



Simulating fish farm enrichment and fallowing impacts reveals unequal biogeochemical recovery of benthic variables

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ABSTRACT: Finfish aquaculture is playing an increasing role in global food provision, with accompanying increases in benthic impacts under intensive pen production systems. Deposited faeces under and near fish pens affect the seafloor environment and biogeochemical functioning. To maintain healthy coastal environments, many fish farms operate by alternating input and fallowing periods to allow benthic coastal receiving environments to recover from excess organic matter inputs. Here, we used flow-through annular flume mesocosms to simulate sustained organic matter inputs to the benthos with a subsequent fallowing period of no inputs. To quantify the effects of excess organic matter loading on benthic receiving environments, we carried out repeated closed-system flux studies to quantify the benthic carbon mineralisation processes, with a focus on benthic oxygen, inorganic and organic carbon, nitrogen, phosphate, and sulphide fluxes, along with the redox state throughout the input and recovery period. We found that recovery periods were input-dependent, with parameters requiring longer fallowing periods to recover following larger inputs. While some benthic parameter fluxes such as dissolved organic carbon, sulphide, and ammonium returned to their pre-input state relatively rapidly (1–2 mo) following cessation of inputs, others such as sediment oxygen demand, ammonium, and redox required longer (>7 mo) to recover. Our results suggest that in situations where the benthic macrofaunal community has been severely impaired, extended fallowing periods may be required in order to permit the biogeochemical composition of the seabed to return to a more natural state, with implications for farm-consenting permits and planning as well as operational fallowing practices.

KEY WORDS: Benthic ecology · Finfish aquaculture · Environmental degradation · Anthropogenic impacts

1. INTRODUCTION

Increase in demand for global food production has resulted in increased exploitation of coastal and shelf sea benthic systems by anthropogenic activities and through food production (Stimpson & Co 2007, Watson et al. 2015). Aquaculture plays a crucial role in global food provision and income security and is a rapidly

growing sector, currently dominated by finfish production (Ottinger et al. 2016, Belton et al. 2018, FAO 2020). The required expansion of aquaculture to meet increasing sustainable protein requirements will result in greater areas of the coast dedicated to fish farms and increased pressure on coastal environments.

Contained farm and pen production of fish results in large depositions of organic-rich particles, primar-

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ily consisting of fish faeces, onto the benthos (Gowen & Bradbury 1987, Buschmann et al. 2006, Bravo & Grant 2018) which, in low-current coastal waters where dispersal of settling particles is minimal, is concentrated directly under or in close proximity to the farms. The magnitude of this benthic enrichment is a function of multiple farm characteristics, including stocking density, feed rates, and the quantity and digestibility of the food and faeces deposited on the seabed (Handley et al. 2020). Additionally, *in situ* environmental conditions also impact deposit dispersal, such as water depth, substrate type, and local hydrodynamics (Hargrave 2010, Holmer 2010, Keeley & Taylor 2011). This input to the sediment affects the benthic environment and biogeochemical functioning under and near the fish pens in a number of ways and is directly dependent on the organic matter input reaching the seabed.

Benthic conditions under farms proceed through a series of predictable stages as organic matter inputs increase (Keeley 2013, Keeley et al. 2015). Under low-input conditions, the benthos can maintain a healthy habitat with active bioturbating macrofauna. Under these conditions, the majority (approximately 80%) of particulate organic matter input is mineralised under oxic conditions by sediment microbes, with the remaining 20% mineralised by benthic macrofauna (Banta et al. 1999, Valdemarsen et al. 2010, Mayor et al. 2012). Benthic metabolism (e.g. O_2 uptake) shows a linear relationship with organic matter input rates: i.e. the greater the deposition rate, the higher the benthic metabolism rate (Holmer & Kristensen 1994, Morrisey et al. 2000, Valdemarsen et al. 2010, 2012). Key to sustainable benthic remineralisation is the benthic assimilative capacity: the rate of deposition of organic matter that maximises total organic carbon (OC) degradation rates while avoiding adverse geochemical and biological conditions (Bravo & Grant 2018), such as sediment and overlying water de-oxygenation, sulphate (SO_4^{2-}) reduction, and loss of the macrofaunal community. There is, therefore, a limit to the amount of fish-farm-derived particulate carbon inputs that can be deposited onto the benthos without negative impacts. When this threshold input is exceeded, increased anoxia can lead to a number of rapid and linked successional changes in benthic fauna and biogeochemistry.

When the assimilative capacity is exceeded, excess inputs may result in increased bacterial biomass and altered bacterial efficiency (Mayor et al. 2012, Tait et al. 2015, Sciberras et al. 2017). Oxygen demand is increased to a point that results in long-term deoxygenation of the sediment and, under certain circum-

stances, the overlying water column (Quijón et al. 2008, Mayor et al. 2012). These changes also lead to disruption in the balance and distribution of reactive nitrogen species (such as ammonium [NH_4-N], nitrite and nitrate [NO_x-N]), with consequences for nitrification, denitrification, and anaerobic NH_4-N oxidation reactions (Garber 1984, Kelly & Nixon 1984, Kemp & Boynton 1984, Sundbäck et al. 1990, Caffrey et al. 1993, Conley & Johnstone 1995, Bannister et al. 2014) that regulate coastal nitrogen budgets (Laverock et al. 2011). These biogeochemical changes impact benthic fauna, reducing biodiversity (Hargrave 2010, Bannister et al. 2014, Zhang et al. 2015). Ultimately, sediments may completely lose the macrofaunal community. Loss of macrofaunal bioturbation also reduces sediment capacity for organic matter degradation (Banta et al. 1999, Kristensen et al. 2012, Valdemarsen et al. 2012, Hale et al. 2017).

When the assimilative capacity is exceeded and excess organic matter input rates continue, the resultant hypoxic or anoxic conditions also cause the accumulation of reduced metabolite species in the sediments, including particulate and dissolved sulphides (Brooks & Mahnken 2003, Holmer et al. 2005, Hargrave et al. 2008, Hargrave 2010, Valdemarsen et al. 2010, Bravo & Grant 2018). Following this process, depletion of porewater SO_4^{2-} may lead to methanogenesis (the production of methane), also exacerbating OC accumulation (Samuelsen et al. 1988, Hall et al. 1990, Holmer & Kristensen 1994, Morrisey et al. 2000, Valdemarsen et al. 2012, Keeley 2013). Ultimately, this self-enforcing build-up of harmful toxins in the sediment may be partly irreversible (Valdemarsen et al. 2012). These over-enriched benthic environmental conditions are undesirable when maintaining a healthy farm and associated environment, so it is important to know how farm characteristics, particularly feeding rates and fish stocking density, relate to benthic impact levels so these can be regulated.

Indeed, finfish farming is highly regulated with strict controls on acceptable benthic (and wider) impacts of farms and degraded, anoxic seabed conditions resulting in breaches of environmental standards (Wilson et al. 2009). However, the rapid expansion of the industry has often left regulatory authorities lagging behind (Peel & Lloyd 2008, Amundsen et al. 2019). In general, it is recommended that benthic conditions under fish farms do not exceed an enrichment stage at which the benthos is still able to assimilate the majority of the OC inputs via oxic pathways. Under acceptable high input levels, species richness may be low, but there remain

large abundances of 1 of 2 active opportunistic species (such as capitellid polychaetes) that are tolerant of high levels of organic deposition (Keeley et al. 2012) and facilitate benthic sediment mixing and maximise bacterial mineralisation. Under these conditions, sediment chemistry may be modified, with small patches of bacterial mats evident but no outgassing observed, and the sediments are not yet azoic (Keeley et al. 2019a). A large biomass of tolerant fauna ensures that the sediments retain a high waste assimilation capacity (Keeley 2013, Handley et al. 2020). Once this maximum assimilative stage is surpassed and organic enrichment inputs exceed the tolerance of the remaining resilient taxa, there will be a reduction in, or even the complete loss of, the infaunal community and their associated bioturbatory sediment oxygenation (Banta et al. 1999); thereafter, organic waste mineralisation rates decrease and organic matter accumulates in the benthos (Keeley & Taylor 2011).

