Vol. 709: 1–15, 2023
https://doi.org/10.3354/meps14285

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 13

Microbial degradation dynamics of farmed kelp deposits from *Saccharina latissima* and *Alaria esculenta*

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ABSTRACT: Seaweed farming is a growing industry worldwide, and its sustainable management requires detailed knowledge about the environmental implications of detrital release. This study investigates benthic degradation of kelp detritus in defaunated mesocosms. The degradation dynamics were investigated over several weeks by resolving O_2 and dissolved inorganic carbon (DIC) fluxes as a function of detritus amendments (0.15 g wet weight [WW] m^{-2} to 1 kg WW m^{-2}), temperature (8 and 15°C), and presence of O_2 for 2 commercially important kelp species: *Saccharina latissima* and *Alaria esculenta*. Kelp fragments were deposited in 2 different ways to simulate oxic and anoxic degradation: on the sediment surface (surface amendments) and just below the oxic surface sediment layer (subsurface amendments). All amendments resulted in high initial O_2 consumption followed by an exponential decrease in O_2 uptake over time. The degradation rates increased linearly with the amount of kelp added for both species and for both types of amendments. *S. latissima* expressed higher decay constants across all experiments and had a higher percentage turnover of carbon. In some instances, microbial priming apparently enabled enhanced degradation of preexisting resilient sedimentary carbon. The absolute degradation rates of kelp were reduced in the absence of O_2, and sulfate reduction resulted in gradual accumulation of iron sulfide. Lower ambient temperature reduced the benthic mineralization rate of both kelp species, particularly during the initial incubation stages. The current study demonstrates the importance of key variables for microbial kelp degradation in marine sediments and their dynamics — variables that should be carefully considered when assessing environmental implications of seaweed farming.

KEY WORDS: Seaweed cultivation · Kelp detritus · Microbial degradation · Benthic fluxes · Microbial priming

1. INTRODUCTION

Seaweed farming has been well established in Asia for decades, and the industry is now expanding to most of the industrialized world (Duarte et al. 2022). In the nothern hemisphere, the sugar kelp *Saccharina latissima*, along with the winged kelp *Alaria esculenta*, thrive naturally and are among the species with the highest commercial potential (Hancke et al. 2018). Kelp farming is generally believed to have little environmental impact. Kelp is an autotrophic organism that relies on carbon dioxide, nutrients, and light to grow; it requires neither fertilizers nor feed during production (Stévant et al. 2017). However, one concern is continuous detritus production from kelp farms and the subsequent export of particulate or-

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ganic matter to the adajcent environment (Fieler et al. 2021). With an expansion of the industry, export of kelp detritus will lead to organic carbon deposition at the seafloor in potentially harmful quantities, depending on the cultivation intensity (Broch et al. 2019). The continously produced detritus originates from erosion of the distal ends of the blade, and kelp detritus includes a wide size range of fragments and intact thalli (Krumhansl & Scheibling 2012, Filbee-Dexter et al. 2018). The quantity of particulate organic export increases with progression of the growth season and has been estimated to account for up to 60% of harvested biomass at the end of the season (Zhang et al. 2012, Fieler et al. 2021). For natural kelp forests, ~40–50% of annual net particulate primary production is exported as organic detritus fractions (Krause-Jensen & Duarte 2016, Pedersen et al. 2020, Pessarrodona et al. 2022). In addition to continuous distal erosion, pulses of drift kelp might be released during storms, harvest, or farm malfunctioning and may create mass deposition events (de Bettignies et al. 2013). Detritus from both cultivated and natural kelp is transported by waves and currents into adjacent habitats (Filbee-Dexter et al. 2018), where it is decomposed by benthic communities or potentially retained in the sediment record (Duggins et al. 1989).

Detritus affects and fuels benthic ecosystems. Microbial processes occurring at the sediment surface are essential for the transformation and fate of deposited kelp detritus. Aerobic microorganisms oxidize organic carbon to carbon dioxide (CO_2) using oxygen (O_2), but in most coastal settings, O_2 only extends a few mm into the sediment (Glud 2008). Deposited kelp can therefore become buried in the anoxic zone of sediments via physical sediment mixing or bioturbation, which affects its degradation dynamics and the involved remineralization pathways. In anoxic sediments, carbon mineralization is typically dominated by sulfate reduction, which produces toxic hydrogen sulfide (H_2S) as an end product (Jørgensen et al. 1990). H_2S can either be oxidized by O_2 or entrapped in reduced iron sulfide (FeS_x), depending on the availability of O_2 and FeO_2H (Jørgensen et al. 1990). In settings with large accumulation of kelp detritus, H_2S production can be extensive, which can lead to the release of harmful H_2S from the seafloor and the formation of sulfide-oxidizing microbial communities (Jørgensen & Revsbech 1985, Glud et al. 2004).

The degradation rate of kelp material is influenced by several environmental factors, such as temperature and O_2 availability. Kelp is generally less degradable than phytoplankton due to its content of complex structural compounds and phenols (Trevathan-Tackett et al. 2015, Filbee-Dexter et al. preprint doi: 10.21203/rs.3.rs-38503/v1). Polyphenol content can vary among kelp species and has been shown to deter microbial attack and reduce the degradability of kelp, especially in anoxic settings (Kristensen et al. 1992, Freeman et al. 2001). Thus, temperature, O_2 availability, and seaweed species-specific carbon compounds are key factors to consider when evaluating the degradation dynamics and environmental implications of detrital deposition.

In this study, we investigated the dynamics of microbial-driven degradation of *S. latissima* and *A. esculenta* in marine sediments (Fig. 1a,b). We hypothesized that the degradation dynamics and the benthic biogeochemical responses following kelp deposition differ for the 2 species, but that specific responses depend on the environmental conditions. Using a series of laboratory experiments, we thus aimed to quantify kelp degradation rates as a function of deposited kelp quantity, O_2 availability, and temperature. We simulated deposition of kelp fragments on top of the sediment, such that they were exposed to oxygen (surface amendments), as well as below the oxic sediment surface (subsurface amendments). The benthic solute exchange in the respective treatments was used to assess microbial mediated degradation, redox dynamics, and carbon sequestration in marine sediments following kelp deposition and to discuss the implications for sustainable kelp farming practices.

2. MATERIALS AND METHODS

2.1. Sample collection

Oslo fjord, Norway is divided into 2 major areas: the inner and outer fjord, which are separated by the 12.0 km long narrow and shallow (19.5 m) Drøbak sill (Staalstrom et al. 2012). Sediment samples were collected close to Drøbak sill just outside the Norwegian Institute for Water Research (NIVA) research station at Solbergstrand, Norway (59° 36″ 57′ N, 10° 39″ 10′ E), on 21–24 May 2019. The temperature at 12 m water depth ranges seasonally from 8 to 15°C (Berge et al. 2015).

Fresh kelp was provided by a Norwegian kelp farm in Trondheim, Norway (Seaweed Energy Solutions; https://seaweedsolutions.com). A total of 2.6 kg of kelp fronds were collected and frozen on May 20, 2019 and transported in frozen cool packs to the laboratory.

