



Alkalinity generation and trace metal dynamics during olivine-based marine enhanced rock weathering in bioturbated sediments

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Abstract.

15 Ocean alkalinity enhancement (OAE) via marine enhanced rock weathering (mERW) of olivine is a proposed strategy for atmospheric carbon dioxide removal (CDR). However, the potential co-release of trace metals to marine ecosystems, most notably nickel (Ni) and chromium (Cr), raises environmental concerns.

Here, we investigated total alkalinity (A_T) release, trace metal dynamics and metal bioaccumulation during mERW using two complementary approaches. First, a 28-day microcosm experiment showed that bioturbation by the lugworm *Arenicola marina* in pure olivine sand enhanced A_T release nearly fivefold and more than doubled the release of dissolved Ni (DNi).
20 Second, in a long-term (> 1 year) mesocosm experiment, we added fine-grained olivine at sediment loading levels of 6% and 10%, and coarse-grained olivine at 10%, to natural intertidal sediments inhabited by *A. marina*. We quantified sediment–water fluxes and porewater concentrations of A_T , DNi, and DCr, and assessed metal accumulation in lugworm tissues. Olivine amendment increased sediment–water A_T fluxes approximately two- to threefold, without significant effects of grain
25 size or loading level. Fine-grained olivine treatments resulted in the highest DNi fluxes and the greatest Ni bioaccumulation in lugworms. Lugworm Ni concentrations increased up to tenfold relative to controls. In contrast, olivine amendment did not increase DCr fluxes and Cr bioaccumulation was minor compared to Ni.

These results show that bioturbation can enhance olivine weathering and that olivine amendment can increase A_T release from natural coastal sediments. However, finer grain size disproportionately increased Ni release and bioaccumulation
30 without a detectable additional A_T benefit. This decoupling suggests that A_T generated by olivine weathering may have been partly offset by suppression of natural sedimentary A_T generation. Under the conditions tested here, coarse olivine therefore provided a more favourable balance between net A_T release and ecotoxicological risks from Ni exposure during mERW.



1 Introduction

Climate change remains one of the most pressing challenges of the 21st century, driven by increasing atmospheric carbon dioxide (CO_2) concentrations (IPCC, 2023; Ripple et al., 2025). To meet the goals set by the Paris Agreement, implementation of carbon dioxide removal (CDR) is needed at large scale, alongside sharp reductions in emissions (Fuss et al., 2014; Gasser et al., 2015; Anderson and Peters, 2016; Sanderson et al., 2016; Rockström et al., 2017). Consequently, a diverse portfolio of CDR approaches is being developed that aim to sequester CO_2 from the atmosphere (Minx et al., 2017, 2018; Amann and Hartmann, 2019).

One CDR approach is ocean alkalinity enhancement (OAE) through marine enhanced rock weathering (mERW). This approach aims to amplify the natural weathering feedback on Earth's climate by dispersing fine-grained silicate rocks in coastal ecosystems (Walker et al., 1981; Schuiling and Krijgsman, 2006; Meysman and Montserrat, 2017; Penman et al., 2020). The dissolution of silicate minerals increases total alkalinity (A_T), which shifts the carbonate system equilibrium of seawater from dissolved CO_2 towards bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}), thus enabling additional atmospheric CO_2 to be stored as dissolved inorganic carbon (DIC) (Taylor et al., 2016; Meysman and Montserrat, 2017; Renforth and Henderson, 2017). The silicate mineral olivine ($\text{Mg}_{(2-x)}\text{Fe}_x\text{SiO}_4$) is considered a prime candidate for mERW, due to its relatively fast dissolution kinetics and its global abundance (Oelkers et al., 2018; Caserini et al., 2022; Geerts et al., 2025a). Before real-world applications of olivine-based mERW can be deployed, the CO_2 sequestration efficiency (i.e. the time scale and magnitude of CO_2 sequestration) and potential environmental impacts need to be carefully scrutinised. A number of recent studies have targeted the former objective, evaluating to what extent secondary reactions, saturation effects, or physical processes may alter dissolution rates and the resulting carbon uptake efficiency (Montserrat et al., 2017; Flipkens et al., 2023b; Bach, 2024; Kreuzburg et al., 2025). Alongside these questions about CO_2 sequestration efficiency, concerns have been raised about the trace metal content of olivine, most notably nickel (Ni) and chromium (Cr), which may pose ecological risks when released upon weathering (Montserrat et al., 2017; Bach et al., 2019; Flipkens et al., 2021). Ni and Cr are naturally present in olivine, with Ni substituting for divalent cations (Fe^{2+} , Mg^{2+}) at concentrations ranging from 0.24 to 1.2 mol%, and Cr typically occurring as chromite (FeCr_2O_4) inclusions at concentrations of 0.02 to 0.66 mol% (Santos et al., 2015; Montserrat et al., 2017; Flipkens et al., 2021).

Consequently, when olivine-rich materials are deposited onto sediments during mERW applications, olivine dissolution could lead to trace metal release and also increase metal bioaccumulation in resident organisms (Meysman and Montserrat, 2017; Flipkens et al., 2021; Zhuang et al., 2025). As such, the ecotoxicological risks of olivine addition and subsequent metal release must be evaluated alongside its carbon removal potential (Bach et al., 2019; Flipkens et al., 2021; Zhuang et al., 2025). Previous studies have indicated potential effects on growth, survival, and reproduction, albeit with varying impacts related to the specific biota involved, exposure time, and olivine grain size (Flipkens et al., 2023a; Vink and Knops, 2023; Flipkens et al., 2024; Jankowska et al., 2024). Still, most of this work is based on relatively short-term exposure under laboratory conditions (Flipkens et al., 2023a; Jankowska et al., 2024) or employs idealised chemical models to constrain



bioaccumulation risks (Vink and Knops, 2023). Therefore, further research is needed on the long-term interaction between olivine and infauna in conditions that more closely mimic the natural situation in which mERW will be conducted.

Here, we investigated A_T release, trace metal dynamics and bioaccumulation following olivine amendment to natural coastal sediments inhabited by the bioturbating polychaete *Arenicola marina* (lugworm), a dominant bioturbator and ecosystem engineer across sandy coastal areas in the North Atlantic (40°N to 70°N) (Cadée, 1976; Flach and Beukema, 1994). We used two experimental approaches. First, we conducted an exploratory microcosm experiment in which lugworms were placed in incubations with pure olivine sand to assess A_T and dissolved nickel (DNi) fluxes and Ni accumulation in lugworm tissues. Subsequently, we performed long-term incubations in an outdoor mesocosm facility to evaluate the effect of olivine amendment on A_T release and trace metal dynamics under semi-natural conditions. We compared fine-grained olivine at sediment loading levels of 6% and 10% with coarse-grained olivine at 10% and an unamended control. In these mesocosms, we quantified sediment–water fluxes and porewater profiles of A_T , DNi, and DCr, and measured metal accumulation in lugworm tissues. Our results on A_T release, trace metal mobilisation, and biological uptake following olivine amendment in coastal sediments provide insights into both the potential and environmental trade-offs of mineral-based OAE.