Determining the potential maximum assimilative capacity of a farm, prescribed by both the characteristics of the farm and the receiving environment, is therefore key to remaining within the required regulatory guidelines. While organic matter input limits will differ by farm, previous investigations into salmon farm organic matter input limits indicate a general transition from aerobic to anaerobic at inputs greater than approximately $2.5 \text{ g OC m}^{-2} \text{ d}^{-1}$ (Hargrave et al. 2008, Hargrave 2010), with persistent anoxia and detrimental benthic effects occurring when inputs exceed $10 \text{ g OC m}^{-2} \text{ d}^{-1}$ (Hall et al. 1990, Hargrave et al. 2008); however, these indicative thresholds do vary. For example, the carbon assimilation capacity of a cold water (8°C) Norwegian deep water fish farm was determined to be $5 \text{ g OC m}^{-2} \text{ d}^{-1}$ (Valdemarsen et al. 2012), and a study on continuous OC loading of benthic sediments showed rapid deterioration of sediments using a loading rate of $4.5 \text{ g OC m}^{-2} \text{ d}^{-1}$ (Valdemarsen et al. 2009). In another study, despite porewater accumulation of sulphides, benthic microbes and macrofauna were capable of metabolising inputs of $3.1 \text{ g OC m}^{-2} \text{ d}^{-1}$ for extended periods of time (Valdemarsen et al. 2009, 2010).

Reducing long-term farm impacts on the benthos requires manipulation of one or more characteristics of the farm and/or the receiving environment; however, many of these changes may decrease the productivity of the farm and therefore its economic profitability. One common method of restricting the benthic impacts of excess organic matter inputs while maintaining stock productivity is to enforce a fallowing period on the fish farm, during which the

farms are destocked and the environment is left to recover. The ability of benthic sediments under and around fish farms to recover during fallowing periods will determine the long-term viability of the particular farm location (Keeley et al. 2015). To maximise farm operations, fallowing periods would ideally be short, with rapid recovery of the benthos to a 'healthy' state: i.e. oxygenated sediment substrate with diverse benthic fauna and no residual solid or porewater sulphides or other detrimental substances (e.g. heavy metals). However, short fallowing periods may not be sufficient to restore benthic sediments to their previous healthy state under some conditions (Macleod et al. 2006). For example, sediment recovery from a heavily impacted methanogenic state can be slow—necessitating long fallowing periods between cohorts (Carroll et al. 2003) and limiting the long-term production potential of a farm (Keeley et al. 2017). This may lead to restocking of farms that have not returned to a baseline assimilative capacity. If benthic sediments are not given the time required to return to a healthy state, they may be unable to assimilate the inputs from each successive growing season without future issues. These recovery processes are highly environment- and situation-specific (Macleod et al. 2007, Borja et al. 2010) and can range from months to years. In more impacted sediments, some studies observed partial recovery within 3–6 mo of fallowing (Brooks et al. 2003, Macleod et al. 2004, Keeley et al. 2019b), although full recovery (return to background conditions pre-farming) can take many years (Hopkins et al. 2004, Keeley & Taylor 2011, Keeley et al. 2014). Sufficient recovery to prevent a rapid return to unfavourable benthic conditions that breach regulations is unlikely during short fallowing periods.

To quantify the assimilative capacity of benthic ecosystems and determine the geochemical effects of excess loading of fish farm inputs with subsequent fallowing, in this study, we used a mesocosm system to simulate sustained organic matter inputs to the benthos. We provided particulate organic matter inputs analogous to a low-input (close to the assimilation capacity of the sediments) and a high-input fish farm to quantify the diagenetic changes and assimilation capacity of soft sediments subjected to continuous loading. Following this, we monitored the post-input recovery of the sediments after cessation of a period of prolonged increased organic input. We quantified benthic OC mineralisation processes, with a focus on benthic oxygen, nitrogen, and sulphide fluxes as well as the redox state throughout the input and recovery period.

2. MATERIALS AND METHODS

To simulate the effect of finfish farms on benthic habitats through input and following recovery periods, a mesocosm experiment was conducted for 2 yr between 21 September 2015 and 27 October 2017. Three treatments ($n = 3$) were simulated in 9 custom-built annular flume incubation chambers (Fig. 1) by manipulating the level of organic inputs (fish faeces) delivered into the mesocosm system.

Each mesocosm consisted of an environmentally controlled (16°C , 0.5% of ambient light), aerated, flow-through annular flume aquarium (500 mm outer diameter, 350 mm inner diameter, 70 mm channel width, 0.092 m^2 enclosed area; Fig. 1A) filled with sediment to a depth of 180 mm (approximately 27 kg of wet 2 mm sieved intertidal sand from an area with no marine farms in the NE Firth of Thames Tikapa Moana-o-Hauraki, New Zealand: 0.28% carbon; 0.03% nitrogen: dry weight Elementar C/N analyser with catalytic combustion MAM 01-1090 estimated initial carbon store density at 4.2 kg C m^{-2}) and covered with approximately 10 l of overlying seawater. The mesocosms were each seeded with 15–25 g of wet sediment from beneath an operating salmon

farm (Marlborough Sounds) to inoculate the system with representative microbial fauna.

The mesocosms were maintained as flow-through systems (Fig. 1A). Recirculation for each flow-through mesocosm was provided by seawater from a dark, aerated, 2000 l temperature-controlled (16°C) header tank that was gravity-fed with controlled flow to each chamber. Outflow water from the chambers was UV-treated, collected in a 50 l aquarium sump with a protein skimmer, and returned to the header tank for recirculation. Approximately 20% of the header tank's water was replaced each week. The flow-through rate was $150\text{--}200\text{ ml min}^{-1}$, providing a full turnover of the water inside the mesocosm approximately every 45 min. A motorised paddle wheel within each annular flume was used to generate a unidirectional flow of $5\text{--}6\text{ cm s}^{-1}$. This current speed was below the surface sediment resuspension threshold.

Each mesocosm was randomly allocated to 1 of 3 treatments: a 'reference' input treatment of $0.15\text{ g OC m}^{-2}\text{ d}^{-1}$, a moderate input treatment of $2.5\text{ g OC m}^{-2}\text{ d}^{-1}$, and a high organic matter input treatment of $12\text{ g OC m}^{-2}\text{ d}^{-1}$. These treatments were based on particulate organic carbon (POC) benthic deposi-

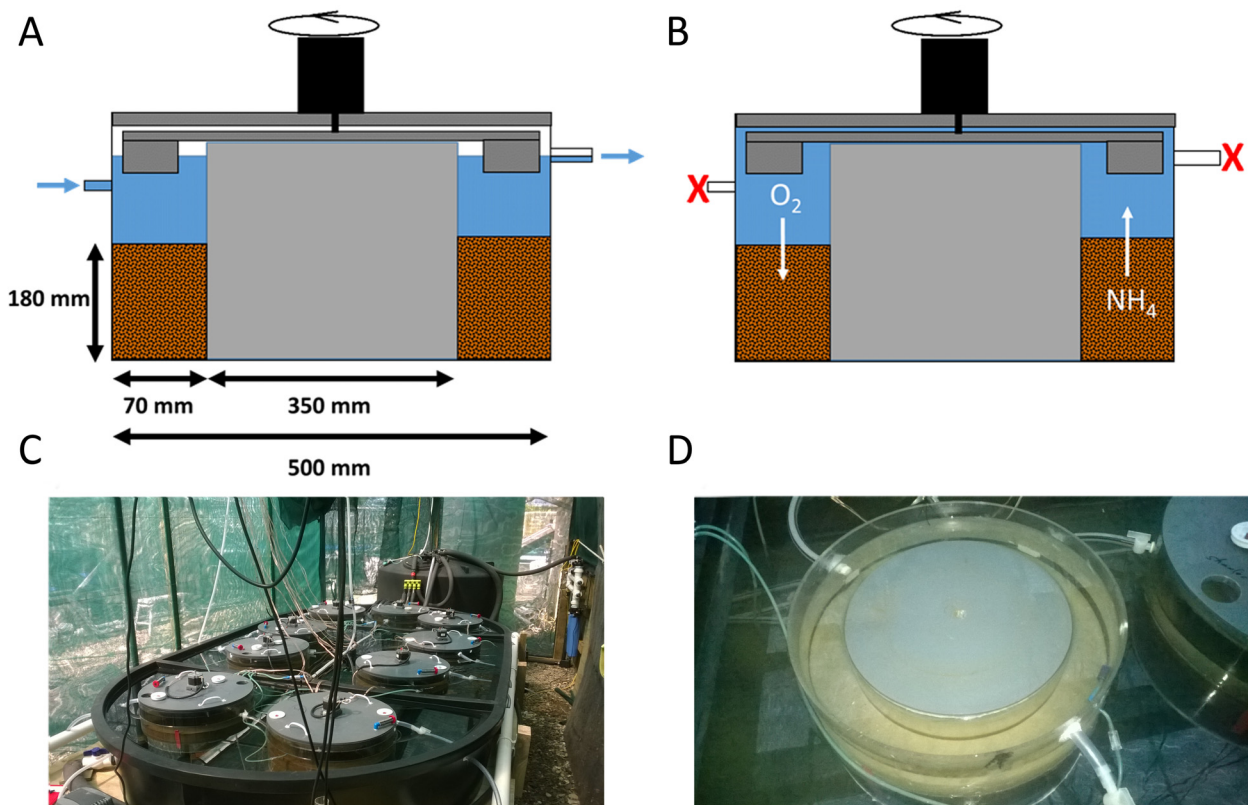


Fig. 1. Schematic of the annular-flume aquaria under (A) long-term experimental and (B) flux-study conditions; (C) the 9 replicate experimental aquaria, and (D) a close-up of an aquarium containing the inoculated sediment showing the seawater ports