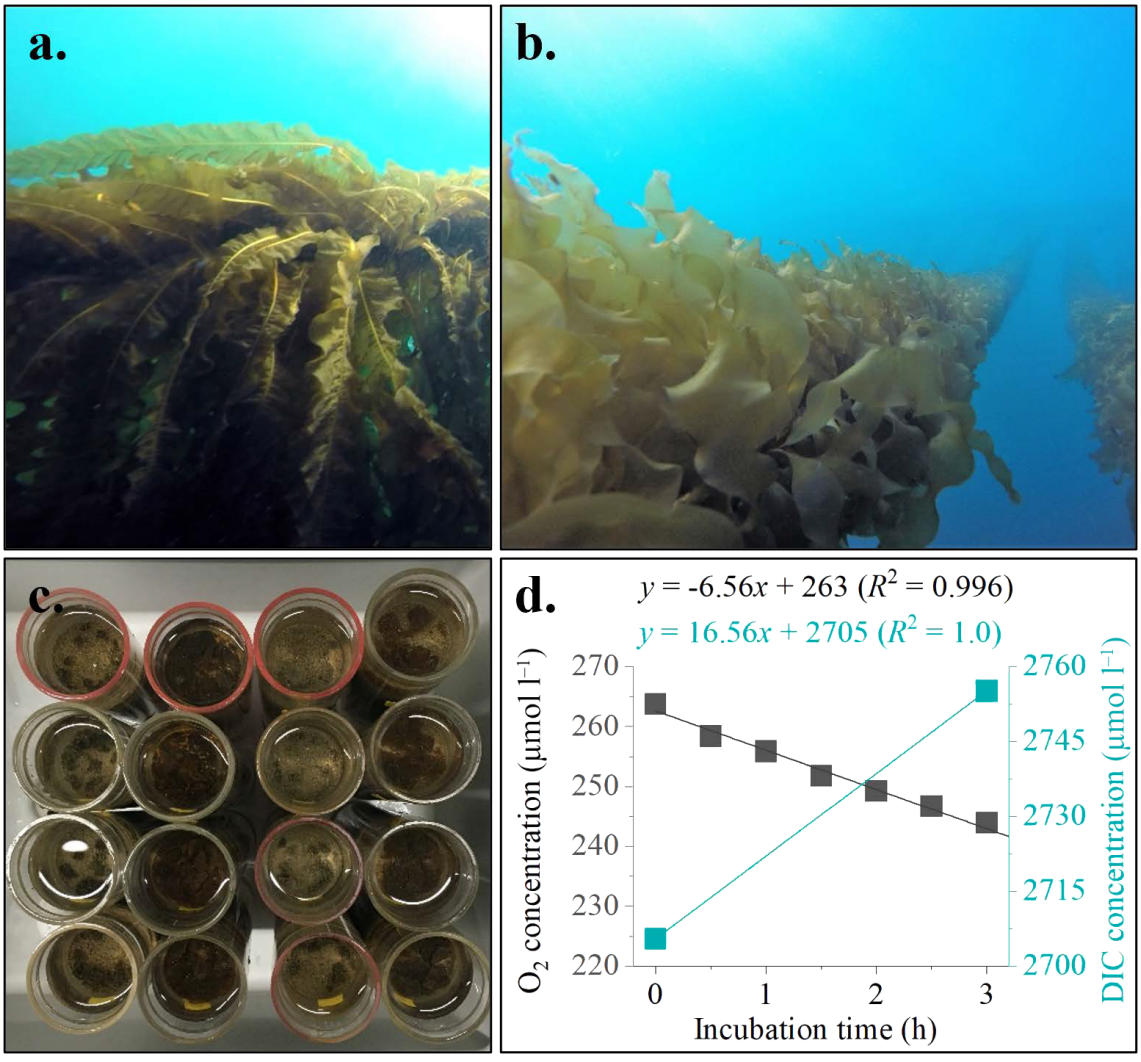

Fig. 1. The 2 species of cultured kelp investigated in the current study (a) *Alaria esculenta* and (b) *Saccharina latissima*. (c) Set of sediment cores with kelp amendments; rotating stirring bars were removed to show sediment surface and amendments. (d) Typical dataset of linearly declining O_2 concentration and the corresponding start and end value of dissolved inorganic carbon (DIC) in a 3 h long incubation

2.2. Sediment sampling

Sediment was collected by SCUBA divers at 12 m water depth using 5.2 cm internal diameter acrylic core liners. Core liners were gently inserted ~15 cm into the sediment, and intact cores were placed into a small crate and carried to the surface (Mogg et al. 2017). During their transportation back to the laboratory in Denmark, sediment cores were kept in racks at ambient temperature (15–20°C) and sealed with rubber stoppers. The cores were then placed in an aquarium room (15°C), and the sediment was initially exposed to anoxia for 10 d. This drove most of the fauna to migrate to the sediment surface, where they were removed using tweezers. Defaunation was required to explore the microbial-driven mineralization of added kelp in relatively similar sediment matrices. Following initial defaunation, cores were transferred to a large aquarium with aerated bottom water collected at the study site in the Oslo fjord (salinity 31.0 ± 1.0). Water height in the sediment cores was adjusted to ~5.0 cm. Prior to the experiments, sediment cores were uncapped and left to acclimatize for 60 d while submerged in sampled seawater at ~15°C. Small magnetic stirrers were fixed inside the cores. The stirring assured mixing of the water column above the sediment. During this initial acclimatization period, any remaining dead fauna

decomposed, and the total oxygen uptake (TOU, see Sections 3.3 and 3.4) was monitored to ensure that a reduced and stable TOU was reached before proceeding with experiments.

2.3. Quantification of carbon mineralization in sediment cores

Benthic carbon mineralization can be approximated by measuring the TOU of sediments, under the assumption that the system is in steady state regarding production and oxidation of reduced substances from anaerobic respiration (Glud 2008). However, during times with high carbon load, O_2 availability decreases, and the reoxidation of reduced substances is delayed, creating a pool of reduced iron sulfides that will be oxidized once O_2 availability increases (Glud et al. 2003). As a result, the O_2 uptake rate typically underestimates the total C-mineralization rate during periods with high organic sediment loading and concurrently overestimates C-mineralization during periods with less organic loading (Therkildsen & Lomstein 1993). The benthic release of dissolved inorganic carbon (DIC) is a more direct measure of the instantaneous C-remineralization rate since CO_2 is the end product of both aerobic and anaerobic respiration and can be measured alongside O_2 uptake (Anderson et al. 1986). Here, we quantify both the exchange rate of O_2 and DIC, which enables direct conversion of the measured flux rates to the concurrent benthic mineralization of organic material in the sediment (Fig. 1c,d). The calculated DIC:O_2 exchange ratio, also termed the respiratory quotient (RQ), provides an indication for the redox conditions at which the organic material is mineralized.

All sediment core incubations were initiated by sealing the cores with a gas-tight cap, leaving a known water volume above the sediment (~5.0 cm water height). Oxygen (% air saturation) was measured non-invasively using a fiber-optic system (Firesting, Pyroscience) following an O_2-sensitive sensor readout spot that was fixed to the underside of the lid and which was in contact with the water during incubation (Camillini et al. 2021). During incubation, the O_2 concentration decreased by about 20% of the initial value, ensuring a distinct linear decline with time (Glud 2008) (Fig. 1d). The individual incubation time ranged from 1 to 8 h, depending on the treatment and conditions. The % air saturation was converted to O_2 concentration (µmol l^{-1}), based on the O_2 solubility at the applied temperature and salinity (Garcia & Gordon 1992). Temperature and salinity were monitored on a regular basis throughout the experiments and varied by less than 1°C and 1, respectively.