2 Materials & Methods

2.1 Olivine physicochemical characterisation

For both experiments in this study, we obtained VANGUARD refractory grade dunite sand from the Sibelco mine in Åheim (Norway). We refer to this sand as olivine throughout the text. The olivine materials were characterised following the methods described by Flipkens et al. (2023a, b). Grain-size distributions were determined by laser diffraction using a Mastersizer 2000 particle-size analyser (Malvern Panalytical, UK). Mineralogical composition of the olivine source rock was determined by powder X-ray diffraction (XRD) using a D8 ECO Advance diffractometer equipped with a LynxEye XE detector (Bruker, Germany), followed by semi-quantitative Rietveld analysis. Specific surface areas were measured by argon adsorption using the Brunauer–Emmett–Teller (BET) method with an Autosorb-1 gas-sorption analyser (Quantachrome, USA). Elemental composition, including Ni and Cr content, was determined by microwave-assisted acid digestion followed by inductively coupled plasma–optical emission spectrometry (ICP–OES; iCAP 6300 Duo, Thermo Scientific, USA). Based on the obtained molar ratios of Mg and Fe, the source rock was characterised as forsteritic olivine (Fo93). The grain size distributions (d_{10} , d_{50} , d_{90}), forsterite content of the source rock (%forsterite), BET specific surface area (A_{BET}), and trace metal content (Ni and Cr) are summarised in Table 1. More details on the physicochemical characterisation protocols are provided in Appendix B, Tables B1 and B2.

Table 1. Physicochemical characteristics and analysis methods for the olivine materials used in the two experiments. The microcosm olivine was used in the exploratory experiment, whereas the fine and coarse olivine were used in the mesocosm experiment. Grain size and elemental composition data ($\mu\text{mol g}^{-1}$ dry weight) are presented as mean $\pm$ SD ($n = 3$ and $n = 5$, respectively). XRD and BET results represent single measurements ($n = 1$). Olivine content refers to the weight fraction of forsterite (Fo93) in the dunite sand source rock.

Property	Method	Microcosm olivine	Fine olivine	Coarse olivine
d_{10} (μm)	laser diffraction	80 ± 0.9	6 ± 0.1	39 ± 1.1
d_{50} (μm)		133 ± 0.3	34 ± 1.6	158 ± 2.1
d_{90} (μm)		211 ± 0.3	112 ± 8.6	317 ± 2.7
Olivine content (wt.%)	XRD	86	69	83
A_{BET} ($\text{m}^2 \text{g}^{-1}$)	BET	0.985	7.329	0.804
Ni ($\mu\text{mol g}^{-1}$ d.w.)	ICP-OES	43 ± 0.8	36 ± 2	38 ± 0.9
Cr ($\mu\text{mol g}^{-1}$ d.w.)		58 ± 3	30 ± 2	23 ± 0.9



2.2 Experimental designs

2.2.1 Microcosm experiment

105 An exploratory microcosm experiment was conducted to evaluate the effect of lugworm activity on the release of A_T and DNi and to assess Ni bioaccumulation. The experiment ran for 28 days in a climate-controlled chamber maintained at $\sim 17^\circ\text{C}$ and dark conditions (Fig. 1a). Eight polymethylmethacrylate (Perspex) cores (10 cm diameter, 20 cm height) were filled with a ~ 9 cm layer of olivine sand and ~ 7 cm of overlying filtered ($0.2\ \mu\text{m}$) seawater of salinity ~ 30 collected in the Oosterschelde. Adult lugworms were sourced from tidal flats in the Oosterschelde basin (The Netherlands).

110 The microcosms were placed in an aquarium tank filled with a bottom layer of ~ 10 cm distilled water, to prevent leakage by providing a counterpressure (Fig. 1a). Cores were open to gas exchange and contained a stirrer to ensure a fully mixed water column at all times. To avoid evaporation of the overlying water in the cores, the aquarium was sealed with a rectangular Perspex sheet fitted with a neoprene rim, preventing atmospheric exchange between the aquarium and the climate cell. The relative humidity inside the aquarium was kept at $\sim 90\%$, by bubbling ambient (outside) air through the water layer at the bottom of the tank. This bubbling also ensured a constant $p\text{CO}_2$ (~ 400 ppm) in the gas phase of the aquarium.

115 After a six-day acclimation period, one adult lugworm each (mean length: 112 ± 6 mm; mean dry weight: 0.276 ± 0.099 g) was introduced on top of the sediment in half of the microcosms (Olivine-BT; $n = 4$), while the others remained without lugworms (Olivine-no BT; $n = 4$). In one microcosm, the lugworm failed to burrow and was replaced with a fresh individual after seven days. Because this microcosm did not have an individual exposed for the full 28-day period, the tissue sample was not included in the trace-metal analysis (see Sect. 2.4.1).

2.2.2 Mesocosm experiment

120 The microcosm experiment was of short duration (28 days) and the substrate was pure olivine sand. To document the long-term impact (i.e., time scale of months to years) under semi-natural conditions (i.e., addition of olivine to natural sediment), a mesocosm experiment was conducted at a dedicated facility for OAE research (VLIZ, Belgium). The mesocosms were operated outdoors under ambient temperature and light conditions, but shielded from rainfall to prevent freshwater dilution. The local climate at the mesocosm facility is temperate maritime with a mean annual air temperature of $\sim 11^\circ\text{C}$, and seasonal
125 variation from 5°C to 18°C (Epicum et al., 2018).