tional rates from a typical New Zealand salmon farm —with deposition of 1–5 kg C m⁻² yr⁻¹ estimated under the farm or at the cage edges and decreasing deposition with distance from the cage edge (Sanford Ltd. 2017, James et al. 2018). To simulate the faecal material that would deposit on the seabed, the fish faeces were repeatedly washed via resuspension and centrifugation until the overlying water was relatively free of coloured dissolved organic material.

The input phase ran for 6 mo, from 21 September 2015 (experimental Day 1) to 4 April 2016 (Day 196), during which processed kingfish faeces (provided by NIWA Northland Marine Research Centre and stored frozen until required) in suspension were added to each mesocosm every 2 d. The kingfish faeces were presumed analogous to pen-production salmon faeces, as they are fed a similar diet (Moran et al. 2009) with comparable physical and biogeochemical properties. Due to the length of the experiment, 2 different batches of kingfish waste were used: Batch 1 (dry weight Elemental C/N analyser: 44.1% C, 7.5% N, 2.2% phosphorous) was added from 21 September 2015 to 28 February 2016 (Day 160); Batch 2 (dry weight: 35.2% C, 7.8% N, no data for phosphorus) was added from 1 March 2016 to 4 April 2016 (inclusive). The change in waste batch did not affect the OC input rate; however, the labile content of the batches may have differed. Note that during the period from 21–30 September 2015, the reference treatment was given an OC input of 0.3 g m⁻² d⁻¹ before being reduced to 0.15 g m⁻² d⁻¹ to better reflect the reference site. This 6 mo input period was then followed by a 20 mo fallow period during which no additional fish waste or organic matter was added to any of the mesocosms.

To determine the effect of continuous loading of fish faeces and following recovery on sedimentary processes, periodic flux studies were carried out within each mesocosm throughout the input period (21 September 2015 to 4 April 2016; first flux study on 2 October 2015: Day 11) and subsequent fallow period approximately every 2 wk until 28 June 2016. Following this date, a further 4 flux studies were carried out until 27 October 2017. For each flux study, the aquaria were switched to a no-flow-through and no-aeration configuration (Fig. 1B) so that sediment oxygen demand (SOD) could easily be measured (Orion Star dissolved oxygen optode; Thermo Fisher Scientific). The paddle wheels maintained unidirectional overlying seawater circulation of 5–6 cm s⁻¹ during flux-study incubations to prevent the creation and measurement of a stationary boundary layer.

The duration of individual flux studies ranged from 40 min to 9 h (depending upon SOD). Overlying seawater column measurements of conductivity, temperature, and pH (Orion Star A220 Series; Thermo Fisher Scientific) were made and samples (0.45 µm filtered) were taken by siphon before and after each flux study and analysed to determine dissolved inorganic carbon (DIC; Thermo Delta Plus Advantage, Gasbench II via a GC PAL autosampler; Dickson et al. 2007), dissolved inorganic nitrogen (NH₄-N and NO_x-N; Astoria simultaneous auto-analysis), dissolved reactive phosphorus (DRP; Astoria simultaneous auto-analysis), and sulphide (S²⁻; APHA 4500-S2-I 22nd ed. 2012, simple acid distillation) concentrations. DIC measurements were taken for the first 3 mo (n = 3) of the fallow period until 15 June 2016. Fluxes were calculated using Eq. (1), where [S] is the solute concentration, V is the overlying seawater volume in the aquarium, A is the surface area of the sediment enclosed (assuming a flat surface), and T is the time at which SOD measurements or nutrient samples were taken.

$$\text{Flux} = \frac{([S]_{\text{final}} - [S]_{\text{initial}}) \times V}{A \times (T_{\text{final}} - T_{\text{initial}})} \quad (1)$$

SOD and DIC production rates were converted to carbon mineralisation (g OC m⁻² d⁻¹). To partition the amount of OC remineralised via different pathways and compare observed fluxes of DIC to those of SOD and SO₄²⁻ reduction, we used the stoichiometry of the oxidation of organic matter by SO₄²⁻, where 2 moles of OC are consumed for 1 mole of SO₄²⁻ respired (Naik et al. 2017).

Sediment redox measurements were made on a random sample of mesocosms (n = 5, 1 reference, 2 medium input, 2 high input) every 2–4 wk. Normally, 2 redox measurements were taken within each chosen replicate chamber and averaged. To take a sediment redox measurement, the reference electrode (Radiometer REF201) was suspended in the bulk water of the mesocosm and the platinum plate electrode (Radiometer M241Pt) inserted into the sediment to a depth of 20 mm (Tantra et al. 2012). Qualitative observations were made on white mat-forming bacterial growth from the beginning of the input period to 8 mo into the following period (30 September 2015 to 11 November 2016).

Surface sediment samples were taken before commencement and at the termination of the incubation to determine organic matter (determined by loss on ignition: sample dried at 103°C then furnace at 400°C) and sediment carbon and nitrogen content (dry weight; Elemental C/N analyser).

All treatment measurements quoted in Section 3 are provided as mean \pm SD of the 3 replicate treatments ($n = 3$) unless otherwise stated.

Our flux measurements allow the weight-specific organic matter decay rates within each mesocosm to be estimated. Whether degraded by free-living microbes or within the guts of metazoa, OC mass is ultimately converted into one of 3 forms: DIC, dissolved organic carbon (DOC), or new living biomass. We had no formal observations of the quantities of living microbial biomass, but we used estimates of the rates of production of DIC and DOC to derive lower-bound estimates of faecal degradation rates. Assuming (1) first-order degradation kinetics, (2) a constant fraction (ϵ , dimensionless) of the decaying material is lost as solute efflux (rather than becoming incorporated into microbial biomass), and (3) no further generation/inputs of additional degradable organic matter to the sediments during the following period, we can calculate the anticipated instantaneous solute carbon (i.e. DIC + DOC) efflux rate ($E(t)$, $\text{g C m}^{-2} \text{d}^{-1}$) using Eq. (2), in which B_0 denotes the initial density of degradable OC (g C m^{-2}) at the start of the following period and t denotes time (d) since the start of the following period:

$$E(t) = \epsilon \cdot k \cdot B_0 \cdot e^{-k \cdot t} \quad (2)$$

At this point, we note that there is no requirement that B_0 must represent only faecal POC. Indeed, the fact that the mesocosms contained some organic matter at the very outset of the experiment implies that B_0 is unlikely to have been entirely composed of fish faeces or particulates deriving from fish faeces. We also acknowledge that assumption (3) is dubious because the mesocosms continued to receive a supply of natural seawater during the following period (and this seawater would have contained at least some metabolizable OC). Nonetheless, Eq. (2) can be transformed to yield Eq. (3):

$$\ln(E(t)) = \ln(\epsilon \cdot k) + \ln(B_0) - k \cdot t \quad (3)$$

Thus, the slope of a regression of ($E(t)$) against time yields an estimate of the specific decay rate (k) for OC in the mesocosm sediments. During the experimental flux studies, we found that the flux of DIC was always from the sediment into the water, but the DOC fluxes were observed both into and out of the sediment. Rather than calculating a specific net decay rate (OC to DIC+DOC), we calculated specific mineralization rates (OC to DIC).