Samples for DIC determinations were extracted from the overlying water at the start and end of each sediment core incubation; 12 ml of water was sampled by a glass syringe, transferred to a gas-tight exetainer, and preserved using 50.0 µl of saturated $HgCl_2$. The water samples were then stored at 15°C in the dark until further analysis by a flow injection analyzer (Hall & Aller 1992). Triplicates of 2 mM $NaHCO_2$ standards were measured every 6 samples to correct for potential drift in the signal. The mean ± SD of 5 sets of triplicates of 2 mM $NaHCO_2$ was 2000 ± 4 µM. Benthic fluxes of O_2 and DIC (mmol m^{-2} d^{-1}) were calculated from the slope of the concentration (C, µmol l^{-1}) change over time (t, h) (dC/dt), accounting for the volume of the enclosed water (V, in m^3) and the sediment area of the cores (A, in m^2), that is, flux = $V/A \cdot dC/dt$.

2.4. Density and organic content of sampled sediment and kelp

Three sediment cores were sliced into 9 sections with 0.5 cm depth resolution between 0.0 and 3.0 cm and 1.0 cm depth resolution between 3.0 and 6.0 cm depth. For each sediment section, sediment density D (g cm^{-3}), water content (%), and weight loss on ignition (LOI,%) were quantified. D was calculated from weight (W, g) and volume (V, cm^3) of wet sediment as $D = W/V$. Water content both for sediment and kelp was calculated as weight loss after drying overnight at 105°C (sediment) and 60°C (kelp) based on the following equation: wet weight (WW) − dry weight (DW)/WW × 100. LOI was calculated after combusting the sediment at 520°C for 6 h (Dean 1974). Carbon and nitrogen content were measured on subsamples of 25.0 mg dried sediment that were transferred into tin capsules for analysis on an elemental analyzer coupled to an isotope ratio mass spectrometer (Delta V Advantage IRMS with Thermo Scientific EA). Water content, LOI and the C:N ratio of kelp material were determined using procedures similar to those for the sediment. Indicated error margins represent SD.

2.5. Experimental setup

2.5.1. Degradation rates of frozen versus fresh kelp material

Since fresh kelp material of similar quality was not available during the entire experimental period, we

decided to use one large batch of frozen kelp material. However, first we tested the potential effect of frozen kelp fronds on the particulate and dissolved organic matter degradation dynamics through a series of degradation experiments in water. Kelp fragments were incubated under dark conditions in 100 ml gas-tight bottles filled with water from the sampling site. The decrease in O_2 over time was monitored similar to procedures for the core incubations. Incubations were performed in triplicates containing either fresh *Saccharina latissima*, frozen *S. latissima*, fresh *Alaria esculenta*, frozen *A. esculenta,* or no kelp (control). Triplicates of 0.8 g WW of each species (1.0 × 1.0 cm pieces) were added to glass bottles containing water (salinity: 31.0 ± 1, temperature 15°C). Glass bottles were fastened onto a rotating plankton wheel, and incubations were conducted 15 times during a 30 d period, with incubation times varying from 1 to 6 h. New glass bottles were used for each incubation to avoid buildup of biofilm on the inside wall of the bottles. After each experiment was terminated, the kelp material was removed and the glass bottles left with gentle air bubbling until the following day to ensure 100% air saturation in the water. The next morning, water was subsampled to determine the O_2 consumption related to degradation of dissolved organic carbon (DOC) that had leaked from the kelp during the experiments. Subsamples were incubated in 12 ml exetainers equipped with an O_2 sensitive sensor spot under the same conditions as for the kelp. This experimental design allowed us to concurrently monitor the degradation kinetics of both frozen and fresh kelp fragments, as well as the O_2 consumption associated with the release of DOC from frozen and fresh kelp. The O_2 consumption associated with the release of DOC was minor when compared to the total O_2 consumption, and freezing did not appear to have a significant impact on the O_2 consumption rates of the 2 targeted species (Fig. A1 in the Appendix). It was concluded that the difference between fresh and frozen material was of minor importance when assessing the benthic degradation dynamics of the 2 kelp species.

2.5.2. Surface amendments — effect of increasing carbon load

To explore the degradation rate of kelp as a function of increasing kelp amendments, 19 defaunated sediment cores were submerged in water from the sediment sampling site and kept at 15°C. For each of the 2 kelp species, 8 cores were amended with: 0.3, 0.5, 0.8, 1.3, 1.5, 1.7, 1.9 and 2.0 g of kelp material (WW). Treatments were not replicated. Three cores were kept unamended as controls. The kelp material consisted of 1.0 × 1.0 cm fragments, and when placed on the sediment surface, the material was kept in place and in contact with the sediment surface using a small mesh. The range of doses and the size of kelp were chosen to mimic typical values for natural settings (Filbee-Dexter et al. 2018, Wernberg & Filbee-Dexter 2018, Fieler et al. 2021); see Section 4. The degradation of kelp was inferred from the benthic exchange rates of O_2 and DIC quantified from 19 individual incubations performed over a 65 d period.

2.5.3. Subsurface amendments — effects of O_2 availability

The O_2 penetration depth (OPD) in the unamended sediment was quantified by microsensor profiling (Revsbech 1989) and was on average (±SD) 0.46 cm ± 0.02 (n = 10). Thus, to test the effect of O_2 availability on the degradation dynamics, kelp pieces were buried >0.5 cm below the sediment surface. This was done by carefully extruding the upper 0.5 cm of the sediment, removing this layer, placing the kelp pieces on the anoxic layer, and then replacing the surface sediment slice. The sediment core was then drawn downwards to 5 cm below the top of the plastic liner and submerged in water from the sediment collection site. This approach was preferred over anoxic incubations in order to maintain realistic environmental conditions after a subsurface deposition mediated by fauna or resuspension events.

The sediment cores were exposed to 5 sets of organic enrichments: 1.0 g WW *S. latissima*, 2.0 g WW *S latissima*, 1.0 g WW *A. esculenta*, 2.0 g WW *A. esculenta,* as well as 3 unamended control cores — all 5 treatments were made in triplicates. The incubation setup was identical to that used in the dose-response experiment described in Section 2.5.2. For the subsurface amendments, 11 individual incubations of each of the 15 sediment cores were conducted within a 41 d period.

2.5.4. Surface amendments — effects of temperature

The effect of temperature on kelp degradation was investigated by incubating sediment with kelp amendments at the sediment surface at 2 different temperatures (8 and 15°C). As above, the experiments were conducted in thermoregulated rooms.

At both temperatures, 3 treatments were applied in triplicates (9 cores): amendment with 1.3 g WW of *S. latissima*, amendment with 1.3 g WW of *A. esculenta,* and finally 3 controls without any kelp addition. Degradation dynamics were assessed by 16 individual incubations of the 9 sediment cores during a 68 d long period.

2.5.5. Determining decay rate constants and applied statistics

To quantify decay constants (k, d^{-1}) for organic carbon being overturned in the respective treatments, an exponential equation, $y = b\,(1 - e^{-kt})$, was fitted to the cumulated O_2 uptake. Non-linear curve-fitting was performed in OriginPro 2022 using a Levenberg-Marquardt iteration algorithm, and the SE of the fitting parameters was scaled with the square root of the reduced chi-squared statistic.