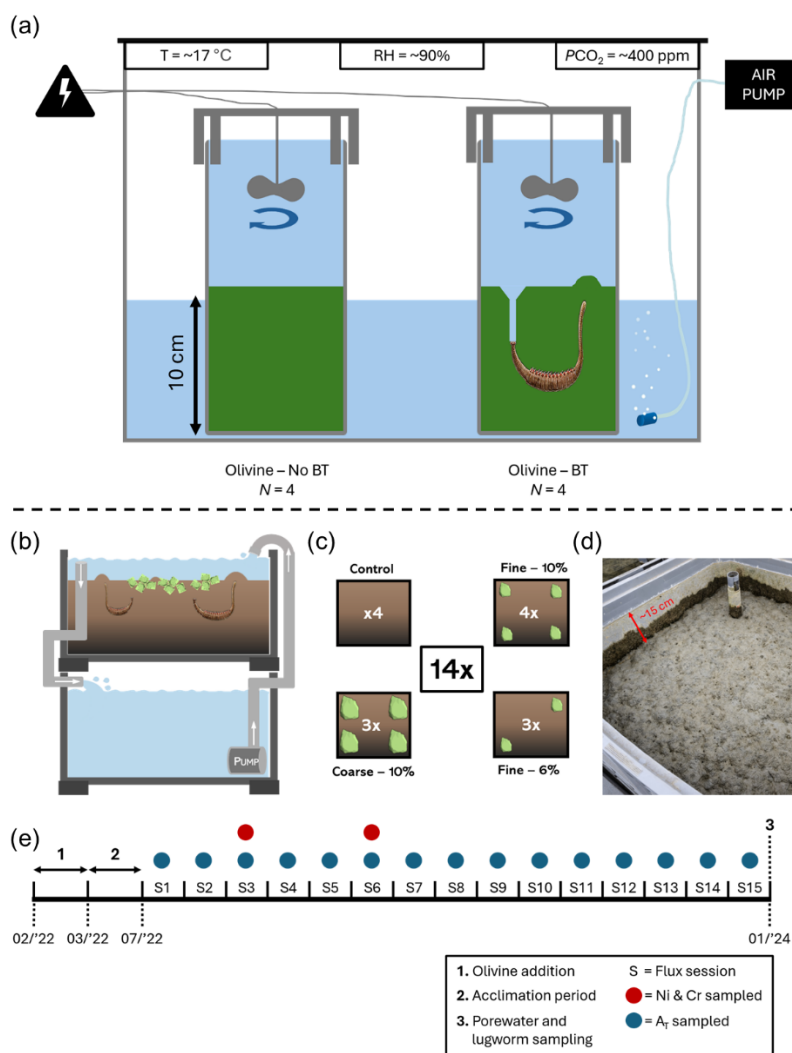


Figure 1. Experimental designs of the microcosm and mesocosm experiments. (a) Schematic representation of the microcosm experimental design. The experiment featured two treatments investigating the effect of bioturbation (BT): Olivine–No BT ($n = 4$) and Olivine–BT ($n = 4$). Temperature (T), relative humidity (RH) and partial CO_2 pressure are noted in the figure. (b) Schematic representation of one mesocosm, consisting of an upper tank with natural intertidal sediment and overlying water, and a lower tank serving as a reservoir, connected by a pump. (c) Overview of the mesocosm treatments: control (no olivine), Coarse–10% ($d_{10}-d_{90}$: 39–317 μm olivine, 10% loading), Fine–10% (6–112 μm olivine, 10% loading) and Fine–6% (6–112 μm olivine, 6% loading). (d) Photograph of a mesocosm during water renewal, showing the sediment surface and approximate overlying water height (~ 15 cm; indicated by red arrow). (e) Experimental timeline showing the addition of olivine, acclimation period, 15 four-week flux sessions (S1–S15), and final sampling. Blue symbols indicate sessions in which total alkalinity (A_T) was measured, red symbols indicate sessions in which trace metal (DNi and DCr) samples were analysed.



Fourteen mesocosms were constructed and operated, which were designed to each mimic $\sim 1 \text{ m}^2$ of natural coastal seafloor. Each mesocosm unit consisted of two tanks ($120 \times 100 \times 57 \text{ cm}$) that are stacked on top of each other (Fig. 1b). The upper
140 tank was filled with $\sim 40 \text{ cm}$ of natural intertidal sediment collected from the Oosterschelde estuary ($51^\circ 27' 31.6'' \text{N}$, $4^\circ 04' 50.4'' \text{E}$) in July 2020. The sediment consisted of very fine sand (median grain size d_{50} : $96 \mu\text{m}$; porosity: 0.41; dry solid phase density: 2.63 g cm^{-3}) and contained 0.23 wt.% organic carbon and 0.24 wt.% inorganic carbon (Rao et al., 2014). Defaunation of the mesocosms was initiated by covering the sediment surface for 2 months with a 0.5 mm thick, gas-impermeable PVC sheet (sold commercially as pond liner). The mesocosms were subsequently filled with coarsely filtered
145 (2 mm) seawater from the Oosterschelde (salinity ~ 30) and water circulation was initiated. The sediment was covered by $\sim 15 \text{ cm}$ of overlying seawater and the lower tank served as a water reservoir (600 L, $\sim 50 \text{ cm}$ water depth) that was connected by a pump to the upper tank. Water was continuously pumped from the lower to the upper tank, and gravitationally drained back to the lower tank, thus ensuring a continuous recirculation between the tanks. In this way, the water overlying the sediment in the upper tank was continuously kept in motion and replenished, and the sediment was covered by a total water
150 column of $\sim 65 \text{ cm}$. The seawater was refreshed approximately every four weeks to avoid excessive accumulation of solutes between individual flux sessions (see below). The water surface remains in contact with the atmosphere, thus allowing for continuous air–sea CO_2 exchange.

After defaunation, the mesocosms were left to acclimate for ~ 6 months in order to establish a geochemical steady-state in the sediment. After this period (May 2021), adult lugworms (*A. marina*; sourced from the sediment collection site) were
155 introduced at natural densities characteristic of the field site ($\sim 40 \text{ individuals m}^{-2}$; Cadée, 1976). The upper tank was exposed to natural light conditions, thus enabling photosynthesis and growth of micro-algae on the sediment surface. This serves as a food source for the sedimentary macrofauna, thus enabling long-term incubation of fauna without starvation or food shortage effects. After lugworm addition, the mesocosms were again left to acclimate for ~ 10 months in order to establish a sedimentary steady-state (now with lugworm bioturbation). In December 2021, an additional set of worms was added to
160 maintain the population level.

Olivine addition to the mesocosms was started in February 2022 and proceeded over a period of ~ 4 weeks. To this end, surface sediment was first collected from a mesocosm, the olivine sand was mixed in an external container, and the resulting slurry mixture was spread back onto the surface of each mesocosm. Four treatments were established (Fig. 1c), which included a control (no olivine added, $n = 4$ mesocosms), fine-grained olivine at 6% loading ($n = 3$), fine-grained olivine at
165 10% loading ($n = 4$), and coarse-grained olivine at 10% loading ($n = 3$). The sediment loadings represent the added olivine mass relative to the estimated dry mass of sediment in the upper 15 cm, which was taken to correspond to the bioturbated layer. Note that control mesocosms were disturbed in a similar way as other treatments (i.e., sediment removal, mixing and spreading), but without olivine addition.