3. RESULTS

3.1. Sediment characteristics

We estimated that each mesocosm initially contained a few 10s of g of POC, given typical sandy sediment porosity of 0.4 g m^{-3} , and that the mesocosms were seeded with approx. 27 kg wet weight of natural sediment with an initial carbon:dry weight (DW) ratio of around $0.0028 \text{ g C g}^{-1} \text{ DW}$ at the outset of the incubations.

After the 6 mo input period and 19 mo following, there was an increase in the carbon and nitrogen content of the sediment surface. Carbon content of the surficial sediment increased from 0.28 to 3.7% in the reference treatment, to 8.2% in the moderate-input treatment, and to 10.3% in the high-input treatment. Sediment percentage nitrogen content increased from 0.03 to 0.28% in the reference treatment, to 1.12% in the moderate-input treatment, and to 1.63% in the high-input treatment. Surficial sediment organic matter content after the experiment was 7.5% in the reference treatment, 16.4% in the moderate-input treatment, and 18.3% in the high-input treatment.

No white mat-forming bacterial growth was observed during the pre-input phase. After inputs commenced, there were visual differences observed in the sediment surface between the 3 treatments. The reference input replicates did not develop any white mat-forming bacterial growth throughout the duration of the experiment. The moderate- and high-input replicates developed white bacterial mats early in the experiment (Day 11 and Day 6, respectively; Fig. 2). Bacterial mats caused a brown discolouration covering the majority of the sediment surface with intermittent development and recession of white-coloured patches in the moderate-input treatment throughout the experiment. In the high-input treatment, a thick layer of white material covering the majority (or all) of the sediment surface was observed by the end of the input period. A colour change to black was observed in the sediment underneath the bacterial mats in both the moderate- and high-input treatments. During the following period, white bacterial mats persisted in the moderate- and high-input treatments. In the moderate-input treatment, the sediment returned to its original colour within a few months, and in the high-input treatment, the thick white bacterial mats receded to small patches while the sediment surface remained dark brown.



Fig. 2. Difference in sediment appearance of the (A) reference treatment, showing no white mat-forming bacterial growth, (B) moderate treatment, showing sparse white mat-forming bacterial growth, and (C) high treatment, showing dense white mat-forming bacterial growth, after 12 d of organic matter inputs

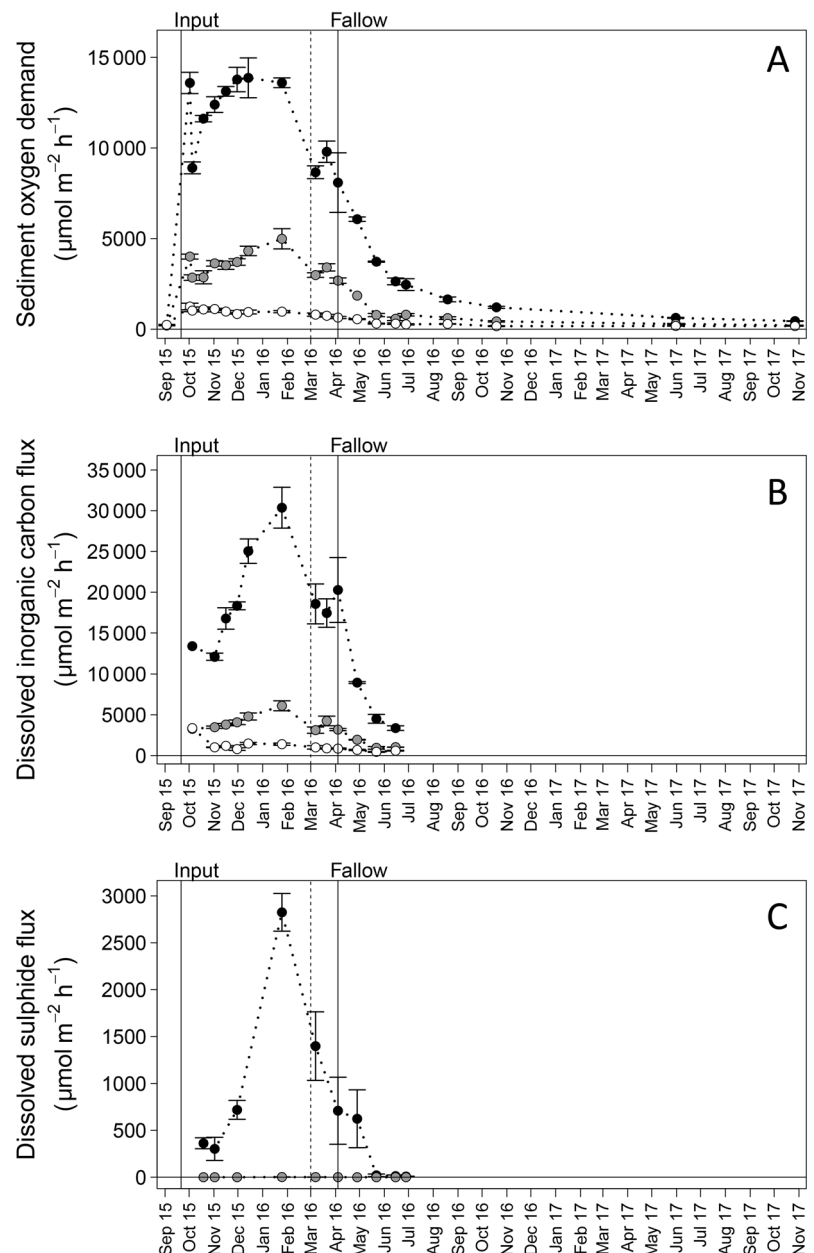
3.2. Fluxes of SOD, DIC, and sulphide

The mean ($n = 8$, all treatments, one flux-study failure) SOD in the chambers before the first addition of organic matter (on 3 September 2015) was $216 \pm 33 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$, with a calculated carbon mineralisation rate of $0.06 \pm 0.01 \text{ g OC m}^{-2} \text{ d}^{-1}$.

Following the commencement of inputs, SOD in all the treatments increased (Fig. 3A, Table S1 in the Supplement at www.int-res.com/articles/suppl/q015p115_supp.xlsx). In all 3 input treatments (reference, medium, and high), during the first flux study (on Day 11, 2 Oct 2015), SOD was higher than that of the following flux studies, showing an initial large increase in SOD in response to the increased organic matter inputs. In the following flux study (on Day 14, 5 Oct 2015), SOD had decreased in all treatments but was still elevated above that measured before organic matter inputs commenced. In the reference treatment, SOD then decreased throughout the input and following periods, return-

Fig. 3. Changes in measured (A) sediment oxygen demand, (B) dissolved organic carbon flux, and (C) dissolved sulphide flux before organic matter input, during the input period, and during the following period in the reference (white), moderate (grey), and high (black) input mesocosm treatments. Dashed vertical line: when the source of treatment inputs changed (see Section 2).

Data are mean \pm SD



ing to pre-input levels after 6.5 mo of fallowing (Fig. 3A, Table S1). In the moderate- and high-input treatments, the initial increase on Day 11 and immediate decrease in SOD was then followed by a gradual increase in SOD, with a second peak in SOD flux approximately 3 (high-input treatment) to 4 (moderate-input treatment) mo after organic matter inputs commenced. The secondary (slightly smaller) peak in SOD measurements was observed in the flux studies just after the change in fish faeces input composition (Day 162, 1 March 2016; Fig. 3A). Following this point, SOD in the moderate- and high-input treatments decreased. After fish faeces inputs ceased during the fallowing period, SOD rates in the moderate- and high-input treatments fell. In the medium-input treatment, SOD rates returned to pre-input levels after 18 mo, whereas in the high-input treatment, SOD rates were not observed to return to pre-input levels during the monitored fallowing period (18 mo).

Similar patterns were reflected in the flux-study DIC measurements. In the reference treatment, the largest DIC flux was measured during the first flux study (on Day 14; Fig. 3B, Table S2), after which measured DIC flux decreased throughout the input and fallowing periods. In the moderate- and high-input treatments, DIC fluxes rose until they peaked on Day 126 (25 Jan 2016, Fig. 3B). Following this point, flux-study DIC measurements decreased during the remainder of the measured input and the fallow periods. During the fallow period, DIC measurements were taken for the first 3 mo. Following this period, due to the absence of reduced species (e.g. sulphide), SOD was assumed to be a representative proxy for carbon mineralisation. This supposition was supported by the convergence of DIC and SOD calculated carbon mineralisation measured during the flux studies being consistent with the cessation of marked effluxes of $\text{NH}_4\text{-N}$ and sulphide (see Figs. 3 & 5).

