.7	296.4	290.4	284.5	278.9
4.0	444.2	432.0	420.4	409.2	398.6	388.5	378.7	369.4	360.5	351.9	343.7	335.9	328.3	321.0	314.0	307.3	300.9	294.6	288.6	282.9	277.3
5.0	441.1	429.1	417.5	406.5	396.0	385.9	376.3	367.0	358.2	349.7	341.6	333.7	326.2	319.0	312.1	305.5	299.0	292.9	286.9	281.2	275.7
6.0	438.1	426.1	414.7	403.8	393.3	383.3	373.8	364.6	355.9	347.5	339.4	331.6	324.2	317.1	310.2	303.6	297.2	291.1	285.2	279.5	274.0
7.0	435.1	423.2	411.9	401.1	390.7	380.8	371.3	362.3	353.6	345.2	337.2	329.6	322.2	315.1	308.3	301.7	295.4	289.4	283.5	277.9	272.4
8.0	432.1	420.3	409.1	398.4	388.1	378.3	368.9	359.9	351.3	343.0	335.1	327.5	320.2	313.1	306.4	299.9	293.6	287.6	281.8	276.2	270.8
9.0	429.1	417.5	406.3	395.7	385.5	375.8	366.5	357.6	349.0	340.8	333.0	325.4	318.2	311.2	304.5	298.1	291.9	285.9	280.1	274.6	269.2
10.0	426.1	414.6	403.6	393.0	383.0	373.3	364.1	355.2	346.8	338.6	330.8	323.4	316.2	309.3	302.6	296.2	290.1	284.2	278.5	273.0	267.6
11.0	423.2	411.8	400.8	390.4	380.4	370.8	361.7	352.9	344.5	336.5	328.7	321.3	314.2	307.3	300.8	294.4	288.3	282.5	276.8	271.3	266.1
12.0	420.3	409.0	398.1	387.8	377.9	368.4	359.3	350.6	342.3	334.3	326.7	319.3	312.2	305.4	298.9	292.6	286.6	280.8	275.1	269.7	264.5
13.0	417.4	406.2	395.4	385.2	375.3	366.0	357.0	348.3	340.1	332.2	324.6	317.3	310.3	303.5	297.1	290.8	284.8	279.1	273.5	268.1	262.9
14.0	414.5	403.4	392.7	382.6	372.8	363.5	354.6	346.1	337.9	330.0	322.5	315.3	308.3	301.7	295.2	289.1	283.1	277.4	271.9	266.5	261.4
15.0	411.7	400.6	390.1	380.0	370.4	361.1	352.3	343.8	335.7	327.9	320.5	313.3	306.4	299.8	293.4	287.3	281.4	275.7	270.2	265.0	259.9
16.0	408.8	397.9	387.4	377.4	367.9	358.7	350.0	341.6	333.5	325.8	318.4	311.3	304.5	297.9	291.6	285.5	279.7	274.0	268.6	263.4	258.3
17.0	406.0	395.2	384.8	374.9	365.4	356.4	347.7	339.4	331.4	323.7	316.4	309.4	302.6	296.1	289.8	283.8	278.0	272.4	267.0	261.8	256.8
18.0	403.2	392.5	382.2	372.4	363.0	354.0	345.4	337.2	329.2	321.7	314.4	307.4	300.7	294.2	288.0	282.1	276.3	270.8	265.4	260.3	255.3
19.0	400.4	389.8	379.6	369.9	360.6	351.7	343.1	335.0	327.1	319.6	312.4	305.5	298.8	292.4	286.3	280.3	274.6	269.1	263.8	258.7	253.8
20.0	397.7	387.1	377.0	367.4	358.2	349.3	340.9	332.8	325.0	317.6	310.4	303.5	296.9	290.6	284.5	278.6	273.0	267.5	262.3	257.2	252.3
21.0	394.9	384.5	374.5	364.9	355.8	347.0	338.6	330.6	322.9	315.5	308.4	301.6	295.1	288.8	282.7	276.9	271.3	265.9	260.7	255.7	250.8