The custom-built mesocosm design enables a detailed monitoring of the sedimentary olivine weathering through time. To
170 this end, we tracked the accumulation of dissolved weathering products in the overlying water of the mesocosm over periods of four weeks, resulting in five timepoints (a so-called “flux session”). After each 4-week flux session, the seawater in the



mesocosms was replaced to restore baseline seawater chemistry before a new flux session was started (Fig. 1d). The experiment spanned a total of 22 months (March 2022–January 2024) and included 15 consecutive flux sessions in total (the first one recorded in July 2022, after 4 months of acclimation). Lugworm activity was monitored weekly by counting fresh adult pseudofeces deposited on the sediment surface. This is a common method to track lugworm density and activity (Flach and Beukema, 1994; Volkenborn and Reise, 2006). Juvenile pseudofeces were additionally counted up to a maximum of 100. The lugworm population gradually declined during the experiment, and so additional lugworms were collected and added to the mesocosms in June and October 2022.

For the purposes of this study, we focus on a selected subset of the recorded flux data. Specifically, two flux sessions (sessions 3 and 6; ~6 and ~9 months after olivine addition, respectively) were used to quantify trace metal (DNi, DCr) fluxes alongside A_T . Additionally, we report A_T data from all 15 flux sessions. Comparisons of A_T and DNi fluxes were based solely on the two sessions where both variables were measured concurrently. In addition to fluxes, we report end-point measurements of porewater (A_T , DNi, DCr) and lugworm tissue metal concentrations (Ni, Cr, Zn), collected in January 2024 (Fig. 1e).

2.3 Seawater sampling and analysis

2.3.1 Microcosm experiment

At the start of the microcosm experiment ($t = 0$), the overlying water in the cores was replaced with air-equilibrated filtered seawater. Overlying water was sampled at six time points (days 0, 1, 7, 14, 21, and 28). Water volumes were kept constant by replacing each sampled volume with an equal amount of filtered seawater. Overlying water samples were processed and analysed for A_T and DNi following the analytical procedures described in Montserrat et al. (2017). Briefly, A_T was determined by automated potentiometric titration using a Titrand system (Metrohm AG, Switzerland). Samples for DNi were acidified with 50 $\mu\text{L mL}^{-1}$ of sub-boiled distilled HNO_3 (65%) and subsequently stored at 4 °C. Before analysis, samples were diluted 20-fold with Milli-Q water, and analysed by high-resolution inductively coupled plasma mass spectrometry (HR-ICP-MS; Element 2, Thermo Scientific).

2.3.2 Mesocosm experiment

Surface water samples were collected on a weekly basis during flux sessions using 50 mL syringes (Terumo Corporation, Japan). For A_T (session 1–15), 50 mL of water was filtered through a 0.8/0.2 μm Supor® syringe filter (PALL®, USA) into a 100 mL HDPE vial (Corning Incorporated, USA) and stored at room temperature for a maximum of one week prior to analysis. For trace metal analysis in sessions 3 (September 2022) and 6 (January 2023), subsamples (10 mL) were transferred into clean 15 mL PP Falcon™ tubes (Corning Incorporated) and acidified with 200 μL of 2% HNO_3 .

A_T was determined in duplicate by potentiometric titration with 0.1 M HCl using an automated titration setup (888 Titrand with 814 USB Sample Processor; Metrohm AG). The titrant was calibrated against certified reference material (batch 209;



OCADS, USA). A_T was calculated from the added titrant volume and electromotive-force measurements recorded with a Unitrode pH electrode (Metrohm AG), using a nonlinear least-squares method as described by Dickson et al. (2007). For
205 quality control, in-house standard filtered seawater samples were analysed at the beginning of each run, after every tenth sample, and at the end of the run. These measurements yielded a relative standard deviation below 2%.

Concentrations of DNi and DCr were determined by ICP-MS (Institute of Geosciences, Christian-Albrechts-University, Kiel, Germany). Acidified samples were diluted 10-fold in ultra-pure 2% HNO_3 (prepared from doubly sub-boiled HNO_3 and ultra-pure water with $18.2\text{ M}\Omega\text{ cm}^{-1}$ resistivity). Concentrations of DNi and DCr were measured on an Agilent 7900 ICP-MS
210 (Agilent Technologies, USA) operated with helium as collision gas. The instrument was tuned and calibrated daily, and indium was added to all solutions as an internal standard. Analytical accuracy was assessed by repeated analysis of NIST 1643f reference material, and reproducibility was determined by replicate preparation and measurement of the same sample yielding relative standard deviations below 10 %.

Porewater was sampled at the end of the mesocosm experiment, i.e., after all 15 flux sessions were concluded (January 2024;
215 Fig. 1e). Rhizon MOM samplers (10 cm, 0.12–0.18 μm pore size; Rhizosphere Research Products BVBA, The Netherlands) were installed through pre-drilled holes in the mesocosm walls. Rhizons were spaced at 2.5 cm to cover depths from –1.5 cm (surface water) to 18.5 cm, thus enabling nine sampling depths. A single porewater sample was collected at each depth from each sampled mesocosm. Rhizons were installed in one or two mesocosms per treatment. Porewater was extracted by connecting 10 mL HENKE-JECT® syringes (Henke Sass Wolf, Germany) to the Rhizons and securing plungers with
220 wooden stoppers to create a vacuum.

Porewater subsamples of ~0.5 mL were collected for trace metal analysis into 1.5 mL Eppendorf® tubes and acidified with 25 μL of 2% HNO_3 (prepared from 65% stock; EMSURE®, Merck KGaA, Germany), then stored at 4 °C until analysis. For A_T analysis, ~5 mL subsamples were collected into clean 15 mL polypropylene (PP) Falcon™ tubes and stored at room temperature until analysis.

225 Porewater DNi and DCr concentrations were determined by ICP-MS (ELCAT research group, University of Antwerp, Belgium). For each sample, a 500 μL aliquot was diluted 20-fold in a 12 mL PP Falcon™ tube using 9.2 mL Milli-Q water ($18.2\text{ M}\Omega\text{ cm}^{-1}$ at 25 °C), 200 μL HNO_3 (67–69%, ICP-MS trace-analysis grade; Thermo Scientific), and 100 μL of yttrium based internal standard solution (10 ppm; Alfa Aesar, USA). Analyses were performed with an Agilent 7850 ICP-MS equipped with an SPS4 autosampler, micro mist nebulizer, and Scott double-pass spray chamber. Calibration standards were
230 prepared from single-element stock solutions (Alfa Aesar), and results were processed with the MassHunter software (v5.2).

Porewater A_T concentrations were determined by potentiometric titration following the same method described for surface water. Prior to titration, samples were weighed and diluted to 50 g final weight using ultrafiltered seawater of known alkalinity (sourced from Stichting Zeeschelp, The Netherlands). Because the available porewater volume was insufficient for replicate titrations, each sample was titrated only once.



