Drifting macrophyte detritus triggers ‘hidden’ benthic hypoxia

Author list: Karl M. Attard1,2,3, Anna Lyssenko3, Iván F. Rodil3,4

Corresponding author: Karl M. Attard karl.attard@biology.sdu.dk

Author affiliations:

1 Department of Biology, University of Southern Denmark, 5230 Odense M, Denmark
2 Danish Institute for Advanced Study, University of Southern Denmark, 5230 Odense M, Denmark
3 Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, 10900 Hanko, Finland
4 Department of Biology (INMAR), Faculty of Marine and Environmental Sciences, University of Cádiz, Puerto Real, Spain

Keywords: benthic ecosystems, primary production, respiration, oxygen fluxes, biodiversity

Abstract

Macrophytes form highly productive habitats that export a substantial proportion of their primary production as particulate organic matter. As the detritus drifts with currents and accumulates in seafloor depressions, it constitutes organic enrichment and can deteriorate O₂ conditions on the seafloor. In this study, we investigate the O₂ dynamics and macrobenthic biodiversity associated with a shallow ~2300 m² macrophyte detritus field in the northern Baltic Sea. The detritus, primarily Fucus vesiculosus fragments, had a biomass of ~1700 g dry weight m⁻², approximately 1.5-fold larger than nearby intact F. vesiculosus canopies. A vertical array of O₂ sensors placed within the detritus documented that hypoxia ([O₂] < 63 µmol L⁻¹) occurred for 23% of the time and terminated at the onset of wave-driven hydrodynamic mixing. Measurements in five other habitats nearby spanning bare sediments, seagrass, and macroalgae indicate that hypoxic conditions were unique to detritus canopies. Fast-response O₂ sensors placed above the detritus documented pulses of hypoxic waters originating from within the canopy. These pulses triggered a rapid short-term (~5 min) deterioration of O₂ conditions within the water column. Eddy covariance measurements of O₂ fluxes indicated that daily photosynthetic production offset up to 81% of the respiratory demands of the detritus canopy, prolonging its persistence within the coastal zone. The detritus site had a low
abundance of crustaceans, bivalves, and polychaetes when compared to other habitats nearby, likely because their low-O$_2$ tolerance thresholds were often exceeded.

1. Introduction

Oxygen availability determines ecosystem health and the biogeochemical function of coastal waters (Diaz and Rosenberg, 2008; Middelburg and Levin, 2009; Breitburg et al., 2018). When in gaseous equilibrium with air, seawater typically contains an O$_2$ concentration ([O$_2$]) between 200-400 µmol L$^{-1}$, depending on the water temperature and the salinity (Garcia and Gordon, 1992). However, both abiotic and biotic processes cause significant departures from equilibrium. The main source of O$_2$ to coastal waters is the atmosphere, where the diffusion of O$_2$ is governed by the air-to-sea gas exchange rate (Berg and Pace, 2017; Long and Nicholson, 2018). In shallow waters and light-exposed seafloor sediments, O$_2$ is produced by primary producers as a by-product of photosynthesis, and it is consumed by consortia of microbes and fauna directly, through aerobic respiration, and indirectly, through the oxidation of reduced substances (Glud, 2008). If O$_2$ consumption exceeds supply for a sufficiently long period, O$_2$ conditions deteriorate and become hypoxic ([O$_2$] < 63 µmol L$^{-1}$). Hypoxia is becoming more common, more intense, and is affecting larger areas of coastal waters, increasingly placing ecosystems and the services they provide at risk (Breitburg et al., 2018). There are several well-known variants of coastal hypoxia (Diaz and Rosenberg, 2008). Seasonal hypoxia, the most common form, typically occurs in summer when warm waters, strong stratification, and high organic enrichment combine to deplete O$_2$ until autumn (Robertson et al., 2016). Periodic O$_2$ depletion, in contrast, occurs more often due to local weather dynamics and tidal cycles but individual events are shorter (Diaz and Rosenberg, 1995), whereas diel cycles with large day-to-night [O$_2$] excursions trigger hypoxia for a few hours daily (Davanzo and Kremer, 1994; Tyler et al., 2009). All events are expected to affect biodiversity and biogeochemical cycling to varying degrees. Seasonal hypoxia and periodic O$_2$ depletion are associated with large-scale mortality of organisms and a switch between retention and removal of bioavailable nutrients such as nitrate, ammonium, phosphate, and toxic hydrogen sulfide (Middelburg and Levin, 2009). Short-term hypoxic events can similarly exceed lethal and non-lethal thresholds for many benthic taxa (Vaquer-Sunyer and Duarte, 2008), although, due to their sporadic nature, their occurrence and impacts are less understood.

Given the importance of O$_2$ in coastal waters, [O$_2$] is one of the most frequently measured environmental parameters. Near-seabed O$_2$ availability is typically measured using long-term stable
O₂ sensors (e.g. optodes, Bittig et al. (2018)) that are moored ~0.5 m above the seafloor, or by performing vertical profiles of water column [O₂] down to ~1.0 m above the seafloor using multiparameter sondes. National monitoring programs such as those maintained by the Swedish Meteorological and Hydrological Institute and the Finnish Environment Institute provide a wealth of essential open-access data, enabling important analyses detailing the prevalence and intensity of coastal hypoxia (Virtanen et al., 2019). Notwithstanding the progress being made in coastal monitoring, it was demonstrated more than 40 years ago that the largest [O₂] gradients may occur just a few cm above the seafloor due to the high reactivity of marine sediments and a strong benthic O₂ demand (Jorgensen, 1980). Hypoxic conditions affecting the seafloor may therefore remain ‘hidden’ if sensors are located higher up in the water column, as is common practice.