No sulphide flux was detected during the reference treatment flux studies throughout the input or fallowing period (Fig. 3C, Table S3). Small sulphide effluxes ($<2 \mu\text{mol m}^{-2} \text{h}^{-1}$) were detected during the moderate-input treatment flux studies after 4 mo of inputs (on Day 126) until the fallowing period. No sulphide effluxes were detected during the fallowing period in the moderate treatment. In the high-input treatment, sulphide efflux was detected from the first sulphide flux-study measurement (on Day 28, 19 Oct 2015). As with the measured SOD and DIC

fluxes, sulphide fluxes in the high-input treatment increased during the input period, peaking on Day 126 and falling once fish faeces inputs changed (Fig. 3C). High-input treatment flux-study sulphide effluxes continued to fall during the fallowing period, returning to baseline levels (no sulphide flux) after 3 mo.

3.3. Fluxes of DOC

During the input period, DOC fluxes in the reference treatment were small compared to the other input treatments and fluctuated around 0 (range: -542.99 to $841.50 \mu\text{mol m}^{-2} \text{h}^{-1}$). In the moderate- and high-input treatments, the sediment was a source of DOC during the input period (Fig. 4, Table S4). During the fallow period, DOC fluxes in the moderate- and high-input treatments decreased and were similar to those of the input treatment, again fluctuating around 0 (range of all treatments: -2017.52 to $2544.19 \mu\text{mol m}^{-2} \text{h}^{-1}$), except during the flux study carried out on Day 333 (19 August 2016), during which the sediments were a sink for DOC (Fig. 4, Table S4).

3.4. Fluxes of nutrients: $\text{NH}_4\text{-N}$, $\text{NO}_x\text{-N}$, and DRP

Reference sediments were a small net sink for $\text{NH}_4\text{-N}$ during the flux studies throughout the experiment (Fig. 5A, Table S5) and a small net source of $\text{NO}_x\text{-N}$ (Fig. 5B, Table S5). In both the moderate- and high-input treatments, sediments were a source of $\text{NH}_4\text{-N}$ and a sink of $\text{NO}_x\text{-N}$ during the flux studies in the input period. As with the other variables, there was an initial peak in $\text{NH}_4\text{-N}$ efflux during an early flux-study experiment (conducted on Day 28, 19 Oct 2015) in both the moderate- and high-input treatments. In the moderate- and high-input treatments, $\text{NH}_4\text{-N}$ ef-

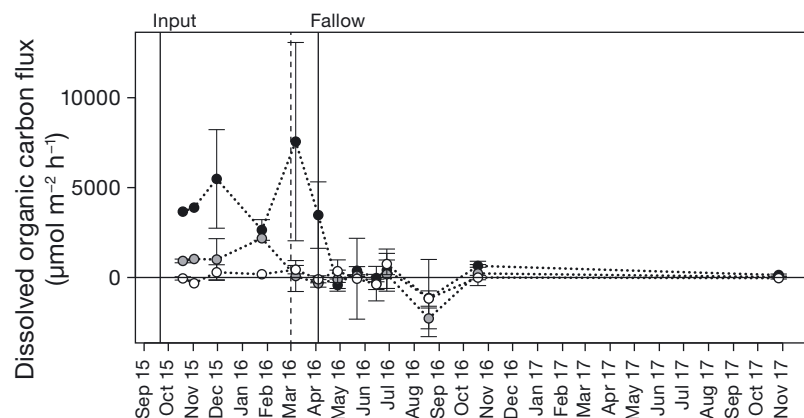


Fig. 4. As in Fig. 3, but for changes in measured dissolved organic carbon

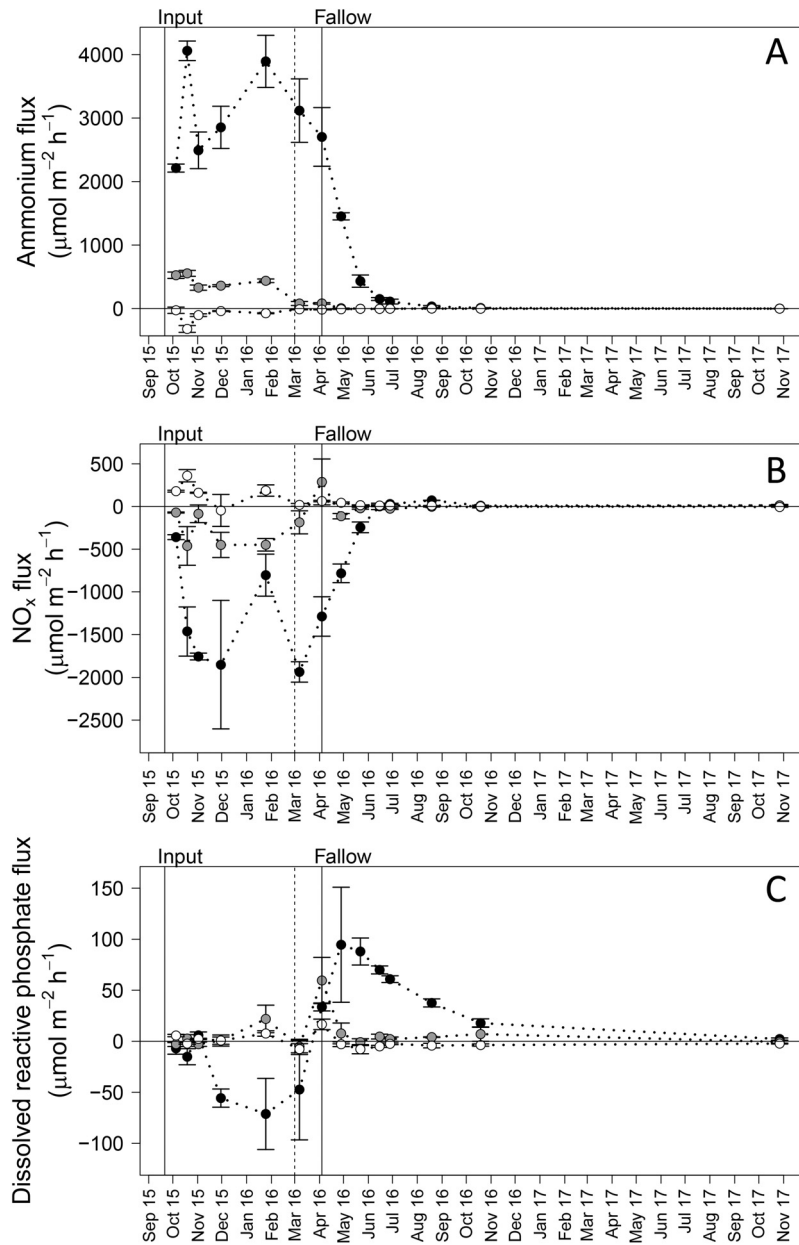


Fig. 5. As in Fig. 3, but for changes in measured (A) ammonium flux, (B) NO_x flux, and (C) dissolved reactive phosphorous flux

fluxes had a second, smaller peak after 126 d of inputs of the first fish faeces batch. After the input of the second fish faeces batch began, $\text{NH}_4\text{-N}$ effluxes fell and continued to decrease during the following period, reaching reference levels in the moderate treatment after 1.5 mo of following and after 18 mo in the high-input treatment. During the fallow period, $\text{NO}_x\text{-N}$ sediment influxes decreased and returned to reference levels immediately in the moderate-input treatment and after 2.5 mo in the high-input treatment.

Sediments were neither a consistent source nor sink of DRP in the reference and moderate treatments (Fig. 5C, Table S5). In the high-input treatment, flux studies measured a net flux of DRP into the sediments during the input phase. The measured DRP sediment influx peaked on Day 126 (the last measurement before the fish faeces inputs changed). There was a net efflux of DRP from the sediments during the following phase, peaking during the first flux study after inputs ceased (Day 220, 28 Apr 2016, 22 d after inputs ceased) and decreasing over the following period, returning to reference levels after 18 mo following.