235 2.4 Lugworm collection, processing and analysis

2.4.1 Microcosm experiment

At the end of the microcosm experiment (day 28), lugworms were collected from the sediment of the bioturbated cores ($n = 3$) for analysis of tissue Ni content. As a control, similarly sized lugworms were collected from the field to compare Ni accumulation ($n = 4$). All individuals were placed in clean seawater for 24 h to depurate gut contents, a duration sufficient to
240 empty ~95% of the gut (De Wilde and Berghuis, 1979). Lugworms were subsequently rinsed under a stereomicroscope and cleaned with a small brush to remove sediment grains from their skin, then frozen at $-20\text{ }^{\circ}\text{C}$ until further processing. Lugworm tissue samples were freeze-dried, weighed immediately to record their dry weight, then digested in 10 mL concentrated HNO_3 using Teflon containers and microwave digestion. The resulting solutions were diluted five-fold with Milli-Q water and analysed for Ni by HR-ICP-MS (Element 2, Thermo Scientific). Indium (2.5 ppb) containing 2% HNO_3
245 was injected simultaneously with the samples as internal standard. To account for matrix effects, the linear slope of the external calibration was corrected with the linear slope of the internal calibration (i.e. standard addition) of one sample.

2.4.2 Mesocosm experiment

At the end of the mesocosm experiment, lugworms ($N = 108$) were collected from all mesocosms by removing a portion of the upper ~10 cm of sediment and passing it through a 1.8 mm brass sieve (W.S. Tyler Co., USA). Individuals were
250 subsequently transferred into 125 mL PP cups (Corning Incorporated) containing seawater from their respective mesocosm and allowed to depurate for 24 h. Following depuration, lugworms were rinsed and cleaned as described for the microcosm experiment, then photographed. Specimens were subsequently transferred to pre-weighed 15 mL PP Falcon™ tubes, weighed to determine wet mass, and stored at $-20\text{ }^{\circ}\text{C}$ until further processing. Lugworm lengths were determined from photographs using the segmented line tool in ImageJ (v1.54g). Because lugworms were introduced at several time points and
255 juvenile recruitment occurred in all mesocosms, individual exposure durations could not be determined. The maximum possible exposure duration was 22 months, corresponding to the interval between the end of olivine addition and endpoint sampling.

Lugworm samples from the mesocosms were freeze-dried at $-58\text{ }^{\circ}\text{C}$ for 72 hours and weighed immediately to determine their dry mass. Individuals were pooled into weight-based batches, digested overnight in HNO_3 (67–69%) at room
260 temperature, and subsequently placed in a hot block at $70\text{ }^{\circ}\text{C}$ for 3–17 hours, depending on weight batch. It should be noted that a small layer of residual sediment was present in 73% of lugworm samples after the acid digest. Digested samples were diluted with 10 mL Milli-Q water and spiked with 100 μL of yttrium internal standard (10 ppm; Alfa Aesar, UK). Ni, Cr, and Zn concentrations were quantified by ICP-MS using the same instrument and procedures as for porewater (ELCAT research group), with Zn included as a reference element expected to remain stable across treatments and to facilitate
265 comparison with literature. Blanks were processed alongside lugworm samples. The accuracy of digestion and analysis was assessed by triplicate measurements of a mussel tissue reference material (ERM®–CE278K). Mean recoveries were 87% for



Ni, 58% for Cr, and 109% for Zn. The relative standard deviations of these measurements were 7.69% (Ni), 1.83% (Cr), and 0.99% (Zn).

2.5 Flux calculations and statistical analyses

270 All statistical analyses were performed in R (version 4.3.3) using RStudio (2026.8.0.187). In the microcosm experiment, sediment–water fluxes of A_T and DNi were calculated separately for each replicate core by fitting quadratic regressions to overlying-water concentrations as a function of elapsed incubation time. All six sampling points (days 0, 1, 7, 14, 21 and 28) were included. Quadratic models were used because the concentration trajectories showed a rapid initial change followed by progressively slower change. Fluxes were derived from the initial slope of each fitted curve. The initial slope was used
275 because progressive solute accumulation in the finite overlying water reservoir could alter concentration gradients and reaction conditions later in the incubation. Regressions and flux calculations were performed using the FLUXER Shiny application in R (Hylén and van de Velde, 2025). Microcosm-specific regression outputs and flux estimates are provided in Table C1.

In the mesocosm experiment, linear mixed-effects models (LMMs) were used to estimate sediment–water fluxes of A_T , DNi
280 and DCr and to assess treatment effects on these fluxes. Prior to analysis, concentrations were corrected for evaporation-driven water loss using a salinity-based correction factor. Elapsed time within each flux session was included as a continuous predictor, with the treatment-specific slopes converted to sediment–water fluxes by accounting for the overlying-water volume and sediment surface area. The 15-session A_T dataset was analysed using a hierarchical treatment structure that first distinguished between the absence and presence of olivine and subsequently accounted for the effect of loading level within
285 the fine-grained treatments and the effect of grain size at 10% loading. Interactions between elapsed time and this treatment structure allowed fluxes to differ among treatments. To account for repeated measurements, random intercepts and slopes for elapsed time were included for sessions and mesocosms nested within sessions. The full model output is provided in Table C2.

The same model structure was initially evaluated for DNi and DCr , but these analytes were measured during only two
290 sessions. Therefore, treating session as a random effect with only two levels resulted in singular fits. To resolve this, session was included as a fixed factor in the two-session analyses, and the four observed treatments were represented without assuming a complete grain-size $\times$ loading factorial design. For DNi , models with and without the session $\times$ treatment $\times$ elapsed-time interaction were compared using a likelihood-ratio test after fitting both models by maximum likelihood (ML). The interaction was retained, and the final DNi model included a random intercept for each mesocosm within each session.
295 To obtain directly comparable A_T estimates to assess the relationship between A_T and DNi fluxes, A_T data from the same two sessions were analysed using the same full session $\times$ treatment $\times$ elapsed-time fixed-effect structure, with random intercepts and temporal slopes for mesocosms within sessions. The final DCr model allowed fluxes to differ between sessions but assumed that treatment effects on fluxes were consistent across sessions, and included a random intercept for each mesocosm



within each session. Full outputs of the final two-session A_T , DNi and DCr models are provided in Tables C3–C5,
300 respectively.