Around two-thirds of the ocean’s photosynthetic biomass is bound in macrophytes growing in shallow waters along the world’s coastline (Smith, 1981). Through seasonal decay, epiphyte growth, grazing, and physical forcing (e.g. waves, currents, ice scouring), macrophytes export a large proportion of their primary production (~40 %) to their surroundings as detritus (Attard et al., 2019a; Krumhansl and Scheibling, 2012; Duarte and Cebrián, 1996). Macrophyte detritus drifts with the currents and accumulates on the shoreline and in low-energy marine environments (e.g. shallow seafloor depressions and in deeper waters), where it constitutes habitat structure and organic enrichment to the receiving habitat (Norkko and Bonsdorff, 1996b). Given high enough abundance, detritus suppresses the diffusion of O₂ from the water column to the sediment surface and it exacerbates O₂ depletion on the seabed as it decays. Large accumulations of unattached ephemeral macroalgae such as the brown algae *Ectocarpus siliculosus* and *Pylaiella littoralis* are common in eutrophic coastal waters such as the Baltic Sea, forming thin mats above the seafloor typically a few centimeters thick (Norkko and Bonsdorff, 1996a). Large accumulations of detritus produced from perennial brown seaweeds have also been observed (Glud et al., 2004). However, the O₂ dynamics within accumulations of drifting detritus and the potential implications for the associated fauna remain poorly understood. Understanding the ecological and biogeochemical implications of drifting macrophyte detritus is particularly important given the ambitions to vastly increase macroalgal farming, which would result in increased deposition of macrophyte detritus on the coastal seafloor (Broch et al., 2019; Broch et al., 2022).

In this study, we investigate the O₂ dynamics and macrobenthic biodiversity associated with a shallow ~2300 m² macrophyte detritus field composed of *Fucus vesiculosus* fragments in the northern Baltic Sea. To assess O₂ production versus consumption rates of the detritus canopy, we
deployed an eddy covariance system on multiple occasions to extract benthic O$_2$ fluxes non-invasively. Using a vertical array of O$_2$ sensors and an acoustic velocimeter, we monitored O$_2$ distribution within the canopy and the hydrodynamics above the canopy to assess the occurrence and intensity of hypoxic events and their links to local hydrodynamics. We performed biodiversity surveys to identify the prevailing taxa, and we compared hypoxic thresholds of these taxa to [O$_2$] measured \textit{in situ} to identify potential stress. Measurements were also performed in five other habitats nearby spanning bare sediments, seagrass, and macroalgae for comparison.

2. Materials and Methods

2.1. Study location

The study was performed in the microtidal Baltic Sea nearby the Tvärminne Zoological Station in SW Finland. Although the focus of our study was to investigate drifting macrophyte detritus, we selected an additional five study sites within the shallow subtidal zone (2-4 m depth) for comparison, representing key habitats in the Baltic Sea: one site with bare sediments, two sites with seagrass (predominantly \textit{Zostera marina}; sheltered and exposed), and two sites with intact macroalgae canopies (predominantly \textit{Fucus vesiculosus}; sheltered and exposed) (Table 1).

Table 1: Environmental conditions and low-oxygen events at the six study sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Deployment start</th>
<th>Deployment duration (h)</th>
<th>Water depth (m)</th>
<th>Water temperature ($^\circ$C)</th>
<th>Minimum O$_2$ ($\mu$mol L$^{-1}$)</th>
<th>Maximum O$_2$ ($\mu$mol L$^{-1}$)</th>
<th>Hypoxia duration (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrophyte detritus</td>
<td>59 811613 N 23 206624 E</td>
<td>29-05-2018</td>
<td>120</td>
<td>3.0</td>
<td>12</td>
<td>0.6</td>
<td>429</td>
<td>27</td>
</tr>
<tr>
<td>Bare sediments</td>
<td>59 841532 N 23 253370 E</td>
<td>20-05-2018</td>
<td>96</td>
<td>3.7</td>
<td>11</td>
<td>307</td>
<td>407</td>
<td>0</td>
</tr>
<tr>
<td>Sheltered \textit{Z. marina}</td>
<td>59 841551 N 23 251203 E</td>
<td>27-05-2018</td>
<td>87</td>
<td>4.0</td>
<td>16</td>
<td>272</td>
<td>333</td>
<td>0</td>
</tr>
<tr>
<td>Exposed \textit{Z. marina}</td>
<td>59 827008 N 23 151976 E</td>
<td>08-06-2018</td>
<td>120</td>
<td>2.9</td>
<td>10</td>
<td>281</td>
<td>437</td>
<td>0</td>
</tr>
<tr>
<td>Sheltered \textit{F. vesiculosus}</td>
<td>59 826856 N 23 209721 E</td>
<td>08-06-2018</td>
<td>120</td>
<td>2.0</td>
<td>10</td>
<td>253</td>
<td>489</td>
<td>0</td>
</tr>
<tr>
<td>Exposed \textit{F. vesiculosus}</td>
<td>59 811359 N 23 207281 E</td>
<td>01-06-2018</td>
<td>116</td>
<td>2.0</td>
<td>9</td>
<td>287</td>
<td>427</td>
<td>0</td>
</tr>
</tbody>
</table>