Statistical analyses were performed to compare decay rates and percent carbon turnover between treatments. A Shapiro-Wilk normality test was used to evaluate whether data were significantly drawn from a normally distributed population. Two-sample *t*-tests established whether the difference between means were significantly different from zero at the 0.05 level. If equal variance could not be assumed, a Welch correction was applied. Statistical tests were performed in OriginPro 2022 (OriginLabs).

3. RESULTS

3.1. Algae and sediment characteristics

The carbon and nitrogen content were slightly higher — while the water content and the C:N ratio was slightly lower — for *Alaria esculenta* than for *Saccharina latissima* (Table 1), similar to previously published values (Schiener et al. 2015, Forbord et al. 2020). The upper 6 cm of sediment showed no distinct vertical gradients in porosity, LOI, and C:N ratios (Table 1). These values are typical of cohesive coastal sediments (Valdemarsen et al. 2014, Röhr et al. 2016, Politi et al. 2019).

Table 1. Water content and C:N of the amended kelp fragments along with sediment (0–6 cm) C:N, density, porosity, and loss on ignition (LOI). Values are mean ±1 SD (n = 11 for kelp samples and n = 27 for sediment samples)

	Water content (%)	C:N	Density (g cm^{-3})	Porosity	LOI (%)
Saccharina latissima	89 ± 2	15.0 ± 2.7			
Alaria esculenta	85 ± 2	12.3 ± 1.3			
Sediment		18.3 ± 2.7	1.8 ± 0.1	0.5 ± 0.1	3.1 ± 1.4

3.2. Effects of increasing organic enrichment on benthic O_2 and DIC exchange

For all incubations with surface amendments, the rate of cumulative O_2 uptake gradually declined over time, and for both kelp species, the cumulative O_2 uptake increased as a function of increasing amount of amended kelp material (e.g. Fig. 2a,b). For surface amendments, cumulated O_2 consumption in the lowest to highest amount of kelp amendment at Day 65 ranged from 1170 to 3456 mmol O_2 m^{-2} for *S. latissima* and from 1325 to 3832 mmol O_2 m^{-2} for *A. esculenta*. The derived decay rate constants remained independent of the amount of organic enrichment and ranged from 0.020 to 0.051 d^{-1} for *S. latissima* (mean ± 1SD = 0.031 ± 0.010 d^{-1}) and from 0.011 to 0.020 d^{-1} for *A. esculenta* (mean ±1 SD = 0.017 ± 0.003 d^{-1}) (Table 2). The mean decay rate for *S. latissima* was significantly higher than *A. esculenta* for the 15°C treatment (t = 3.800, df = 8.399, Pr > |t| = 0.005) (Table 2).

The DIC release rate quantified for 3 kelp amendments of each species (0.0, 1.3, 2.0 g WW) exhibited similar dynamics as the O_2 consumption rate. The cumulative DIC release at Day 65 ranged from 2804 to 4670 mmol DIC m^{-2} for *S. latissima* (Fig. 2d) and from 3158 to 4629 mmol DIC m^{-2} for *A. esculenta* (Fig. 2c).

The DIC:O_2 exchange ratio as derived from the individual incubations showed substantial variation but no clear temporal development. The mean DIC:O_2 exchange ratio of all incubations with surface kelp amendments amounted to 1.3 (*S. latissima*: 1.3 ± 0.4 and *A. esculenta*: 1.2 ± 0.4), while values for the controls amounted to 1.5 ± 0.7 (Fig. 2e,f). The large variations among the respective treatments as well as the controls indicated a relatively large core-to-core variation, confounding any potential minor trend or difference across treatments.

The total carbon turnover after 65 d increased linearly with increasing organic enrichment for both species, and the response exhibited no sign of substrate saturation, which would likely manifest as an asymptote in the dose-response relationship of Fig. 3. The smaller range in organic enrichment as expressed in carbon equivalents for *S. latissima* reflects

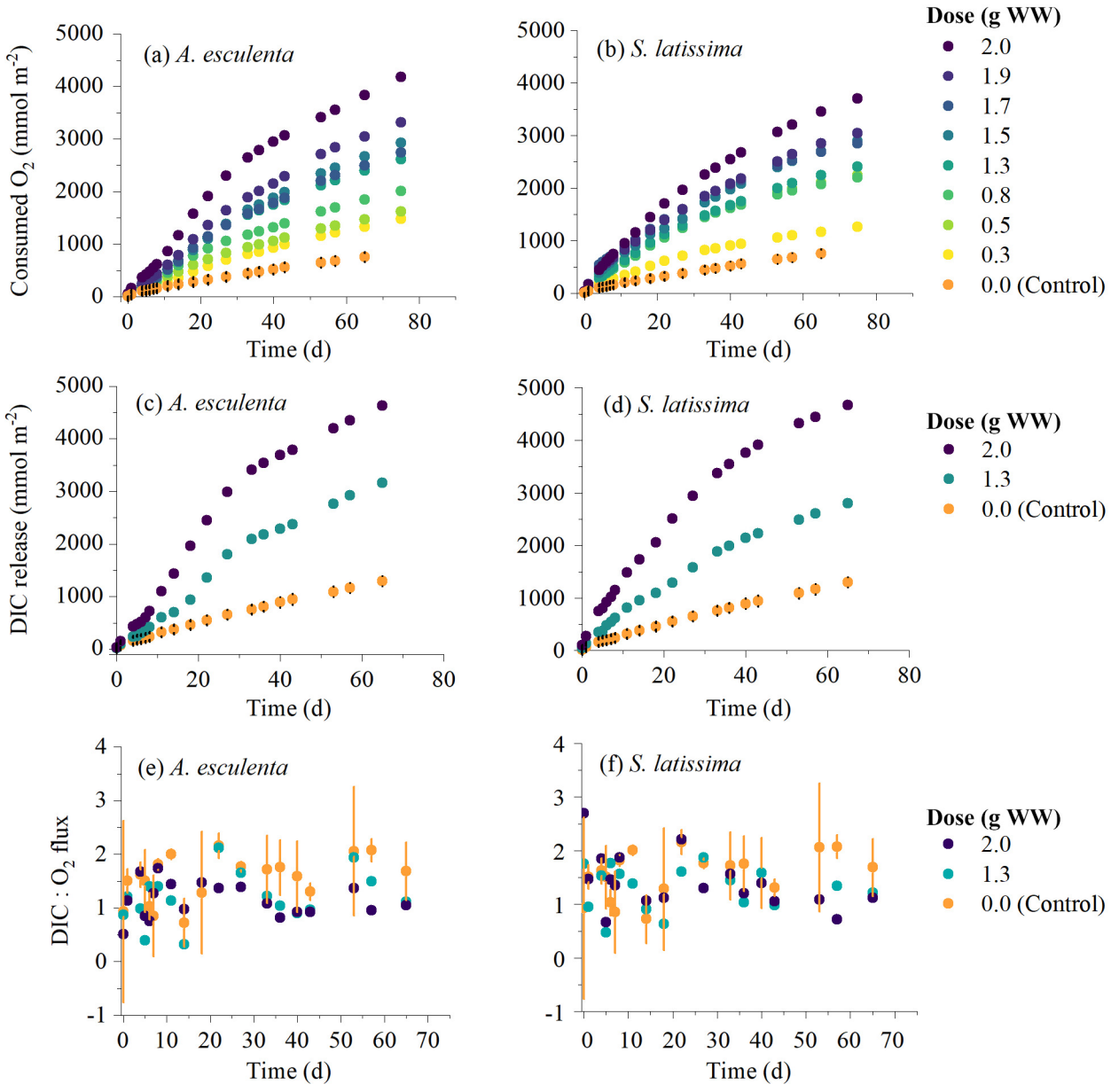

Fig. 2. (a,b) Cumulated O_2 consumption, (c,d) dissolved inorganic carbon (DIC) release, and (e,f) the resulting DIC:O_2 ratio for the exchange rates measured during incubations of sediment cores amended with different doses of kelp material at the sediment surface from the 2 targeted species (*Alaria esculenta* and *Saccharina latissima*) at 15°C. Incubations with kelp amendments made without replications; control incubations without kelp amendment made in triplicate. Error bars (mean ±1 SD) presented where relevant. WW: wet weight

the higher water content and lower carbon content (%) as compared to *A. esculenta* (Table 1).