22.0	392.2	381.8	371.9	362.4	353.4	344.7	336.4	328.5	320.8	313.5	306.5	299.7	293.2	287.0	281.0	275.2	269.7	264.3	259.1	254.1	249.3
23.0	389.5	379.2	369.4	360.0	351.0	342.4	334.2	326.3	318.7	311.5	304.5	297.8	291.4	285.2	279.3	273.5	268.0	262.7	257.6	252.6	247.9
24.0	386.8	376.6	366.9	357.6	348.7	340.2	332.0	324.2	316.7	309.5	302.6	295.9	289.6	283.4	277.5	271.9	266.4	261.1	256.0	251.1	246.4
25.0	384.1	374.0	364.4	355.2	346.4	337.9	329.8	322.1	314.6	307.5	300.7	294.1	287.8	281.7	275.8	270.2	264.8	259.5	254.5	249.6	244.9
26.0	381.5	371.5	361.9	352.8	344.0	335.7	327.7	320.0	312.6	305.5	298.7	292.2	285.9	279.9	274.1	268.5	263.2	258.0	253.0	248.2	243.5
27.0	378.8	368.9	359.5	350.4	341.7	333.4	325.5	317.9	310.6	303.6	296.8	290.4	284.2	278.2	272.4	266.9	261.6	256.4	251.5	246.7	242.1
28.0	376.2	366.4	357.0	348.0	339.5	331.2	323.4	315.8	308.6	301.6	294.9	288.5	282.4	276.5	270.7	265.3	260.0	254.9	250.0	245.2	240.6
29.0	373.6	363.9	354.6	345.7	337.2	329.0	321.2	313.8	306.6	299.7	293.1	286.7	280.6	274.7	269.1	263.6	258.4	253.3	248.5	243.8	239.2
30.0	371.0	361.4	352.2	343.4	334.9	326.9	319.1	311.7	304.6	297.8	291.2	284.9	278.8	273.0	267.4	262.0	256.8	251.8	247.0	242.3	237.8
31.0	368.5	358.9	349.8	341.1	332.7	324.7	317.0	309.7	302.6	295.9	289.3	283.1	277.1	271.3	265.8	260.4	255.3	250.3	245.5	240.9	236.4
32.0	365.9	356.5	347.4	338.8	330.5	322.5	314.9	307.7	300.7	294.0	287.5	281.3	275.4	269.6	264.1	258.8	253.7	248.8	244.0	239.4	235.0
33.0	363.4	354.0	345.1	336.5	328.3	320.4	312.9	305.6	298.7	292.1	285.7	279.5	273.6	268.0	262.5	257.2	252.2	247.3	242.6	238.0	233.6
34.0	360.9	351.6	342.7	334.2	326.1	318.3	310.8	303.7	296.8	290.2	283.9	277.8	271.9	266.3	260.9	255.7	250.6	245.8	241.1	236.6	232.2
35.0	358.4	349.2	340.4	332.0	323.9	316.2	308.8	301.7	294.9	288.3	282.0	276.0	270.2	264.6	259.3	254.1	249.1	244.3	239.7	235.2	230.9
36.0	355.9	346.8	338.1	329.7	321.7	314.1	306.7	299.7	293.0	286.5	280.3	274.3	268.5	263.0	257.7	252.5	247.6	242.8	238.2	233.8	229.5
37.0	353.5	344.4	335.8	327.5	319.6	312.0	304.7	297.7	291.1	284.6	278.5	272.5	266.8	261.4	256.1	251.0	246.1	241.4	236.8	232.4	228.2
38.0	351.0	342.0	333.5	325.3	317.4	309.9	302.7	295.8	289.2	282.8	276.7	270.8	265.2	259.7	254.5	249.5	244.6	239.9	235.4	231.0	226.8
39.0	348.6	339.7	331.2	323.1	315.3	307.9	300.7	293.9	287.3	281.0	274.9	269.1	263.5	258.1	252.9	247.9	243.1	238.5	234.0	229.7	225.5
40.0	346.2	337.4	329.0	320.9	313.2	305.8	298.7	292.0	285.4	279.2	273.2	267.4	261.8	256.5	251.4	246.4	241.6	237.0	232.6	228.3	224.1