2.2. O$_2$ dynamics of benthic habitats

To investigate the near-bed O$_2$ dynamics and its environmental controls, we equipped a tripod frame with a suite of sensors consisting of three cross-calibrated dissolved O$_2$ loggers with inbuilt temperature compensation (HOBO U26-001, Onset), 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 O2 loggers have a factory-specified accuracy of ± 6 µmol L⁻¹ from 0 to 250 µmol L⁻¹, ± 16 µmol L⁻¹ from 250-625 µmol L⁻¹, a resolution of 0.6 µmol L⁻¹ and a 90% response time (T₉₀) < 2 min. The O2 and conductivity sensors were mounted onto a 75 cm-long stainless steel rail affixed to the tripod leg (Fig. 1). The sensors were secured to the rail at various heights above the seabed using rail mount clamps. For the study sites with canopies, two sensors were set inside the canopy; one sensor was ~5 cm above the seafloor and one was close to the top of the canopy (15-25 cm). The third sensor was placed in the water above the canopy (~35 cm above the seafloor). The tripod was deployed by divers from a small boat and was carefully positioned on the seafloor using a lift bag. The exact sensor heights were noted by the divers once the instrument was on the seafloor. The instrument was left to record data for 3-5 days at each site. The velocimeter sampled three-dimensional flow velocity continuously at 8 Hz, whereas the O2, temperature, conductivity, and PAR sensors recorded data every minute.

To investigate O2 dynamics and its environmental drivers, all sensor time series were aligned in time and analyses were performed to investigate vertical gradients in O2 distribution, diel O2 excursions, and boundary-layer hydrodynamics. We assessed the occurrence of hypoxia (O2 < 63 µmol L⁻¹) by quantifying the magnitude (lowest O2 value) and the duration (in hours) of hypoxic events. The high-frequency velocity data were used to calculate mean flow velocity magnitude ($U$) as the sum of streamwise ($u$) and traverse ($v$) components, as $U = \sqrt{u^2 + v^2}$. 

![Image a](https://doi.org/10.5194/bg-2022-119)

![Image b](https://doi.org/10.5194/bg-2022-119)

![Image c](https://doi.org/10.5194/bg-2022-119)
2.3. Benthic $O_2$ fluxes

An aquatic eddy covariance system was deployed at the detritus site to quantify benthic $O_2$ fluxes at the canopy-water interface on three occasions (June 2017, September 2017, and May 2018). The eddy covariance setup was identical to the tripod frame described above, with the addition of a fast-response ($T_{90} < 0.3$ s) $O_2$ microsensor setup for covariance measurements (Mcginnis et al., 2011). The hardware and data processing techniques are described in detail in Attard et al. (2019b). This instrument can capture the entire range of flux-contributing turbulent eddies within the benthic boundary layer, and this information is used to approximate the benthic $O_2$ flux non-invasively (Berg et al., 2003; Berg et al., 2022). The instrument recorded co-located measurements of the vertical velocity ($w$) and the $O_2$ concentration ($C$) at 32 Hz, and the data were processed using a multiple-step protocol detailed in Attard et al. (2019b) to extract and quality-check benthic fluxes. The data streams for $w$ and $C$ were decomposed into mean and fluctuating components using Reynolds decomposition, as $w = \bar{w} + w'$ and $C = \bar{C} + C'$ (Berg et al., 2003). The turbulent flux ($J_{EC}$) was then computed in units of mmol $O_2$ m$^{-2}$ h$^{-1}$ as $J_{EC} = \overline{w'C'}$, where the overbar represents a period of 15 min. The turbulent flux was then summed with a storage correction term to calculate the total benthic flux ($J_{benthic}$, mmol $O_2$ m$^{-2}$ h$^{-1}$) (Rheuban et al., 2014), as:

$$J_{benthic} = J_{EC} + \int_0^{h_{day}} \frac{\partial C}{\partial t} dz$$

The storage correction term was defined as an average of the $O_2$ sensors located within and above the canopy (Camillini et al., 2021). The high-frequency time series were also analyzed to identify any pulses of low $O_2$ waters originating from within the canopy and propagating up into the water column.

2.4. Benthic metabolic rates

The $O_2$ flux time series was separated into individual 24 h periods (midnight to midnight). The daytime flux ($Flux_{day}$, mmol $O_2$ m$^{-2}$ h$^{-1}$) was computed as a bulk average of fluxes measured when PAR > 1.0 $\mu$mol m$^{-2}$ s$^{-1}$. The nighttime flux ($Flux_{night}$, mmol $O_2$ m$^{-2}$ h$^{-1}$) was calculated as the average of the remaining fluxes, when PAR < 1.0 $\mu$mol m$^{-2}$ s$^{-1}$. These two values and the number of daylight hours ($h_{day}$) were used to estimate the daily photosynthetic rate, termed the gross primary
production (GPP, in mmol O$_2$ m$^{-2}$ d$^{-1}$), as $GPP = \text{Flux}_{\text{day}} + abs(\text{Flux}_{\text{night}}) \times h_{\text{day}}$, and daily respiration ($R$, in mmol O$_2$ m$^{-2}$ d$^{-1}$), as $R = abs(\text{Flux}_{\text{night}}) \times 24$, assuming a light-independent respiration rate. The daily balance between $GPP$ and $R$, termed the net ecosystem metabolism ($NEM$, in mmol O$_2$ m$^{-2}$ d$^{-1}$) was estimated as $NEM = GPP - R$ (Attard et al., 2019b).