3.5. Sediment redox state

Sediment redox potential remained positive during the whole period of the experiment in the reference treatment. Following 56 d of inputs (on 16 Nov 2015), sediment redox decreased; however, once organic matter inputs ceased, sediment redox returned to pre-input levels (Fig. 6, Table S6). In the moderate treatment, organic matter inputs caused a decrease in the sediment redox potential compared to that of the reference treatment. Sediment redox continued to decrease during the input phase, becoming negative after 56 d. After inputs ceased, sediment redox increased again and continued rising through the following period observed (until 20 d after inputs ceased); however, it did not return to levels similar to those observed in the reference treatment. In the high-input treatment, sediment redox was negative throughout the whole input period. After organic matter inputs ceased, sediment redox rose but did not return to positive values even by the end of the observed following period (220 d of following).

3.6. Carbon loading and mineralisation summary

During the input period, we estimated that 31.2, 492.5, and 2364 g m^{-2} of POC were added to the ref-

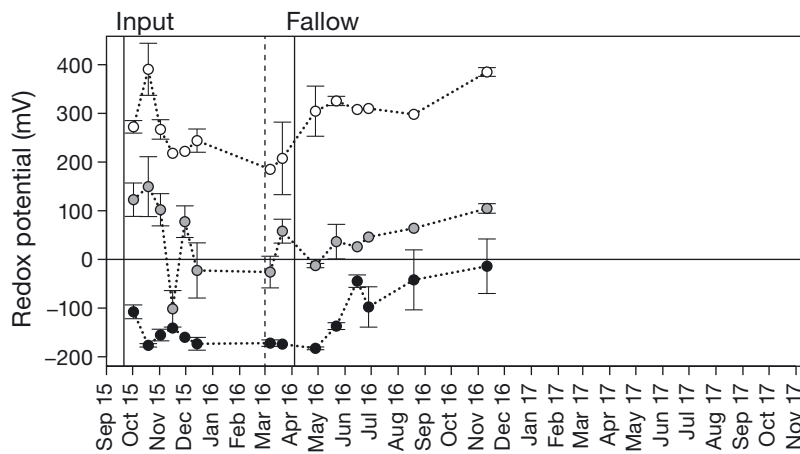


Fig. 6. As in Fig. 3, but for changes in measured sediment redox potential

erence, moderate-, and high-input treatments, respectively. From mean SOD and DIC fluxes, by the end of the input period, we estimated that 64.0, 236.0, and 1118.3 g m⁻² of that carbon was mineralised and a further 41.0, 90.5, and 319.0 g m⁻² was mineralised during the observed following period in the reference, moderate-, and high-input treatments, respectively (Fig. 7).

We observed hysteresis in sediment loading and unloading carbon metabolism rates. For example, in the high-input treatment, the mean SOD initially increased at a rate of $19 \pm 1.5 \mu\text{mol m}^{-2} \text{d}^{-2}$ ($n = 3$) and mean DIC fluxes increased at a rate of $13 \pm 6.5 \mu\text{mol m}^{-2} \text{d}^{-2}$ ($n = 3$). Upon following, the mean SOD rates decreased at a rate of $-3.9 \mu\text{mol m}^{-2} \text{d}^{-2}$ ($n = 1$) and mean DIC fluxes decreased at a rate of $-7.7 \pm 1.9 \mu\text{mol m}^{-2} \text{d}^{-2}$ ($n = 3$) (Fig. 6). Note that we believe the discrepancy between the calculated net loss of benthic carbon from the reference treatment sedi-

ments with an observed accumulation of carbon in the sediment is due to the pool of carbon provided in the initial sediments (estimated 4.2 kg C m⁻²) and additional carbon introduced in the overlying seawater, which was mixed between all mesocosms via a shared 2000 l header tank. This is an unfortunate limitation in the design of this experiment.

For the reference treatments, the mesocosm-specific mineralization rate of the OC in the sediments (as inferred from the time-course of DIC efflux) ranged between 0.003 and 0.009 g C d⁻¹ (though none of these coefficients proved significantly different from zero at the 95% confidence level). For the intermediate-dosage chambers, the range was 0.015–0.019 g C d⁻¹, but only the intermediate value (0.015 g C d⁻¹) proved to be significantly different from zero at the 95% confidence level. Across the high dosage chambers, the range was 0.022–0.029 g C d⁻¹, and all estimates proved to be significantly different from zero at the 95% level.

3.7. Partitioning mineralisation

In the reference treatments, carbon efflux rates inferred from SOD were closely correlated with the measured DIC effluxes (Fig. 7). This indicates that the majority of the carbon was remineralised via oxic pathways and/or any reduced electron acceptors produced were quickly reoxidised at the sediment surface (Valdemarsen et al. 2009). Similarly, in the moderate- and high-input treatments during the early input phase, before the impacts of sediment organic matter addition become apparent, SOD-estimated remineralisation was consistent with that inferred from measured DIC fluxes (Fig. 7). In the moderate-input treatment, SOD-estimated remineralisation and observed DIC fluxes diverged after approximately 3 mo of inputs. In the high-input, these estimates diverged after just 1 mo of inputs (Fig. 7). In these strongly reducing conditions (i.e. where SO₄²⁻ reduction is occurring), the amount of dissolved oxygen consumed underestimates carbon mineralisation. The ob-

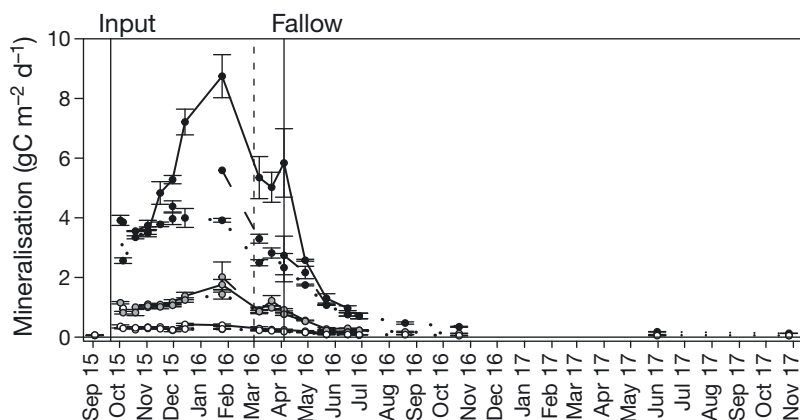


Fig. 7. As in Fig. 3, but for changes in carbon mineralisation estimated using sediment oxygen demand (dotted line), sediment oxygen demand + dissolved sulphide flux (dashed line), and dissolved inorganic carbon flux (solid line)

served difference between the summed estimated SOD and sulphide mineralisation pathways and that estimated by DIC fluxes indicates that reduction of non-sulphur species was also serving as a pathway for anoxic remineralisation under the large organic matter loading (Fig. 7).

4. DISCUSSION

The data show that using SOD as a proxy for diagenesis under high organic loading conditions can underestimate total carbon mineralisation. For example, at peak mineralisation rates under the high loading treatment, the estimated SOD rate was 2-fold lower than that implied by a naïve interpretation of the measured DIC fluxes. Oxygen represents the most favourable and abundant electron acceptor available; however, within enriched benthic sediments in a low-oxygen environment, this oxidant may only penetrate millimetres beneath the sediment surface and will soon be depleted. Below this level, the degradation of organic matter inputs is therefore mainly mediated anaerobically by microbes using nitrate, manganese, and iron oxides or SO_4^{2-} as electron acceptors (Canfield et al. 1993, Glud 2008). However, over the longer term, the initial pools of even these alternative electron acceptors will become exhausted (fully reduced), and continued mineralisation becomes dependent upon the resupply of oxygen and/or fresh sources of alternative electron acceptors. Typically, this resupply arises through diffusive processes augmented by macrofauna-mediated bioturbation (Banta et al. 1999, Valdemarsen et al. 2009).