All final models underlying the reported flux estimates and bootstrap confidence intervals were fitted by restricted maximum likelihood (REML) using `lmer()` from the `lmerTest` R package (3.1.3). Maximum likelihood (ML) was used only for the DNi model comparison described above. Model convergence and singularity were evaluated using optimizer diagnostics and `isSingular()` from the `lme4` package (1.1.35.3). Degrees of freedom and p -values for fixed-effect tests and targeted contrasts
305 of fitted temporal slopes were calculated using Satterthwaite's approximation. For DNi , session-specific fitted slopes were obtained using `emtrends()` and compared using `contrast()` from the `emmeans` package (1.10.4). Targeted contrasts of fitted temporal slopes were used to evaluate the treatment comparisons reported in the Results. Treatment-specific flux estimates were calculated from the fitted temporal slopes and converted from $mmol$ to $\mu mol\ m^{-2}\ day^{-1}$ for DNi and DCr . For each of the four final models, 95% confidence intervals were obtained from 10,000 parametric bootstrap simulations using
310 `bootMer()` from `lme4` (`type = "parametric"`, `use.u = FALSE`). Targeted contrast intervals were calculated by applying the corresponding contrasts within each bootstrap simulation, thereby retaining covariance among the fitted slopes. Model-derived flux estimates and bootstrap confidence intervals, targeted treatment contrasts, and bootstrap diagnostics are reported in Tables C6, C7 and C8, respectively.

In both experiments, the relationship between fluxes of A_T and DNi was compared with the theoretical ratio expected from
315 stoichiometric olivine dissolution. The theoretical ratio was calculated separately for each olivine material using its measured Ni content, XRD-derived olivine fraction and the molar mass of Fo_{93} olivine ($145.11\ g\ mol^{-1}$), assuming production of 4 $mol\ A_T$ per mole of olivine dissolved.

Metal concentrations (Ni , Cr , Zn) in lugworm tissue samples from the mesocosms were analysed without exclusion of any data points. Although some individuals exhibited strongly elevated concentrations, these values were retained as there was
320 no technical or biological justification for exclusion. To account for the non-normal distribution of the data and presence of extreme values, differences among treatments were assessed with a non-parametric Kruskal–Wallis test. Pairwise post-hoc comparisons using a Dunn's test with Bonferroni correction were executed to assess treatment-level differences. Statistical significance was set at $p < 0.05$. Median values are reported throughout, as they better represent central tendencies in skewed datasets.



325 3 Results

3.1 Microcosms: release of A_T and DNi from olivine sand and Ni bioaccumulation

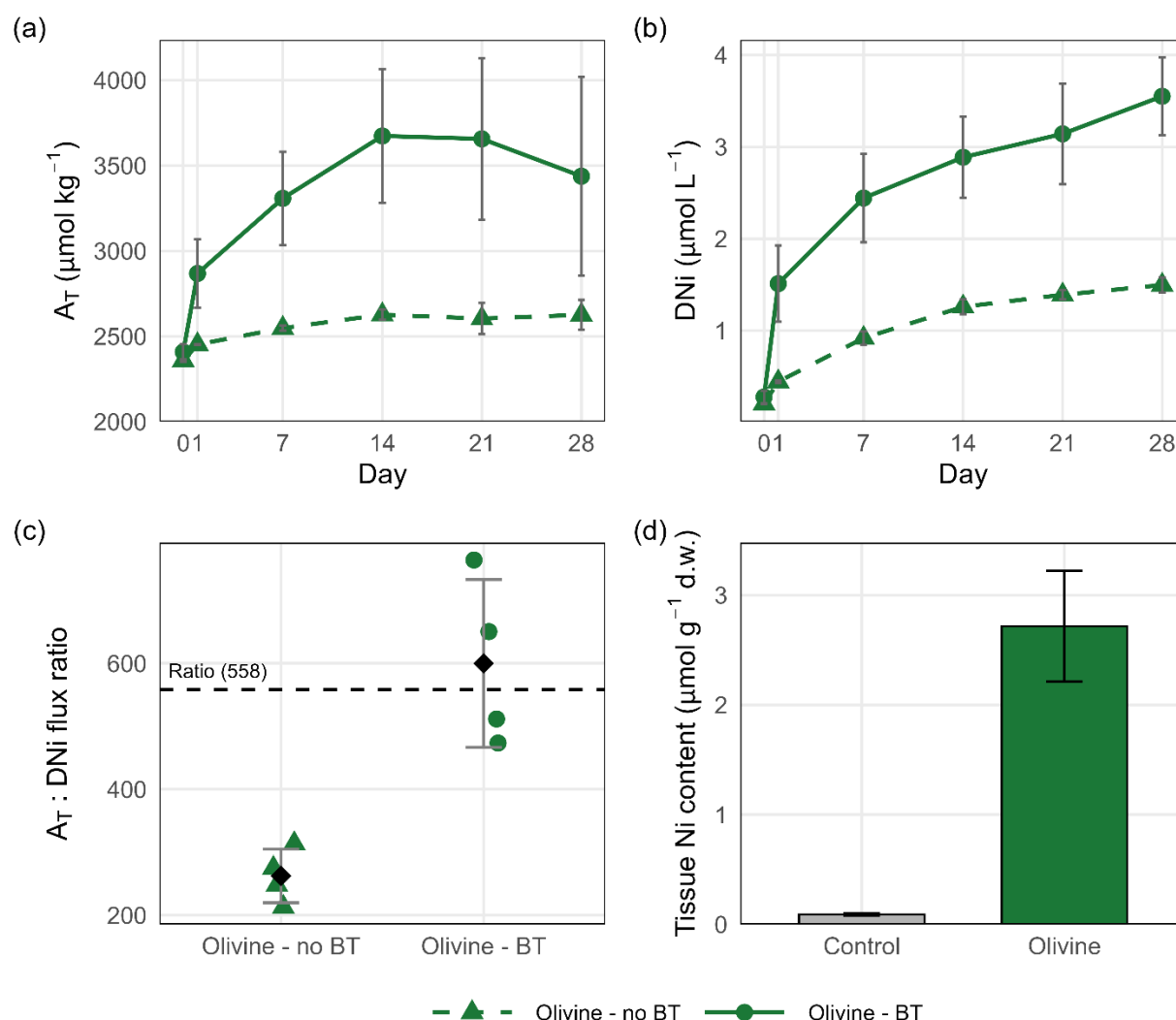


Figure 2. (a, b) Overlying water concentrations of total alkalinity (A_T ; $\mu\text{mol kg}^{-1}$) and dissolved nickel (DNi; $\mu\text{mol L}^{-1}$), respectively, during the 28-day microcosm experiment in absence (no BT, triangle) and presence (BT, circle) of lugworm bioturbation. Points show treatment means and error bars indicate SD ($n = 4$). (c) Flux ratios of A_T : DNi, where green symbols reflect individual microcosms, black diamonds and error bars indicate treatment means and SD. The dotted black line represents the theoretical ratio (558) expected from stoichiometric dissolution of the source rock. (d) Ni content of lugworm tissues ($\mu\text{mol g}^{-1}$ d.w.) after 28 days exposure to olivine sand (green; $n = 3$) compared to field-collected controls (grey; $n = 4$). Bars indicate means and error bars indicate SD.