The relationship between seafloor PAR and the in situ benthic O$_2$ flux was investigated using light-saturation curves. Hourly O$_2$ fluxes were plotted against the corresponding near-bed incident PAR and the relationship between the two was investigated using a modified tangential hyperbolic function by Platt et al. (1980), as $O_2 \text{flux} = P_m \times \tanh(\frac{\alpha I}{P_m}) - R$, where $P_m$ is the maximum rate of hourly gross primary production, $\alpha$ is the initial quasi-linear increase in O$_2$ flux with PAR, $I$ is near-bed irradiance (PAR), and $R$ is the dark respiration rate. The photosaturation parameter, $I_k$ ($\mu$mol PAR m$^{-2}$ s$^{-1}$) was derived as $P_m/\alpha$. Non-linear curve fitting was performed in OriginPro 2020 using a Levenberg–Marquardt iteration algorithm, until a Chi-Squared tolerance value of 1E-9 was reached (Attard and Glud, 2020).

2.5. Biodiversity sampling

At all six sites, we aimed to obtain a quantitative understanding of the abundance, biomass, and species richness of macrophytes and macrofauna (infauna and epifauna). The different habitats required different sampling strategies, since four sites were sedimentary (bare sediments site, two seagrass sites, and the detritus sites) and two sites were rocky (two macroalgal sites) (Rodil et al., 2019).

At the time of our study, the detritus site had a ~20-cm thick detritus mat covering the seabed sediments. The detritus canopy was sampled using large stainless steel core liners (inner diameter = 19 cm; $n = 4$) capable of cutting through the mat, and the collected samples were transferred into a fine-mesh bag. In the laboratory, the detritus was rinsed through a 0.5 mm sieve to collect the associated epifauna. Samples of algal detritus were dried at 60°C for 48 hours and the biomass was calculated as dry weight /m$^2$.

Macroinfauna at the four sedimentary habitats was sampled using six sediment cores (inner diameter = 5.0 cm, depth = 15 cm). The samples were sieved through a 0.5 mm sieve and animals were stored in alcohol for later identification. At the seagrass sites, representative macrophyte samples were collected by divers from an area around the tripod frame at the end of the deployment using four randomly-placed quadrats (20 x 20 cm). The seagrass within each quadrat was gently
uprooted and was transferred into a net-bag. In the laboratory, the samples were rinsed through a 0.5 mm sieve to collect all the associated epifauna. The animals were stored in alcohol for later identification, 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 in m². The above- and below-ground macrophyte biomass was separated, dried at 60°C for 48 hours and weighed.

At the rocky sites, *F. vesiculosus* individuals (*n* = 4) were randomly collected from around the instrument in fine-mesh bags. Randomly-placed quadrats (1 m², *n* = 4) were used to quantify the number of *F. vesiculosus* individuals per m². At the laboratory, the collected *F. vesiculosus* samples were carefully rinsed through a 0.5 mm sieve to collect the epifauna. The height of the *F. vesiculosus* canopy was determined from the average length of the sampled individuals. Both *F. vesiculosus* and epiphytes were separated to the extent possible, dried at 60 °C for 48 h and weighed. To collect any macrofauna on the bare rock beneath the *F. vesiculosus* canopy, Kautsky-type samplers were placed on the seafloor and the 20 cm x 20 cm area was gently scraped using a spoon into a fine-mesh sampling bag. In the laboratory, all the macrofauna from the four replicates were sieved through a 0.5 mm sieve and stored in alcohol.

The fauna from all habitats was sorted, identified to species level, counted, and weighed. The wet weight for each species was noted with 0.0001 g accuracy. In cases where the fauna occurred in very high numbers, the sample was placed in a water-filled tray and divided into eight sectors. Four sectors were randomly chosen to calculate abundance and biomass. The length of gastropods and bivalves was measured from anterior to posterior axis using Vernier callipers (accuracy = 0.01 mm) for conversion to ash-free dry mass (AFDM). The AFDM of bivalves and gastropods was calculated using established relationships between length and weight for Baltic Sea fauna (Rumohr et al., 1987).

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 multidimensional scaling (nMDS, with fourth-root-transformed data) to visualize macrofauna assemblages between sites. ANOSIM based on the Bray-Curtis similarity matrix was also performed in Primer (site as a fixed factor, 4999 random sample permutations) to compare differences in macrofauna abundance and biomass between sites.
3. Results

3.1. Environmental conditions

Average water depth ranged from 2.0 m to 4.0 m at the six study sites, and average water temperature ranged from 9 °C to 16 °C during the study period (Table 1). Hypoxic conditions were only detected at the detritus site. Bottom-water [O$_2$] at the detritus site ranged from 1 µmol L$^{-1}$ to 429 µmol L$^{-1}$, with hypoxic conditions occurring for 27 h out of the 120 h long deployment (i.e. for 23 % of the time) (Table 1). At the five other measurement sites, [O$_2$] were well above hypoxic conditions, with overall concentrations following diel patterns and ranging from 250 µmol L$^{-1}$ to 490 µmol L$^{-1}$ (Table 1).