3.3. Effect of subsurface amendments on benthic O_2 and DIC fluxes

In the subsurface amendment experiments, cumulated O_2 consumption also increased with increasing organic enrichment from 433 to 617 mmol m^{-2} for *S. latissima* and from 390 to 500 mmol m^{-2} for *A. esculenta* (after 41 d, Fig. 4a,b). The cumulated DIC release followed the same pattern, but with an elevated response compared to the cumulated O_2 uptake (Fig. 4c,d). The values ranged from 643 to 964 mmol m^{-2} for *S. latissima* and from 453 to 744 mmol m^{-2} for *A. esculenta* for the 2 respective amendments, while the DIC:O_2 exchange ratio in the control incubations remained at 1.3 ± 0.6 and remained similar to the DIC:O_2 exchange ratio of

Table 2. Decay rate constants (k, d^{-1}) for the surface and subsurface amended experiments along with the % C turnover of amended material after 41 d of incubation. Global means are compared statistically among species. In all treatments, mean decay rate constants and % C turnover rates in *Saccharina latissima* were significantly larger than corresponding values for *Alaria esculenta*. Where relevant, values are reported as mean ±1 SD. WW: wet weight

	Organic dose (g WW)	*S. latissima* (k, d^{-1})	*A. esculenta* (k, d^{-1})	*S. latissima* (% C turnover)	*A. esculenta* (% C turnover)
15°C surface	0.3	0.051	0.019	128	55
	0.5	0.035	0.019	276	49
	0.8	0.030	0.018	171	49
	1.3	0.025	0.019	112	50
	1.5	0.020	0.015	124	49
	1.7	0.034	0.011	117	40
	1.9	0.025	0.015	106	47
	2.0	0.025	0.020	133	70
Mean ±1 SD		0.031 ± 0.010	0.017 ± 0.003	146 ± 56	51 ± 9
15°C subsurface	1.0	0.041 ± 0.007	0.018 ± 0.010	70 ± 17	22 ± 10
	2.0	0.034 ± 0.009	0.012 ± 0.009	61 ± 3	21 ± 7
Mean ±1 SD		0.038 ± 0.013	0.015 ± 0.010	66 ± 10	22 ± 8
8°C surface	1.3	0.005 ± 0.000	0.002 ± 0.001	46 ± 20	29 ± 6

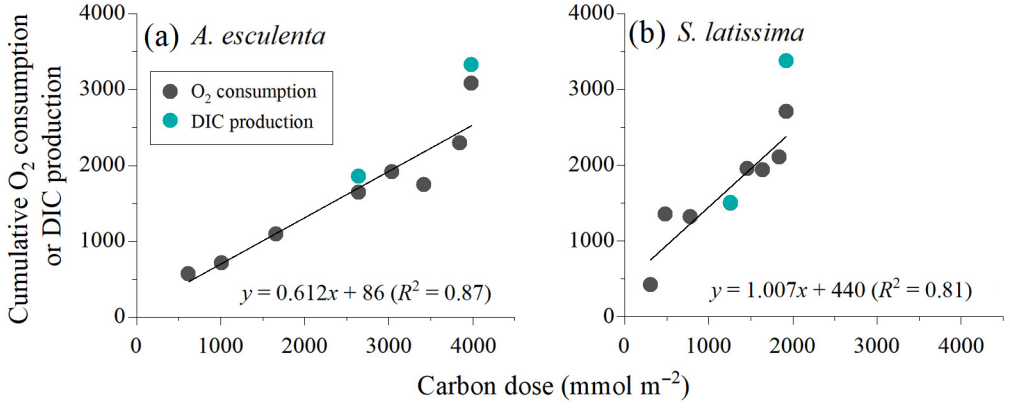

Fig. 3. Cumulated O_2 consumption and dissolved inorganic carbon (DIC) release after 65 d of incubations as a function of kelp amendments for (a) *Alaria esculenta* and (b) *Saccharina latissima*. Data fitted with a linear regression

the control incubations of the previous incubations experiments. The subsurface kelp amendments thus resulted in elevated DIC:O_2 exchange ratios of 2.4 ± 0.7 for both kelp species (Fig. 4e,f). This suggests that O_2 was not supplied sufficiently fast to oxidize reduced products from anaerobic degradation (H_2S and FeS_x) which accumulated as an O_2 debt in the sediment during all incubations with subsurface amendments. The total amount of organic material overturned after 41 d (the extent of the incubations with subsurface amendments) as assessed by cumulative DIC release was 65 ± 11% (mean ±1 SD, n = 4) for *S. latissima* and 22 ± 7% (mean ±1 SD, n = 4) for *A. esculenta*, with means being significantly different (t = 6.781, df = 6, Pr > |t| = 0.000).

3.4. Effect of temperature on benthic O_2 fluxes

The cumulated O_2 consumption of 1.3 g WW kelp deposited at the sediment surface at 8 and 15°C are illustrated in Fig. 5. The cumulative O_2 consumption in the 15°C experiment increased rapidly from the first day, but rates gradually declined until the end of the experiment where the incubations with *S. latissima* and *A. esculenta* reached 1497 and 1640 mmol m^{-2}, respectively.

In contrast, the cumulative O_2 consumption in the 8°C experiment exhibited a lag phase until Day 11. By the last day of the experiment, the cumulative values of *S. latissima and A. esculenta* had only reached 484 and 788 mmol m^{-2}, respectively, and the derived decay rate constants (k) at the lower temperature were