4.1. Impact of organic enrichment on benthic condition

The sediments under fish farms experience a high amount of organic loading, leading to anoxia and changes in benthic geochemical cycling, adversely impacting the benthos and overlying water column and the health of nearby ecosystems (Brooks & Mahnken 2003). Our moderate-input treatment used a loading rate of $2.5 \text{ OC m}^{-2} \text{ d}^{-1}$, which has been proposed as an upper limit for the assimilative capacity of sediment (Black et al. 2008, Keeley et al. 2013). In this treatment, we observed small $\text{NH}_4\text{-N}$ fluxes from the sediment but no meaningful or persistent sediment sulphide efflux. While benthic OC increased during the input period, the sediments did not ex-

hibit the geochemical symptoms of sediments that have exceeded their assimilative capacity. The moderate-input treatment is probably close to the sustainable level of inputs under the flow and temperature conditions of the input period (Hargrave 2010, Holmer 2010), as the sediments did not exhibit the geochemical symptoms of sediments that have exceeded their assimilative capacity or malfunctioned. Many of the geochemical indicators return to reference rapidly following cessation of inputs. This is in the absence of any bioturbating macrofauna with benthic mineralisation rates driven by diffusive and microbial processes. It is likely that benthic mineralisation rates would be higher in the presence of an active bioturbating infaunal community (Welsh 2003). The observations made in the treatments with moderate organic matter input levels ($2.5 \text{ g OC m}^{-2} \text{ d}^{-1}$) support the assumption that this is the approximate threshold beyond which changes within the benthic community (of soft sediments) begin to manifest themselves (Black et al. 2008, Keeley et al. 2013).

In the high-input treatment, the sediments and associated microbial community have the capacity to utilise up to $8.7 \pm 1.2 \text{ g C m}^{-2} \text{ d}^{-1}$ (maximum rate: $10.2 \text{ g C m}^{-2} \text{ d}^{-1}$; Fig. 6). This peak rate was measured shortly before the original batch of fish waste became exhausted and a second batch was brought into play. Unfortunately, therefore, we can not determine whether the subsequent decline in mineralisation was driven by (1) a gradual exhaustion of sediment sulphate (and other electron acceptors) and/or accrual of toxic metabolites in the porewaters or (2) a change in the lability of the incoming organic matter. As SO_4^{2-} depletes, there is the potential for toxic metabolites to accumulate in sediment porewater, which eventually hampers further microbial mineralisation. In previous studies, this has led to methanogenesis and decreased mineralisation rates (Valdemarsen et al. 2012).

Large carbon mineralisation rates (DIC fluxes up to $25 \text{ mmol m}^{-2} \text{ h}^{-1}$, SOD up to $15 \text{ mmol m}^{-2} \text{ h}^{-1}$) indicate benthic over-enrichment and eutrophication. High DIC fluxes relative to SOD indicate the prevalence of anaerobic pathways during the peak production periods, facilitated by bacteria mediating SO_4^{2-} reduction (Hargrave et al. 2008, Valdemarsen et al. 2009). This is supported by the measurement of large sediment effluxes of sulphide ($>2.5 \text{ mmol m}^{-2} \text{ h}^{-1}$), showing SO_4^{2-} reduction is occurring in the sediment, with accumulation of reduced species in the sediment porewater. These anaerobic pathways account for a large proportion of organic matter miner-

alisation in coastal sediments (Jørgensen 1982, Valdemarsen et al. 2010), and measurement of sulphide in sediment porewater or overlying benthic seawater is an indicator of biological response to organic enrichment from aquaculture or unfavourable anoxic conditions (Brooks & Mahnken 2003, Hargrave et al. 2008, Valdemarsen et al. 2010, Keeley et al. 2013). When carbon mineralisation is anaerobically microbially driven, oxygen levels are too depleted for the persistence of macrofaunal organisms in natural benthic environments. Further, accumulated sulphide in sediment porewater is toxic to benthic organisms (Pearson & Rosenberg 1978, Bagarinao 1992), with decreased benthic macrofaunal (Banta et al. 1999) and microbial (Valdemarsen et al. 2012) activity reducing the benthic environment's capacity for organic matter degradation.

Coupled large $\text{NH}_4\text{-N}$ effluxes ($>3 \text{ mmol m}^{-2} \text{ h}^{-1}$) and $\text{NO}_x\text{-N}$ fluxes into the sediment ($>1.5 \text{ mmol m}^{-2} \text{ h}^{-1}$) indicate a decrease in sedimentary $\text{NO}_x\text{-N}$, caused by nitrate reduction and ammonification, with anaerobic denitrification utilising nitrate derived from the overlying water. These geochemical variable values are of a similar magnitude to those measured under a deep water (190 m) fish farm in Norway (Valdemarsen et al. 2012)—where farm-derived organic matter inputs of approximately $4.9 \text{ g C m}^{-2} \text{ d}^{-1}$ led to DIC fluxes of approximately $7.5 \text{ mmol m}^{-2} \text{ h}^{-1}$, SOD of $8.1 \text{ mmol m}^{-2} \text{ d}^{-1}$, and $\text{NH}_4\text{-N}$ effluxes of $0.7 \text{ mmol m}^{-2} \text{ d}^{-1}$ —and measurements under a high-capacity salmon farm (31–40 m water depth), where similar fluxes were observed following organic matter inputs during the post-fallow period and at distances $>600 \text{ m}$ from the farm (Keeley et al. 2019b). While the effects we observed are significant compared to the inputs ($28 \text{ g C m}^{-2} \text{ d}^{-1}$) and impacts (e.g. SOD $140 \text{ mmol m}^{-2} \text{ d}^{-1}$) measured under the high-capacity salmon farm, our high-input treatment ($12 \text{ g C m}^{-2} \text{ d}^{-1}$) and the associated impacts are relatively low (Keeley et al. 2019b). Without assessing the effects on benthic macrofauna, it is difficult to assess the relative condition of our experimental treatments versus *in situ* observations (e.g. the enrichment stages of Keeley 2013); however, the decreased benthic redox values and bacterial mat growth suggest very high to excessive enrichment.

4.2. Impact of fallowing on benthic condition

The degradation in seabed condition as a result of excess organic matter inputs from overlying fish farms can lead to a breach of environmental stan-

dards and adverse economic consequences for aquaculture farms, requiring production limitation, fallow periods, or even farm removal (Carroll et al. 2003, Keeley et al. 2017). Fallowing is a strategy that temporarily removes organic inputs through deactivation of the farm to facilitate recovery and can increase long-term farm productivity and sustainability (Keeley et al. 2015).

We found that after cessation of organic matter inputs and commencement of fallowing, changes in SOD in the medium- and high-input treatments indicated that recovery processes may proceed at a slower rate than initial rates of impact. This suggests hysteresis in the system, and as initial microbial responses to organic matter inputs increase benthic assimilation capacity, these large mineralisation rates are not sustained as the carbon pool is depleted and microbial assimilative capacity decreases. When required (i.e. when assimilative capacity and acceptable benthic conditions have been exceeded), fallowing may need to be implemented for longer than the farm has been active to enable all benthic geochemical species to return to acceptable levels such that reactivation of the farm would not cause rapid degeneration of the benthic state. This has economic repercussions for finfish farms that regularly exceed acceptable benthic conditions and require fallowing.

The geochemical recovery processes we observed (in the absence of macrofauna) can be characterised by a series of key observed changes over the short (0–6 mo), medium (6–12 mo), and long term (12 mo onwards). We showed that significant geochemical remediation can take place in the short term following the cessation of inputs. Nitrogenous species fluxes ($\text{NH}_4\text{-N}$, $\text{NO}_x\text{-N}$) returned to reference input levels within approximately 2 mo in the moderate-input treatment and 6 mo in the high-input treatment.

The absence of large sulphide fluxes in the reference and moderate treatments indicates no marked accumulation of reduced elemental species in the sediments as a result of the organic matter inputs. In the high-input treatment, sediment sulphide fluxes decreased rapidly following cessation of inputs and returned to reference levels (i.e. no sulphide flux), indicating a decrease in sulphide generation. Some sedimentary variables did not return to pre-input levels within the observed recovery period. In particular, SOD and the DRP efflux all remained elevated and sediment redox remained suppressed, even after 18 mo of fallowing. These observations could indicate re-oxidation of sulphidic and other electron acceptors at the sediment surface before release into the overlying water with partial chemical recovery of

the sediments, or that the pool of SO_4^{2-} in the sediment has become depleted, such that there is no more SO_4^{2-} to generate sulphide from.

Larger DRP flux rates in the moderate- and high-input treatments for the duration of the observed fallow period (18 mo) indicated that sub-surface sediments remained depleted of oxygen even at the end of the 18 mo fallow period. The majority of phosphorus provided in commercial fish feed is lost to the environment. Fish retain only ~40% of phosphorus provided in modern commercial fish feeds, with the remainder excreted (Wu 1995, Pearson & Black 2001, Sugiura 2018); therefore, these excess phosphorus inputs, derived from both sinking fish food and faeces, have potentially long-lasting impacts on benthic health under farms and may contribute to eutrophication in adjacent areas with associated excess nitrogen release (Hung et al. 2008, Jiang et al. 2012).