3.2. Oxygen dynamics in detritus canopies

The oxygen measurements within the detrital canopy document a highly dynamic O$_2$ environment driven by light availability and flow velocity (Fig. 2). Within the upper layers of the canopy (i.e. ~10 to 25 cm above the seafloor), [O$_2$] and temporal dynamics largely follow diel patterns driven by light availability, with large ~250 µmol L$^{-1}$ diel excursions in O$_2$. In the upper canopy region, the [O$_2$] was lowest in the morning (~160 µmol L$^{-1}$) and highest in the evening (~430 µmol L$^{-1}$). In all cases, [O$_2$] within the upper canopy region was above hypoxic thresholds. However, under low average flow velocities < 2 cm s$^{-1}$, [O$_2$] within the lower canopy region (< 10 cm) deviated substantially from the conditions above. No diel variations in O$_2$ were observed during these periods, and [O$_2$] rapidly became hypoxic for sustained periods (> 24 h long), with [O$_2$] being very low (< 10 µmol L$^{-1}$) during ~10 hr (~8 % of the time) (Fig. 2). As hypoxia persisted throughout the night under low flow velocities, low [O$_2$] extended upwards into the canopy. Hypoxic conditions ended at the onset of higher mean flow velocities of ~7 cm s$^{-1}$, which initiated a rapid (i.e. within 1.5 hr) oxygenation of the entire canopy.
Fig. 2: (a) Flow velocity measured by the velocimeter 10 cm above the detritus canopy and (b) O$_2$ distribution within the canopy as resolved by three O$_2$ sensors located at 3 cm, 10 cm, and 35 cm above the seafloor.

3.3. Pulses of hypoxic waters

High-frequency O$_2$ measurements performed 10 cm above the detritus canopy document transient pulses of hypoxic water originating from within the canopy and propagating upwards into the water column (Fig 3). Such pulses typically followed quiescent weather and occurred at the onset of increased flow velocities. It took $< 1$ min to reduce [O$_2$] in the water column from 220 $\mu$mol L$^{-1}$ to 65 $\mu$mol L$^{-1}$. Subsequently, a recovery period followed where O$_2$ gradually increased back to previous concentrations over a ~5 min period. These rapid variations in water column [O$_2$] were not captured by the slow-response O$_2$ optode sampling at 1 min intervals.
3.4. Benthic O$_2$ fluxes and detritus metabolic rates

The eddy covariance measurements at the detritus site produced three days of continuous flux data in June 2017, three days of data in September 2017, and five days of data in June 2018. Benthic O$_2$ fluxes documented a dynamic O$_2$ exchange rate driven by light availability and flow velocity (Fig. 4). During quiescent periods with low flow velocity < 2 cm s$^{-1}$, a clear diel signal in the O$_2$ flux was observed, indicating substantial primary production associated to the detritus canopy. Higher flow velocities stimulated O$_2$ uptake rates by up to 5-fold, indicating that canopy ventilation through mixing increased O$_2$ uptake (Fig. 4).
Fig 4: Eddy covariance O₂ fluxes measured 10 cm above the canopy in September (a-c) and June (d-f). Oxygen consumption rates during quiescent periods (panels a and d) were 3.3- and 4.5-fold lower than fluxes measured during more turbulent periods (panels b and e), indicating that canopy ventilation through mixing stimulated O₂ uptake.

Hourly O₂ fluxes ranged from -22 mmol O₂ m⁻² h⁻¹ at night to 13 mmol O₂ m⁻² h⁻¹ during the day and showed a distinct diel cycle in response to sunlight availability (Fig. 5). Daily R ranged from 26 to 97 mmol O₂ m⁻² d⁻¹, and daily GPP was between 15 and 74 mmol O₂ m⁻² d⁻¹. Daily R exceeded GPP in all 11 measurement days (net heterotrophic), with NEM ranging from -7 to -32 mmol O₂ m⁻² d⁻¹ (Fig. 5). The deployment average (± SD) GPP:R for the detritus canopy was 0.77 ± 0.04 in June 2017 (n = 3), 0.55 ± 0.02 in September 2017 (n = 3), and 0.77 ± 0.00 in June 2018 (n = 5), and the global mean was 0.71 ± 0.11 (n = 11).
There was a significant positive relationship between near-bed incident PAR and the benthic O₂ flux (Fig. 6). Light-saturation curves fitted to hourly data from all deployments indicated a maximum gross primary production rate ($P_m$) of $5.14 \pm 0.56 \text{ mmol } \text{O}_2 \text{ m}^{-2} \text{ h}^{-1}$, an $\alpha$ of $0.03 \pm 0.01$, and a R rate of $1.92 \pm 0.26 \text{ mmol } \text{O}_2 \text{ m}^{-2} \text{ h}^{-1}$. Light saturation ($I_k$) of the detritus canopy occurred at irradiances greater than $\sim 170 \text{ µmol } \text{PAR m}^{-2} \text{ s}^{-1}$. 
Fig. 6: Relationship between all hourly in situ benthic O₂ fluxes at the detritus site and light availability from the three flux datasets measured. A modified photosynthesis-irradiance curve by Platt et al. (1980) is shown together with 95% confidence bands.