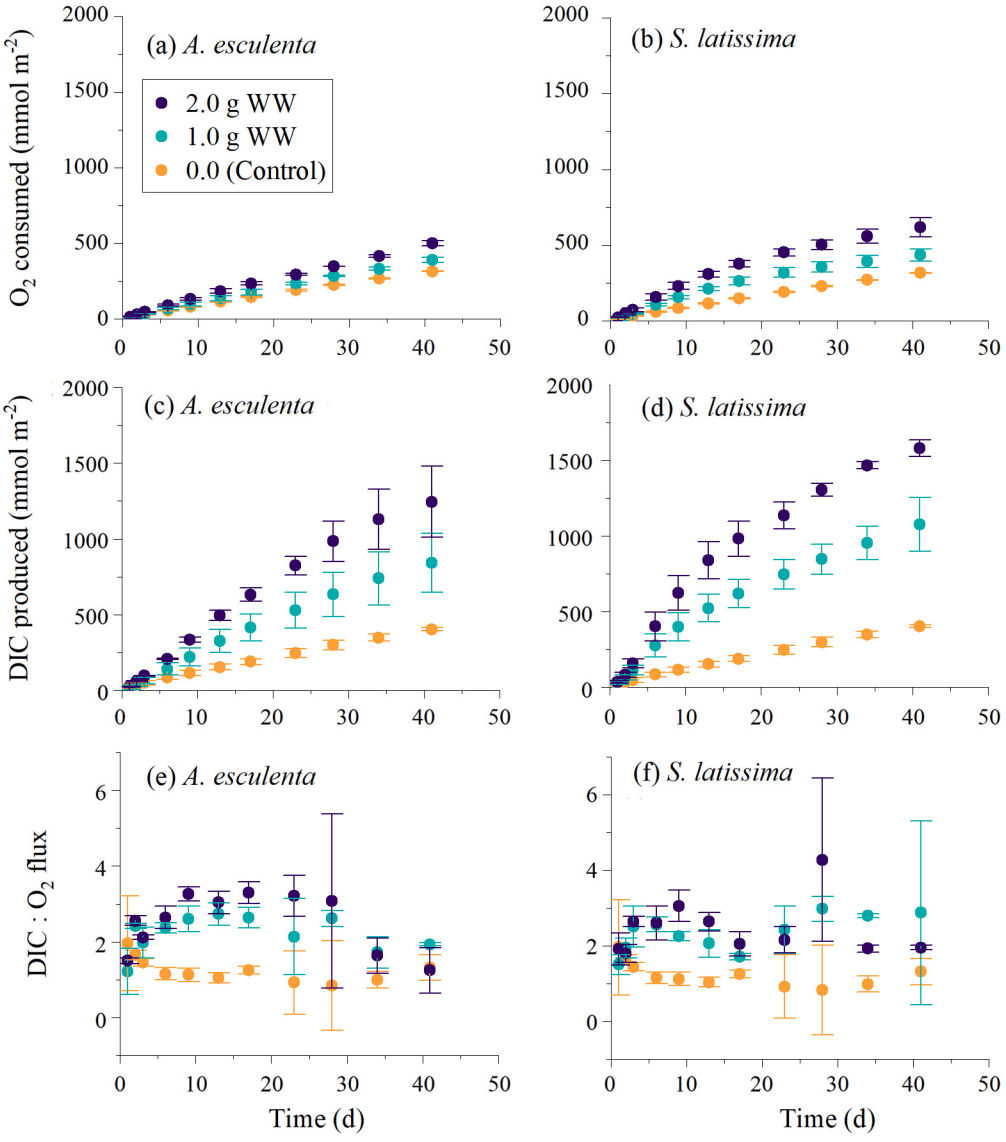

Fig. 4. (a,b) Cumulated O_2 consumption, (c,d) dissolved inorganic carbon (DIC) release and (e,f) resulting DIC:O_2 ratio for the exchange rates measured during triplicate incubations of sediment cores with subsurface amendments of different doses of kelp material from the 2 targeted species (*Alaria esculenta* and *Saccharina latissima*) at 15°C. Error bars (mean ±1 SD) presented where relevant. WW: wet weight

reduced by a factor of ~8 (Table 2). Higher temperature resulted in significantly more C being turned over for both *S. latissima* (t = 4.597, df = 9, Pr > |t| = 0.022) and *A. esculenta* (t = 3.616, df = 8.996, Pr > |t| = 0.006) (Table 2). Unfortunately, we did not make concurrent measurements of the DIC exchange rates in the temperature experiments.

3.5. Mass balance and species' differences

To assess the relative amount of kelp material that had been mineralized in the respective treatments, we compiled values after 41 d for all incubation, which was the duration of the shortest experiment, subtracted the mean control, and scaled the values to the absolute amount of kelp that had been added (Table 2, Fig. 6). For the surface amendments, we converted the measured O_2 fluxes to carbon equivalents using the measured DIC:O_2 exchange ratios from the respective incubations, while values for the subsurface amendments were based on the directly measured DIC exchange rates. The amount of *S. latissima* material that had been mineralized ranged from 46 to 276% across all experiments, while the range for *A. esculenta* material that had been miner-

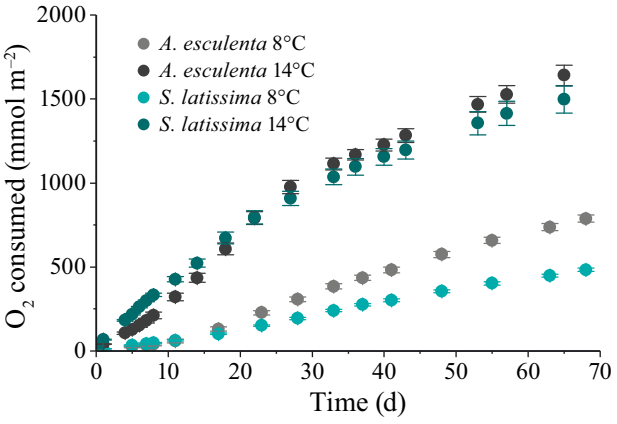

Fig. 5. Cumulated O_2 consumption over the 70 d long incubations with kelp from the 2 targeted species (*Alaria esculenta* and *Saccharina latissima*) amended to the surface sediments at 8 and 15°C. Error bars indicate ±1SD

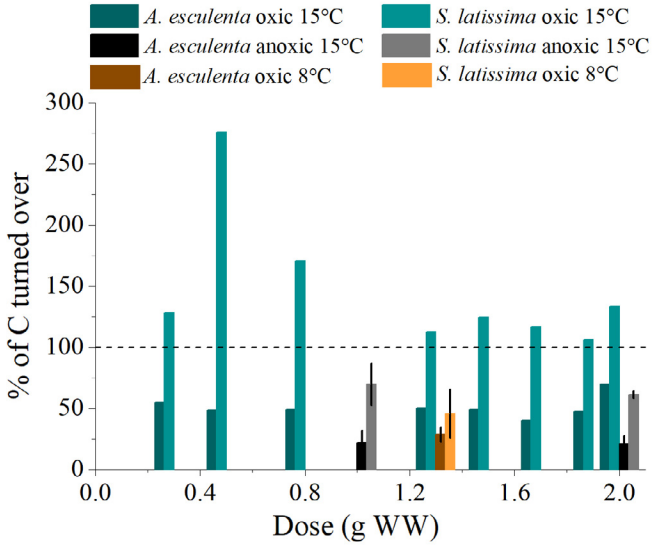

Fig. 6. Relative proportion of organic carbon mineralized 41 d (the shortest incubation period applied) after kelp amendments (*Alaria esculenta* and *Saccharina latissima*) at the respective environmental conditions. Values are corrected for control incubations without amendments; oxic versus anoxic conditions refer to whether kelp was amended at the sediment surface (oxic) or below the oxic surface layer (see Sections 2.5.2 and 2.5.3 for details). Error bars for the 'anoxic' incubations represent SD of triplicate incubations. Horizontal dashed line indicates 100% of the amended kelp has been overturned. Conversion between O_2 consumption and carbon mineralization are based on the measured respiratory quotient (see Sections 3.2 and 3.3 for details). WW: wet weight

alized ranged from 21 to 70%. The mean % C turnover for *S. latissima* treatments under oxic conditions was significantly higher than *A. esculenta* at 15°C (t = 4.734, df = 7.328, Pr > |t| = 0.002) and at 8°C (t = 3.244, df = 4, Pr > |t| = 0.032) (Table 2). The relative amount of kelp degraded during the surface amendments expressed considerably more variation than the subsurface amendments (Table 2, Fig. 6).