Table 2. Fluxes of A_T ($\text{mmol m}^{-2} \text{ day}^{-1}$) and DNi ($\mu\text{mol m}^{-2} \text{ day}^{-1}$) in microcosms without bioturbation (Olivine – no BT) and with bioturbation (Olivine – BT). Values represent means $\pm$ SD ($n = 4$).

Flux	Olivine – no BT	Olivine - BT
A_T ($\text{mmol m}^{-2} \text{ day}^{-1}$)	1.8 ± 0.2	8.9 ± 2.0
DNi ($\mu\text{mol m}^{-2} \text{ day}^{-1}$)	6.8 ± 0.5	15.1 ± 3.2

In the non-bioturbated microcosms (Olivine – no BT), a slow and gradual accumulation of A_T was observed in the overlying water. In contrast, in the bioturbated microcosms (Olivine – BT) A_T increased markedly during the first day, followed by continued accumulation until day 14 (Fig. 2a), whereafter concentrations decreased again. A very similar response was observed for DNi in both treatments, with slow and gradual accumulation in the non-bioturbated microcosms and stronger release during the first day, followed by continued accumulation in the bioturbated microcosms (Fig. 2b). Consistent with these concentration patterns, the resulting initial A_T flux was nearly fivefold higher and the initial DNi flux was more than twice as high in the bioturbated compared to the non-bioturbated microcosms (Tables 2, C1).

In the non-bioturbated microcosms (Olivine – no BT), the flux ratios of $A_T : \text{DNi}$ were consistently below the theoretical ratio of 558. In contrast, the ratios in the bioturbated microcosms (Olivine – BT) centred around the theoretical value, with a mean of ~ 600 that only slightly exceeded the ratio expected from stoichiometric olivine dissolution (Fig. 2c).

Following tissue trace metal analysis, the lugworms retrieved from the olivine sand in the bioturbated microcosms contained ~ 30 times more Ni ($2.7 \pm 0.5 \mu\text{mol g}^{-1} \text{ d.w.}$) than the control specimens that were collected in the field ($0.09 \pm 0.01 \mu\text{mol g}^{-1} \text{ d.w.}$) (Fig. 2d).

3.2 Mesocosms: sediment–water A_T fluxes and porewater concentrations

Across all 15 flux sessions, olivine addition significantly increased A_T fluxes relative to the control treatment ($p < 1e-7$; Fig. 3a; Table C2). The highest estimated A_T flux was observed in the Fine–6% treatment ($5.18 \text{ mmol m}^{-2} \text{ day}^{-1}$; 95% CI: 4.02–6.35), more than twice that in the control ($1.89 \text{ mmol m}^{-2} \text{ day}^{-1}$; 95% CI: 0.79–2.95). Similarly elevated A_T fluxes were observed in the Fine–10% ($4.76 \text{ mmol m}^{-2} \text{ day}^{-1}$; 95% CI: 3.69–5.84) and the Coarse–10% treatment ($3.96 \text{ mmol m}^{-2} \text{ day}^{-1}$; 95% CI: 2.77–5.10). Model-derived flux estimates and their bootstrap confidence intervals are provided in Table C6. Neither olivine loading level nor grain size significantly affected A_T fluxes ($p = 0.50$ and $p = 0.20$, respectively; Table C7). Elevated A_T concentrations were observed in the porewater of the olivine-amended sediments, reaching up to $\sim 4000 \mu\text{mol kg}^{-1}$ in the Fine–10% and Coarse–10% treatments vs. $\sim 3400 \mu\text{mol kg}^{-1}$ in the control (Fig. 5a).

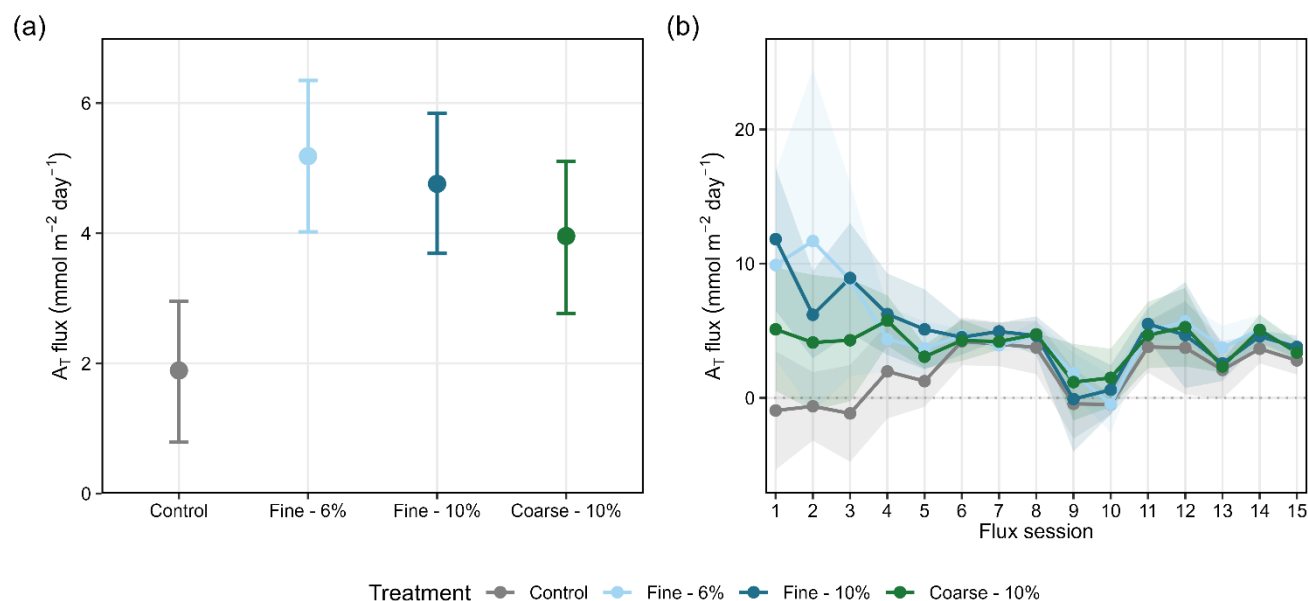


Figure 3. Sediment–water fluxes of total alkalinity (A_T ; $\text{mmol m}^{-2} \text{day}^{-1}$) across all 15 flux sessions of the mesocosm experiment. **(a)** Treatment-specific flux estimates derived from the linear mixed-effects model. Error bars denote 95% confidence intervals obtained from 10,000 parametric bootstrap simulations. **(b)** Mean A_T fluxes per treatment during each flux session. Points represent means, and shaded areas indicate $\pm$ SD.