Appendix B.

The sensors' mean correction values and the reference sensor 6.

Sensor number	DO µmol L^{-1}
1	-1,73622
2	0.090581712
3	-4.073715749
4	-1.23952
5	-2.2953
6	0

Appendix C.

Duration and frequency of low O_2 events (<63 µmol l^{-1} or 2 mg L^{-1}) at the site Detritus.

Date	Start time	End time	Duration
1.6.2018	13:12	13:24	12 min
1.6.2018	13:29	13:47	18 min
1.6.2018	15:53		
2.6.2018		3:42	11h 49 min
2.6.2018	4:42	6:56	2h 14 min
2.6.2018	7:28	8:13	45 min
2.6.2018	8:21	9:05	44 min
2.6.2018	9:08	19:22	10h 14 min
4.6.2018	12:28	12:40	12 min
4.6.2018	12:51	13:28	37 min

Appendix D. The benthic macrofauna species that were found in this study.

Species found in this study

x = The abundance of the particular species
Red colour = The most abundant species

	Location	Ångbåt	Ångbåt	Hendriksberg	Spikarna	Spikarna	Vindskären
	Description	Bare sediment	Seagrass habitat, sheltered	Seagrass habitat, exposed	Detritus covering seabed	*F.vesiculosus* habitat, exposed	*F. vesiculosus* habitat, sheltered
	Site	Bare	SGsh	SGex	Detritus	FUex	FUsh
Group							
Crustacea	*Amphibalanus improvisus*		x				
	Asellus aquaticus						x
	Corophium spp.		x				
	Gammarus spp.		x	x		x	x
	Idotea balthica			x	x	x	x
	Idotea chelipes			x		x	x
	Idotea granulosa		x	x		x	x
	Jaera albifrons		x	x		x	x
	Cladocera						x
	Copepoda						x
	Ostracoda sp.						x
	Mysid					x	x
Bivalves	*Cerastoderma glaucum*		x	x			
	Parvicardium haunience		x	x			
	Macoma balthica	x	x	x	x	x	x
	Mya arenaria		x	x			
	Mytilus trossulus x edulis		x	x	x	x	*x*
Gastropods	*Hydrobia ulvae*	x	x	x	x	x	*x*
	Lymnea sp.		x		x	x	
	Potamopyrgus antipodarum	x	x				
	Theodoxus fluviatilis	x	x	x	x	x	*x*
Polychaeta	*Hediste diversicolor*		x	x			
	Halicryptus spinulosus						*x*
	Marenzelleria spp.	x	x	x			
	Nematoda						*x*
	Oligochaeta		x	x			x
	Pygospio elegans						x
Others	Chironomus sp.		x	x		x	x
	Coleoptera larvae						x
	Odonata						x
	Cyanophtalma obscura						x
	Hydrachnidae	x					x

Appendix E. All the vegetation species that were found at studied sites.

Vegetation species found in this study

x = The abundance of species attached to the substrate
* = Only as a drifting form of algae and unattached epiphytes

	Location	Ångbåt	Ångbåt	Hendriksberg	Spikarna	Spikarna	Vindskären
	Description	Bare sediment	Seagrass habitat, sheltered	Seagrass habitat, exposed	Detritus covering seabed	*F.vesiculosus* habitat, exposed	*F. vesiculosus* habitat, sheltered
	Site	Bare	SGsh	SGex	Detritus	FUex	FUsh
Plants	*Potamogeton perfoliatus*		x				
	Potamogeton pusillus			x			
	Stuckenia pectinata			x			
	Zostera marina		x	x			
	Zannichellia spp.			x			
Charales	*Tolypella nidifica*			x			
Algae	*Chorda filum**						x
	Ceramium tenuicorne					x	x
	Cladophora aegogrophila						x
	*Cladophora glomerata**					x	x
	*Cladophora rupestris**						x
	Dictyosiphon foeniculaceus						x
	Ectocarpus siliculosus					x	x
	Elachista fucicola					x	x
	*Eudesme virescens**					x	x
	Fucus vesiculosus					x	x
	*Fucus vesiculosus**				x		
	*Furcellaria lumbricalis**				x		
	Membraneous green algae					x	x
	Pilayella littoralis					x	x
	Polysiphonia fibrillosa						x
	Rhizoclonium sp.*						x
	*Stictyosiphon tortilis**						x
	Ulvae sp.*					x	x
	Vaucheria sp.					x	
	Zygnema sp*						x
	Drifting unrecognized dead algae				x	x	x
Bryozoa	*Electra crustulenta*					x	x

Appendix F. A closer look at the timeline from the detritus site with hypoxic conditions appearing below 63 µmol L^{-1}.