4. DISCUSSION

4.1. Benthic mineralization and lability of kelp detritus

All incubations with kelp amendments exhibited a relatively high initial mineralization rate that gradually decreased over the course of the incubations. This presumably reflects a gradual decline in the amount and lability of the added kelp during the long-term incubation periods. The mineralization rate increased linearly with the amount of organic enrichment, and the derived decay rate constants appeared to be independent of the enrichment. However, the derived k-values for the 2 kelp species documented contrasting degradation dynamics, with k-values for *Saccharina latissima* being up to 3-fold higher than those for *Alaria esculenta* (Table 2). This, in combination with the observation that a larger proportion of *S. latissima* was turned over relative to *A. esculenta* over the same period, suggests that *S. latissima* is overall more degradable, reflecting a higher lability of this species' biomass. *A. esculenta* has been reported to contain more than twice the amount of polyphenols than *S. latissima* (Schiener et al. 2015, Roleda et al. 2019). Polyphenols are known to deter herbivory and microbial colonization and therefore may prolong the degradation period of phenol enriched detritus (Nagayama et al. 2002, Goecke et al. 2010). Thus, in addition to the C:N ratio, the content of structurally complex organics probably defines the lability of these 2 species, and macroalgae species in general. Reduced benthic O_2 depletion associated with microbial degradation of more refractory deposits from *A. esculenta* may thus be less severe and have less environmental impacts than the degradation of similar deposits by labile *S. latissima*. Inspection of the sediment at the end of the experimental period confirmed that while fragments of *A. esculenta* still were visible and relatively intact, fragments of *S. latissima* were completely disintegrated and apparently more efficiently degraded. *A. esculenta* would therefore be expected to persist over longer periods of time.

The derived k-values in our study generally align with previously published data, but available values generally show large variability (Table 3). However, they are lower than those recently reported on

Table 3. Decay rate constants for different additions of organic material determined under a range of laboratory conditions and methodological approaches. Decay rates by Pedersen et al. (2005) and Pedersen et al. (2021) mean ±1 SE (n = 3) whereas the remaining rates are mean ±1 SD

Decay rate constant (k, d^{-1})	Temp. (°C)	Applied procedure	Organic material	Reference
0.018	15	Surface amendment	*Fucus serratus*	Kristensen & Mikkelsen (2003)
0.01	15	Subsurface amendment	*F. serratus*	Kristensen & Mikkelsen (2003)
0.054	16	Surface amendment	*Chondrus crispus*	Kristensen et al. (1992)
0.038 ± 0.022	10	Litterbags in tanks, hypoxic	*Laminaria hyperborea*	Pedersen et al. (2021)
0.009 ± 0.005	10	Litterbags in tanks, oxic	*L. hyperborea*	Pedersen et al. (2021)
0.019 ± 0.011	15	Litterbags in tanks, hypoxic	*Sargassum muticum*	Pedersen et al. (2005)
0.016 ± 0.002	15	Litterbags in tanks, hypoxic	*Halidrys siliquosa*	Pedersen et al. (2005)
0.160	20	Surface amendment	*Mussel deposits*	Giles & Pilditch (2006)
0.031 ± 0.010	15	Surface amendment	*Saccharina latissima*	Present study
0.017 ± 0.003	15	Surface amendment	*Alaria esculenta*	Present study
0.005 ± 0.000	8	Surface amendment	*S. latissima*	Present study
0.002 ± 0.001	8	Surface amendment	*A. esculenta*	Present study
0.038 ± 0.013	15	Subsurface amendment	*S. latissima*	Present study
0.015 ± 0.010	15	Subsurface amendment	*A. esculenta*	Present study

degradation dynamics of *Laminaria hyperborea* exposed to similar environmental conditions (Pedersen et al. 2021). Here, the authors report a decay rate constant of up to 0.183 d^{-1} during the first week, followed by a 10-fold decrease in oxic conditions at 10°C, which is 2- to 3-fold higher than the average decay rate constants for *S. latissima* obtained in our study (Tables 2 & 3). These differences might partly reflect the different species investigated as well as differences in methodology. Pedersen et al. (2021) derived the decay from the mass loss of particulate kelp detritus fragments, while in our study we utilized O_2 and DIC fluxes for the entire benthic compartment with the kelp detritus being embedded in intact benthic sediments. This latter methodological approach better represents *in situ* seafloor conditions but may stimulate microbial colonization in the sediment. Thus, the decay rate constants will additionally include remineralization of dissolved organic matter and other preexisting sedimentary carbon pools. The lower decay rates found in our study are consistent with the decay of more refractory carbon pools in the sediment (Tables 2 & 3). When comparing the decay rate constants obtained in our study to the spectrum of organic matter found in marine settings under similar environmental conditions, the decay rate constants are comparable to those of other common brown macroalgae such as *Fucus serratus*, *Halidrys siliquosa*, *Chondrus crispus*, and *Sargassum muticum*, whereas decay rates of mussel biodeposits are around 10-fold larger (Table 3). The deposits from fish farms include both feed and fecal pellet with initial faster decay due to the high lability of feed and the pre-colonization of gut bacteria from the fish in fecal pellets (Piedecausa et al. 2012). In contrast to kelp amendments, carbon mineralization below fish farms appears to be saturated with substrates due to high loading, stimulating sediment sulfide emission and large reduction in macrofauna abundance (Holmer & Kristensen 1992, Holmer et al. 2003).

4.2. Benthic carbon mineralization and microbial priming

Generally, 50% of the surface amended *A. esculenta* was mineralized after 41 d. However, surprisingly, the organic material mineralized in 7 out of 8 surface amendments with *S. latissima* at 15°C exceeded the amount of added kelp (Table 2, Fig. 6). We argue that this additional turn-over of organic material is related to stimulated degradation of preexisting organic material in the sediment. The sequential microbial degradation of organic material is initiated by extracellular enzymes, which also can hydrolyze accumulated resilient organic material in the sediment, a phenomenon known as microbial priming (Arndt et al. 2013). This is particularly relevant after enrichment with highly labile organic material (Guenet et al. 2010, Bengtsson et al. 2018) and thus presumably more prevalent in the amendments with *S. latissima*. The mean organic matter content of the ambient sediment amounted to ~3% DW and could well balance the additional mineralization rate that were encountered. Therefore, additional benthic O_2 consumption due to potential

microbial priming likely has important implications for C burial and sequestration in the coastal zone and should be considered when assessing environmental impacts of highly labile kelp deposits.