3.5. Macrobenthic diversity and abundance

The detritus site had a biomass of accumulated macrophyte (*F. vesiculosus*) detritus of 1666 ± 223 g dry weight m⁻² (mean ± SE, n = 4), approximately 1.5-fold larger than nearby intact *F. vesiculosus* canopies (Table 2). Detritus accumulation in the five other habitats was around 100-fold smaller.

The area of the detritus site estimated using Google Earth was 2300 m², amounting to 3,832 kg dry weight of *F. vesiculosus* fragments. Macrofauna abundance ranged from 2719 ± 854 ind. m⁻² at the bare sediments site to 17259 ± 2421 ind. m⁻² at the sheltered *F. vesiculosus* site (mean ± SE, n = 4) (Table 3). Macrofauna biomass ranged from 6 ± 2 g m⁻² at the bare site to 41 ± 9 g m⁻² at the exposed seagrass site (mean ± SE, n = 4), and the number of species ranged from 6 to 23, with the lowest values measured at the bare sediments and detritus sites, and the highest values at the sheltered *F. vesiculosus* site (Table 3).

At the detritus site, there was a low abundance of epifaunal crustaceans when compared to other habitats with canopies. Key species, such as the amphipod *Gammarus spp.* were notably absent, and isopods such as *Idotea spp.* were present in low abundance (Table A1). Similarly, there was a notable absence of bivalves such as the soft-shelled clam, *Mya arenaria*, and the cockle *Cerastoderma glaucum*. Polychaetes such as *Hediste diversicolor* and *Marenzelleria spp.* were also absent from the detritus site but present in other sedimentary habitats (Table A1). The nMDS ordination of the macrofaunal assemblages indicated a clear separation of points representing the different habitat sites (ANOSIM: R² = 0.865; p < 0.001). The assemblages from the bare sand and the detritus sites formed separated site groupings compared to the vegetated sites (‘*Fucus*’ and ‘seagrass’, both exposed and sheltered). Within the vegetated sites, the assemblages of the ‘seagrass sheltered’ and the ‘*Fucus* sheltered’ sites were the most different (Fig. 7).
Table 2: Vegetation abundance and biomass (dry weight) at the six study sites. Abundance is shoots per m² for seagrass and individuals per m² for *F. vesiculosus*. Values are mean ± SE.

<table>
<thead>
<tr>
<th>Site</th>
<th>Abundance per m²</th>
<th>Above-ground biomass (g m⁻²)</th>
<th>Belowground biomass (g m⁻²)</th>
<th>Detritus (g m⁻²)</th>
<th>Biomass other species (g m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrophyte detritus</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1666 ± 223</td>
<td>-</td>
</tr>
<tr>
<td>Bare sediments</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sheltered <em>Z. marina</em></td>
<td>768 ± 92</td>
<td>21 ± 2</td>
<td>8 ± 1</td>
<td>58 ± 13</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td>Exposed <em>Z. marina</em></td>
<td>2565 ± 164</td>
<td>69 ± 7</td>
<td>25 ± 3</td>
<td>16 ± 2</td>
<td>0.2 ± 0.2</td>
</tr>
<tr>
<td>Sheltered <em>F. vesiculosus</em></td>
<td>16 ± 2</td>
<td>1244 ± 58</td>
<td>-</td>
<td>55 ± 11</td>
<td>-</td>
</tr>
<tr>
<td>Exposed <em>F. vesiculosus</em></td>
<td>16 ± 2</td>
<td>1112 ± 119</td>
<td>-</td>
<td>20 ± 2</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 3: Macrofauna abundance, biomass (ash-free dry weight), and number of species at the six study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Infauna abundance (ind. m⁻²)</th>
<th>Epifauna abundance (ind. m⁻²)</th>
<th>Total abundance (ind. m⁻²)</th>
<th>Infauna biomass (g m⁻²)</th>
<th>Epifauna biomass (g m⁻²)</th>
<th>Total biomass (g m⁻²)</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrophyte detritus</td>
<td>4175 ± 2885</td>
<td>493 ± 37</td>
<td>4668 ± 2885</td>
<td>5 ± 3</td>
<td>5 ± 0</td>
<td>9 ± 3</td>
<td>6</td>
</tr>
<tr>
<td>Bare sediments</td>
<td>2719 ± 854</td>
<td>-</td>
<td>2719 ± 854</td>
<td>6 ± 2</td>
<td>-</td>
<td>6 ± 2</td>
<td>6</td>
</tr>
<tr>
<td>Sheltered <em>Z. marina</em></td>
<td>6110 ± 787</td>
<td>3020 ± 874</td>
<td>9110 ± 1176</td>
<td>30 ± 6</td>
<td>2 ± 0</td>
<td>33 ± 6</td>
<td>18</td>
</tr>
<tr>
<td>Exposed <em>Z. marina</em></td>
<td>6959 ± 620</td>
<td>3316 ± 772</td>
<td>10275 ± 990</td>
<td>31 ± 8</td>
<td>10 ± 2</td>
<td>41 ± 9</td>
<td>16</td>
</tr>
<tr>
<td>Sheltered <em>F. vesiculosus</em></td>
<td>-</td>
<td>17259 ± 2421</td>
<td>17259 ± 2421</td>
<td>-</td>
<td>11 ± 2</td>
<td>11 ± 2</td>
<td>23</td>
</tr>
<tr>
<td>Exposed <em>F. vesiculosus</em></td>
<td>-</td>
<td>3551 ± 609</td>
<td>3551 ± 609</td>
<td>-</td>
<td>7 ± 2</td>
<td>7 ± 2</td>
<td>12</td>
</tr>
</tbody>
</table>
Fig. 7: A non-metric multidimensional scaling (nMDS) ordination of the macrofaunal assemblages indicated a clear separation of points representing the different habitat sites. The assemblages from the bare sand and the detritus sites formed separate site groupings compared to the vegetated sites.