Sustained increased SOD and a long-term decreased sediment redox state indicate the persistence of anoxic metabolites in the sediment. Our chambers lacked any macrofauna (which promote the reintroduction of oxygen into the sediments through bioturbation), and this may have slowed recovery, but those macrofauna would also be scarce or absent in any real-world heavily impacted sediments, and the patterns we observed were similar to those described in the field during fallowing (Brooks et al. 2003, Keeley et al. 2019b).

The implication is that full geochemical recovery is expected to take several years and may be limited by the rates at which macrofauna can re-occupy the sediments (Borja et al. 2010, Keeley et al. 2015) and at which the slowest recovering biogeochemical species return to reference levels. In a cycle within which farms are stocked for a short period (1–2 yr) and then fallowed, if benthic inputs remain within a certain threshold (e.g. that of the moderate input level in this study), then recovery could be possible during a subsequent short (1 yr) fallowing period. If benthic inputs greatly exceed those that can be assimilated during active farm operation and a subsequent extended recovery/fallowing period (e.g. that of the high input level in this study), long-term degradation of the benthic habitat can be expected as benthic impacts accumulate. Farms operated in this way will increasingly require active interventions to prevent deterioration of the benthic habitat and adverse impacts from farming activities.

For farms that are run on a long-term basis without a defined cycle of operation and fallowing, regular monitoring is important to determine farm management responses if benthic habitat quality declines as

a result of sustained organic matter inputs. A better understanding of the processes in the early stages of seafloor recovery provides valuable farm management information and is essential for evaluating and designing long-term fish farm management and fallowing strategies (Brooks et al. 2003, Macleod et al. 2006, Lin & Bailey-Brock 2008, Keeley et al. 2015), particularly where multiple cycles of inputs and fallowing are desired, as there may be cumulative impacts (Macleod et al. 2007, Keeley et al. 2015). Additionally, benthic health monitoring strategies during fallowing that do not consider all biogeochemical aspects of environmental quality may conclude that the benthic receiving environment has recovered following excess inputs where long-term effects still remain.

4.3. Specific degradation rates for fish faeces

Initial consenting processes for fish farms often require an assessment of potential effects at the seabed. Often, models are used to simulate likely spatial patterns of organic matter deposition ($\text{mass m}^{-2} \text{d}^{-1}$), and inferences are then drawn as to the probable magnitudes of benthic faunal change by reference to empirical observations from other farms and mesocosm studies. Since faeces sink rapidly (relative to water depths and specific faecal decay rates), the first-time deposition footprint can be reliably approximated without taking into account faecal decay. Furthermore, in low-energy environments (ones where resuspension is rare), the first-time deposition rate is a reliable indicator of the long-term net deposition rate at all locations. However, now that farmers are seeking to place farms in areas of higher current flows and/or greater wave energy, there is a greater need to consider resuspension and the long-term fate of faeces. Indeed, rather than focussing on deposition rates, it may be more relevant to focus on quantifying the net incremental mass of organic matter sitting in/on the seabed (mass m^{-2}) and/or the associated implied SOD ($\text{g O}_2 \text{m}^{-2} \text{d}^{-1}$) arising from the decay of that incremental mass of organic matter. Regardless of whether the focus is on the incremental density of organic matter at the seabed or incremental SOD, it becomes crucial to establish plausible bounds for faecal mineralisation rates.

Our estimates for the fallow-period-specific mineralization rates of OC to DIC in the mesocosms were highest for those chambers which experienced the highest prior faecal loading rates and lowest in those chambers which experienced the lowest prior load-

ing rates. In the reference and intermediate chambers, the flux of DOC was often into the sediments during the fallowing period. This suggests ongoing microbial growth that was, at least in part, fuelled by OC stemming from the header-tank seawater. Nonetheless, in the high-loading treatment, the sediment was primarily a source of DOC, suggesting that microbial degradation of faecal matter outweighed microbial growth and respiration using seawater-derived DOC. We infer that the assumptions (especially since there was no further generation/input of additional degradable organic matter to the sediments during the fallowing period) that underlie Eqs. (2) and (3) are invalid for the reference and intermediate loading chambers but at least approximately true for the high-loading chambers.

In the high-loading chambers, the inferred (SOD and DIC flux-based) specific mineralisation rates were around $0.02\text{--}0.03\text{ g C m}^{-2}\text{ d}^{-1}$. That value is high in comparison with specific degradation rates for most 'raw' terrestrial vegetation but close to the median specific rate for phytoplankton (Enríquez et al. 1993). Our estimate of the specific mineralization (to CO_2) rate is around half of the specific particulate mass loss rate (to $\text{CO}_2 + \text{DOC} + \text{particulates} < 0.075\text{ }\mu\text{m}$) that Thusty et al. (2000) estimated from mass-loss studies in short-term incubations with fresh fish faeces. It is expected that the specific rate for mineralisation to CO_2 is smaller than an independent estimate of degradation (the sum of fragmentation, dissolution to dissolved organic form, and mineralisation to CO_2). Nonetheless, it also seems probable that faecal matter is composed of a range of materials with differing degrees of lability. Indeed, we found that SOD in the moderate- and high-input treatments decreased after the change in fish faeces batch, possibly indicating that the organic matter in the second faecal batch was less labile. By making only short-term incubations, Thusty et al. (2000) focussed on degradation of the more labile fractions. In contrast, we derived an estimate of the overall specific microbial mineralization rate of the material.

We note that both our study and that of Thusty et al. (2000) excluded detritivorous macrofauna. Keeley et al. (2019b) measured DIC fluxes emanating from cores taken from sediments under/around Norwegian fish farms. They concluded that close to the farms, the macrofaunal and microbial CO_2 production rates (integrated to 5 cm core depth) were of similar magnitudes, even though close to the farm, macrofaunal respiration usually exceeded microbial respiration. Keeley et al.'s (2019b) data imply a specific decay rate of approximately $0.09\text{ g C m}^{-2}\text{ d}^{-1}$.

Regulators and coastal managers require an understanding of natural ecosystem complexity, diversity, and resilience and how this is modified by the cumulative effects of on-site activities of aquaculture (Science Advisory Group 2011, Handley et al. 2020). In New Zealand and elsewhere, the global marine fish-farming industry is actively seeking to expand (New Zealand Government 2019, Naylor et al. 2021, New Zealand Government 2021). This expansion is dependent on the development and maintenance of productive farms in receiving environments that are resilient to substantial benthic inputs of organic matter (Keeley 2013, Keeley et al. 2019b). The regulatory processes that govern the establishment and operation of fish farms differ across jurisdictions, but it is often the case that applications for new fish farms propose progressive expansion of the farm's production capacity (Naylor et al. 2021). Each step-wise expansion is contingent upon the farm having been operating at full (currently permitted) production capacity for a specified minimum period leading up to the expansion decision without having breached the agreed environmental standards. Additionally, evidence may be required to demonstrate that the environment has sufficient residual 'processing capacity' to withstand/accommodate the incremental loading that will accompany any further expansion of farming operations.

Regulations that govern fish farming often require a fallowing period between successive fish crops, but the duration of this period is sometimes chosen with a view to breaking host–pathogen and/or host–parasite life cycles rather than ensuring the seabed's macro-faunal community and biogeochemical functions remain viable. As such, fallowing periods are sometimes no more than a few weeks. Our results suggest that in situations where the benthic macro-faunal community has been severely impaired, much longer fallowing may be required to permit the biogeochemical composition of the seabed to return to a more natural state. Our study does not reveal whether a full return to a natural biogeochemical state can be achieved before the macro-faunal community itself has largely recovered. Models that explicitly seek to explore the relationship between accruing seabed impact during the crop phase and subsequent seabed recovery during fallowing will help farmers and regulators make well-informed decisions during the planning and consenting stages. This will reduce the risk that the environment suffers unwarranted harm and prevent the establishment of farm developments that will prove environmentally unsustainable. However, it will be important to es-

establish reliable empirical relationships between incremental organic matter at the seabed (and/or incremental SOD) and biogeochemical and benthic macro-faunal responses.

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