4.3. Aerobic versus anaerobic degradation of kelp material

The overturn of organic material as assessed from the O_2 and DIC exchange rates were markedly higher in incubations with surface amendments. This presumably reflect the higher efficiency of aerobic versus anaerobic respiration (e.g. Kristensen et al. 1995). In most studies, the assessment of benthic carbon mineralization is derived from the benthic O_2 consumption rate, and the RQ used for converting O_2 consumption to equivalents of carbon mineralization varies extensively in the literature. For aerobic respiration of pelagic phytodetrital material RQ is generally considered to be in the range of 0.67–0.78 (Tanioka & Matsumoto 2020), while assessments for macroalgae are in the range of 0.6–1.2 (Carvalho & Eyre 2011). However, the DIC:O_2 exchange associated with benthic mineralization might differ considerably from this range, depending on the types of detrital material undergoing mineralization, potential carbonate dissolution/precipitation dynamics, O_2 consumption via nitrification and the redox dynamics of benthic iron sulfide pools (e.g. Jørgensen et al. 2022). Exchange rates of DIC:O_2 in coastal or shelf sediments are typically in the range of 1.0–1.3 (Boucher et al. 1994, Stahl et al. 2004, Glud et al. 2016). This range scales well with values encountered for surface amendment of the current study, which on average amounted to 1.3 ± 0.4 for *S. latissima* and 1.2 ± 0.4 for *A. esculenta*, giving confidence in our procedure for converting O_2 exchange rates to kelp mineralization rates during surface amendments.

In the subsurface amendments, the DIC:O_2 exchange for both kelp species increased to an average of 2.4 ± 0.7. This implies that DIC from anaerobic mineralization following organic enrichment was produced faster than O_2 was supplied. Reduced products from the anaerobic degradation therefore accumulated in the sediment. Based on the distinct smell of sulfide and the darkening of the sediment from light grey to black, which is indicative of FeS, we conclude that sulfate reduction contributed significantly to anaerobic degradation. Sulfide is highly toxic to higher fauna; hence, stimulated sulfate reduction following subsurface deposition of kelp constitutes an important environmental risk. The negative impacts of organic enrichment can be alleviated by sulfide oxidation if the seabed is well oxygenated or has high content of iron oxides that can bind the free sulfide as iron sulfides (Jørgensen et al. 1990). Therefore, it will be relevant to quantify and monitor the level of oxidized iron in areas of kelp farming. In natural settings, bioturbation is important for efficient re-oxidization of reduced product from anaerobic mineralization, and the unusually high DIC:O_2 encountered in our study might partly reflect the initial defaunation of our sediment cores. To fully explore the linkage between degradation of kelp deposits, H_2S and FeS_x dynamics, natural benthic infauna communities must be included, but this represents a major experimental challenge and would probably require large-scale mesocosm studies placed directly in the environment.

4.4. Temperature

Short-term and seasonal variations in temperature are important factors regulating microbial respiration and the efficiency of carbon degradation in costal settings (Grant 1986, Thamdrup et al. 1998, Hancke & Glud 2004). Reducing the ambient temperature from the *in situ* value of 15 to 8°C extended the period where surface amended kelp detritus remained visually intact and markedly reduced the initial decomposition rate. Even though the mineralization rate at low temperature, after an initial lag period, gradually approached the values observed at the higher temperature, only 45.6% ± 19.9 of *S. latissima* and 28.7% ± 5.9 of *A. esculenta* additions were mineralized after 65 d. The corresponding values at 15°C were 112.3 and 50.3%. Similarly, the derived decay rate constant at 8°C was ~8 times lower than the values at 15°C (Table 2). Short-term lowering of the temperature thus reduced the mineralization intensity and the O_2 demand of the sediment. The current study only reflects conditions following a temporary reduction in temperature as induced by hydrodynamic-driven changes of water masses. Longer-term or seasonal changes in temperature will induce a change in the microbial community structure, favoring better temperature-acclimated and adapted microbial communities (Sagemann et al. 1998, Thamdrup et al. 1998, Hancke & Glud 2004, Robador et al. 2016). Several studies have documented that substrate availability is more important than temperature and that turnover or preservation of organic carbon in permanently cold regions are similar to values encountered in warmer regions exposed to similar deposition rates

(Meyer-Reil & Koster 1992, Nedwell et al. 1993, Arnosti et al. 1998). However, the current study demonstrates that short-term reductions in temperature will make benthic communities more resilient to the potential detrimental effects of kelp mineralization — an effect that might be enhanced also by the increased O_2 solubility at lower temperatures.

4.5. Perspectives and recommendations

We have applied a standardized microcosm procedure to assess microbial degradation dynamics of kelp detritus and quantified the importance of the most relevant environmental drivers, such as the amount of organic matter enrichment, anaerobic vs. aerobic mineralization, and ambient temperature. These investigations provide important insights on benthic responses and factors to acknowledge during sustainable kelp farming of 2 commercially relevant species in defaunated sediment. However, natural settings are highly variable and macrofauna can play an important role for the biogeochemical function of benthic habitats. The study provides detailed quantitative insight on the degradation dynamics, revealing some surprising findings such as microbial priming, which may enhance the degradation of resilient organic material in the sediment counteracting climate beneficial burial of carbon equivalents. However, as for most laboratory studies, our investigations cannot be directly transferred to complex and environmentally dynamic *in situ* conditions. The next step for exploring environmental effects of kelp deposition would be to assess benthic responses in complementary large-scale megacosms or non-invasively by the eddy covariance approach (Berg et al. 2022).

Acknowledgements. We thank Hartvig Christie for dive assistance and seaweed energy solution for supplying freshly harvested kelp for the study. We also thank the Nordcee Lab, especially Anni Glud, for laboratory assistance. This study was funded by the Research Council of Norway grant no 267536 (KELPRO). In addition, E.H.B., K.A. and R.N.G. were supported by grants from the European Research Council grant no 669947(HADES-ERC), Danish National Research Foundation grant no DNRF145(HADAL), and the Danish National Research Council (FNU7014-00078).

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Appendix.

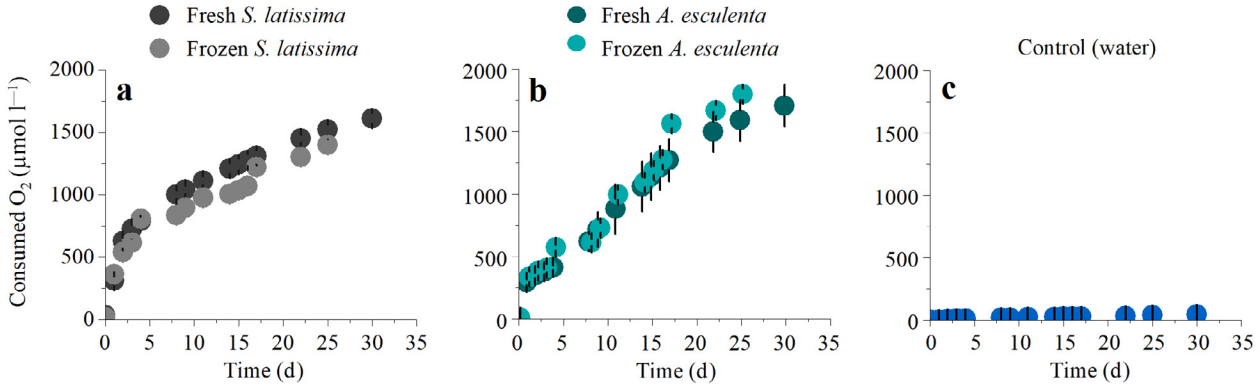

Fig. A1. Cumulative O_2 consumption during parallel incubations of suspended fresh and pre-frozen kelp material from the (a,b) 2 targeted species and (c) during parallel controls without kelp. Error bars indicate SD of triplicate measurements

Editorial responsibility: Robinson Fulweiler, Boston, Massachusetts, USA
Reviewed by: 3 anonymous referees

Submitted: August 24, 2022
Accepted: March 7, 2023
Proofs received from author(s): April 4, 2023