4. Discussion

4.1. Detritus metabolism rates

The eddy covariance measurements document a highly active detrital canopy that photosynthesized as well as respired. High daily rates of GPP of up to 75 mmol O₂ m⁻² d⁻¹ and R of 100 mmol O₂ m⁻² d⁻¹ are comparable to some of the most productive habitats in the area, such as dense seagrass meadows (*Zostera marina*) and intact canopies of bladder wrack (*Fucus vesiculosus*) (Attard et al., 2019b). These results indicate that shallow detritus accumulation zones are not just regions of organic matter remineralization, but rather they synthesize substantial amounts of organic matter through primary production. The range in daily GPP:R from 0.53 to 0.81 indicates that primary production can offset a substantial proportion of the respiratory demand, which extends the persistence of detritus in the coastal zone. These observations are consistent with the laboratory study by Frontier et al. (2021), who determined that following detachment, kelp (*Laminaria hyperborea* and *L. ochroleuca*) fragments retain physiological and reproductive capabilities for up to several months. Carbon retention within the coastal zone and export to deeper, sedimentary accumulation regions would therefore be larger than would be predicted by decomposition theory alone. Similarly, slow, and incomplete degradation of algae detritus under low O₂ conditions, which could occur, for instance, in the bottom layers of detrital canopies or in the large anoxic basins of...
the Baltic Sea (Conley et al., 2009), would increase carbon retention, transfer, and sequestration potential (Pedersen et al., 2021).

4.2. ‘Hidden’ benthic hypoxia

Our in situ measurements performed over a few days in late spring document that subtidal detritus accumulation zones uniquely experience dynamic O₂ conditions driven by sunlight availability and flow velocity, with rapid O₂ oscillations and frequent periods of hypoxia (Table 1). Hypoxic conditions were largely restricted to the lower ~5 cm of the canopy and were only revealed by sensors placed directly above the sediment surface (< 5 cm distance). At the onset of wave-driven mixing, hypoxic waters from within the canopy propagated upwards into the water column and were registered by fast-response O₂ sensors located 10 cm above the canopy (~35 cm above the seafloor). This observation suggests that the O₂ conditions inside the entire canopy and even in the water column directly above can reach hypoxic conditions for a few minutes (Fig. 4). Such pulses, however, were not registered by the slow-response O₂ optodes with a factory-specified T₉₀ < 2 min. The minimum O₂ concentration observed by these sensors placed at 10 cm and 35 cm above the seafloor was 158 and 229 µmol L⁻¹, respectively, and thus well above hypoxic conditions.

The importance of measuring O₂ close to the seafloor was demonstrated more than 40 years ago by Jorgensen (1980), who developed a small sled that could be towed slowly across the seafloor to map spatial gradients in O₂ at < 5 cm distance to the seabed. Since then, other researchers have investigated the distribution of dissolved constituents such as O₂ and nutrients in the benthic boundary layer using motor-driven sliders that transport sensors vertically towards the seafloor (Holtappels et al., 2011). These studies document that solute gradients are largest near the seafloor, because the seafloor is a strong solute sink or source, and turbulent diffusivities are low. For practical reasons, however, coastal monitoring programs measure O₂ further away from the seafloor. It is therefore likely that hypoxia in the coastal zone is currently underestimated because large-scale models are based on measurements performed higher above the seafloor (0.5-1.0 m) (Virtanen et al., 2019).

4.3. Biodiversity and oxygen dynamics in detritus canopies

Despite being considered a temporary habitat, detritus was found in abundance at our study site on all occasions in May, June, and September. This type of habitat is likely quite widespread in the Baltic. Topographical depressions with limited water exchange occupy ~1350 km² or ~11% of the...
northern Baltic Sea (Virtanen et al., 2019). During a recent seasonal study, we observed the highest abundance of detritus at our study site in summer and autumn, coinciding with high southerly winds that erode intact canopies in shallower waters (Attard et al., 2019a). However, we also observed significant canopy erosion in winter when a substantial biomass of *F. vesiculosus* froze into sea ice and got dislodged once the ice broke up (Fig. 8). Therefore, some degree of drifting detritus might be common throughout the year. Drifting detritus constitutes a significant habitat structure. Given high enough biomass, however, detritus canopies can be a challenging habitat for most species. Dense canopies induce drag, suppress local turbulence, and curb the exchange of O$_2$ and other nutrients between the benthic boundary layer and the seafloor (Hansen and Reidenbach, 2017). If O$_2$ consumption within the canopy and underlying sediments exceeds O$_2$ supply from the water column, low-O$_2$ conditions develop, resulting in hotspots of anoxia and hydrogen sulfide production, inducing mortality of sedentary species (Norkko and Bonsdorff, 1996a; Glud et al., 2004; Norkko et al., 2013). At our study site, hypoxic conditions uniquely occurred at the detritus site and for around a quarter of the deployment time (Table 1). We can expect these conditions to be particularly challenging for crustaceans, the most hypoxia-sensitive macroinvertebrate group (Vaquer-Sunyer and Duarte, 2008). Indeed, we only found one crustacean species at this site- the isopod *Idotea balthica* (Table A1)- which is mobile and can tolerate hypoxic conditions for a few hours (Vetter and Dayton, 1999). All other invertebrates observed at the detritus site were mollusks (Table A1), the most hypoxia-tolerant marine invertebrate group (Vaquer-Sunyer and Duarte, 2008). Other tolerant species include the blue mussel *Mytilus trossulus x edulis* that can survive > 300 h of anoxia (Jorgensen, 1980), although the survival of larvae depends on its developmental stage (Diaz and Rosenberg, 1995). Similarly, the mudsnail *Peringia ulvae* is highly mobile and can survive > 150 h of anoxia (Jorgensen, 1980; Norkko et al., 2000).

Overall, the dynamic O$_2$ conditions in detrital canopies seem to be challenging for most species in this region of the Baltic Sea, with lethal and non-lethal thresholds frequently being exceeded on timescales of hours to days. We currently have a poor understanding of the extent of ‘hidden’ hypoxia in coastal waters, because O$_2$ measurements are performed at some distance away from the seabed. While this is a practical approach that is done to minimize sensor fouling and damage, it does not reveal the full extent of coastal hypoxia. If implemented widely, sensor arrays, as described herein, and sensor elevators (e.g. Holtappels et al. (2011)) can fill in this knowledge gap and provide important insights into the ecological status and biogeochemical cycling that is needed for the sustainable management of coastal ecosystems.
Fig. 8: substantial detritus accumulation was observed in late winter (March 2021) when *F. vesiculosus* froze into sea ice and got dislodged once the ice broke up. (Photo by Alf Norkko)
Table A1. Species list for the five studied sites. Presence is indicated by ‘x’.

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Macrophyte detritus</th>
<th>Bare sediment(s)</th>
<th>Sheltered Z. marina</th>
<th>Exposed Z. marina</th>
<th>Sheltered F. vesiculosus</th>
<th>Exposed F. vesiculosus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustacea</td>
<td><em>Amphibalanus improvisus</em></td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Asellus aquaticus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Corophium</em></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Gammarus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Idotea balitica</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Idotea chelipes</em></td>
<td></td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Idotea granulosa</em></td>
<td></td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Jaera albifrons</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Cladocera</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Copepoda</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Ostracoda</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Mysid</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Bivalvia</td>
<td><em>Cerastoderma glaucum</em></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Parvicardium haunience</em></td>
<td></td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Mya arenaria</em></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Mytilus trossulus edulis</em></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Theodoxus fluviatilis</em></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

Preprint. Discussion started: 19 May 2022
© Author(s) 2022. CC BY 4.0 License.
<table>
<thead>
<tr>
<th>Polychaeta</th>
<th><em>Hediste diversicolor</em></th>
<th>x</th>
<th>x</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Halicryptus spinulosus</em></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Maranzelleria spp.</em></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Nematoda</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Oligochaeta</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Pygospio elegans</em></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Others</td>
<td><em>Chironomus sp.</em></td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Coleoptera larvae</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Odonata</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td><em>Cyanophthalma obscura</em></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>Hydrachnidae</td>
<td>x</td>
<td></td>
</tr>
</tbody>
</table>
Author contribution

All authors contributed significantly to designing the research, funding the study, collecting the data, analyzing samples and data, and interpreting the results. KMA wrote the paper with input from all authors.

Competing interests

The authors declare that they have no conflict of interest.

Data availability

All data presented in this paper will be made available in a FAIR-aligned data repository upon acceptance of the paper.

Acknowledgements

Colleagues at the Tvärminne Zoological Station provided help with fieldwork and logistics. Anni Glud at the University of Southern Denmark constructed the oxygen microsensors used in this study. Elina Virtanen at the Finnish Environmental Institute (SYKE) provided spatial data used to estimate the potential extent of detritus canopies. The Walter and Andrée de Nottbeck Foundation supported this work through a postdoctoral fellowship to KMA and through a Masters fellowship to AL. Further funding for this project was provided by research grants from the Academy of Finland (project ID 294853), the University of Helsinki and Stockholm University strategic fund for collaborative research (the Baltic Bridge initiative), and Denmark’s Independent Research Fund (project ID 7014-00078). This study has utilized research infrastructure facilities provided by FINMARI (Finnish Marine Research Infrastructure network, The Academy of Finland, project ID 283417).
References