Beyond the treatment effects, A_T fluxes varied considerably among mesocosms within treatments and across flux sessions, with the greatest variability occurring during the first 6 months of the experiment (Fig. 3b). During this period, which encompassed the first five recorded flux sessions, mean differences between the control and olivine-amended mesocosms were also most pronounced. From session 6 onwards, differences between the mean A_T fluxes of the control and the olivine treatments remained below $\sim 2 \text{ mmol m}^{-2} \text{day}^{-1}$. The session-specific model fitted for comparison with the trace metal fluxes illustrated this change (Fig. 4a; Table C3). During session 3 (~ 6 months after olivine addition), the estimated A_T flux was lowest in the control ($-1.16 \text{ mmol m}^{-2} \text{day}^{-1}$) and highest in the Fine-6% ($8.80 \text{ mmol m}^{-2} \text{day}^{-1}$) and Fine-10% ($8.93 \text{ mmol m}^{-2} \text{day}^{-1}$) treatments, while Coarse-10% showed an intermediate flux of $4.29 \text{ mmol m}^{-2} \text{day}^{-1}$. By session 6 (~ 9 months after olivine addition), the estimated A_T fluxes were nearly identical in the control ($4.21 \text{ mmol m}^{-2} \text{day}^{-1}$) and Coarse-10% ($4.28 \text{ mmol m}^{-2} \text{day}^{-1}$) treatments, while those of Fine-6% ($4.64 \text{ mmol m}^{-2} \text{day}^{-1}$) and Fine-10% ($4.52 \text{ mmol m}^{-2} \text{day}^{-1}$) were only slightly higher. The associated 95% confidence intervals are reported in Table C6.

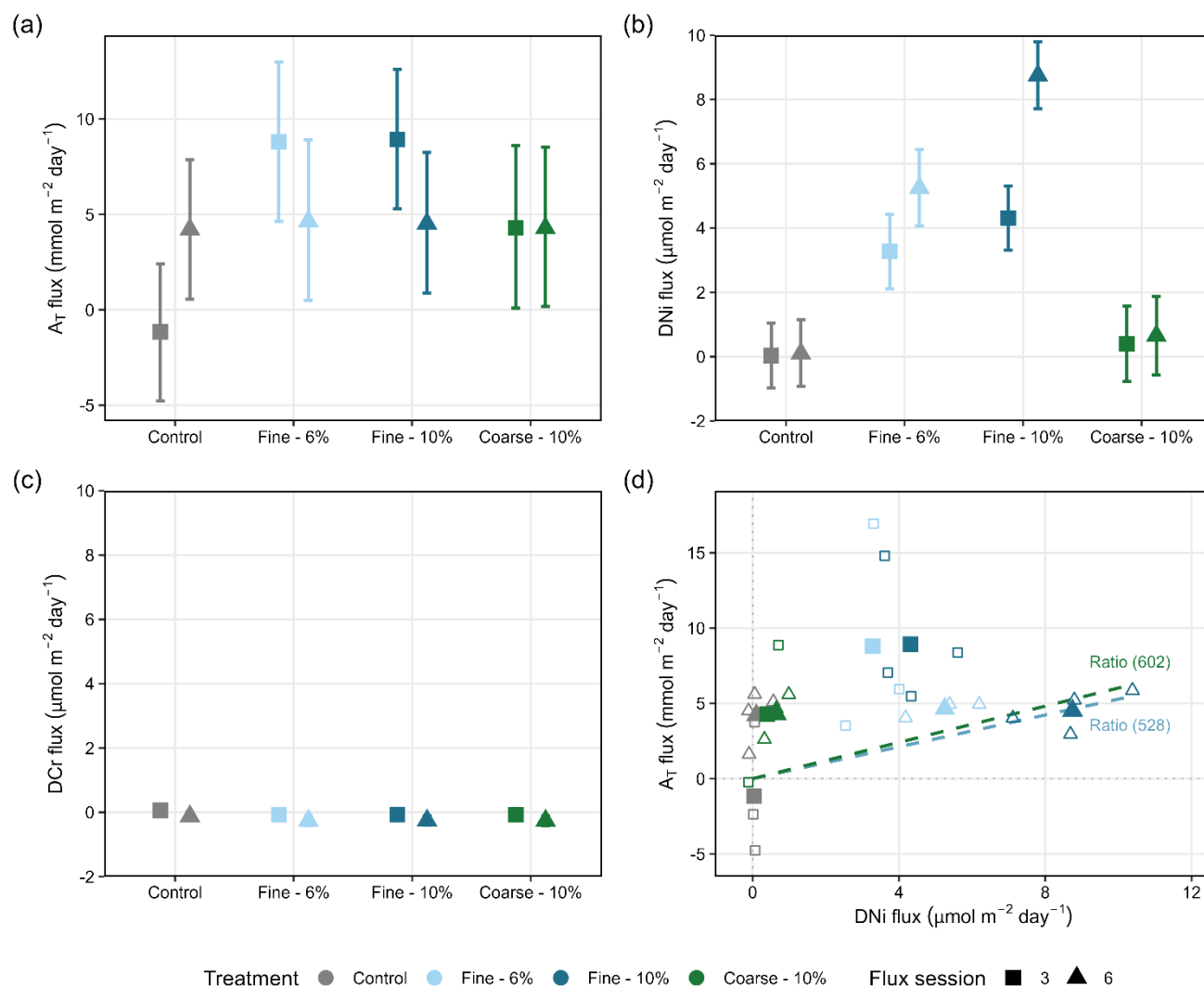


Figure 4. Sediment–water flux estimates during flux sessions 3 (squares) and 6 (triangles) for (a) total alkalinity (A_T ; $\text{mmol m}^{-2} \text{ day}^{-1}$), (b) dissolved nickel (DNi ; $\mu\text{mol m}^{-2} \text{ day}^{-1}$), and (c) dissolved chromium (DCr ; $\mu\text{mol m}^{-2} \text{ day}^{-1}$) across the four mesocosm treatments. Points in panels (a)–(c) represent flux estimates from linear mixed-effects models, and error bars denote 95% confidence intervals obtained from 10,000 parametric bootstrap simulations. (d) Scatterplot showing the relationship between DNi and A_T fluxes during sessions 3 and 6. No control correction was applied. Large filled symbols represent model-derived flux estimates, whereas small open symbols represent fluxes for individual mesocosms. The dashed blue and green lines show the theoretical relationships expected if the observed A_T and DNi fluxes were derived entirely from stoichiometric dissolution of the source rock, corresponding to molar $A_T : DNi$ ratios of 528 for fine (blue) and 602 for coarse (green) olivine.

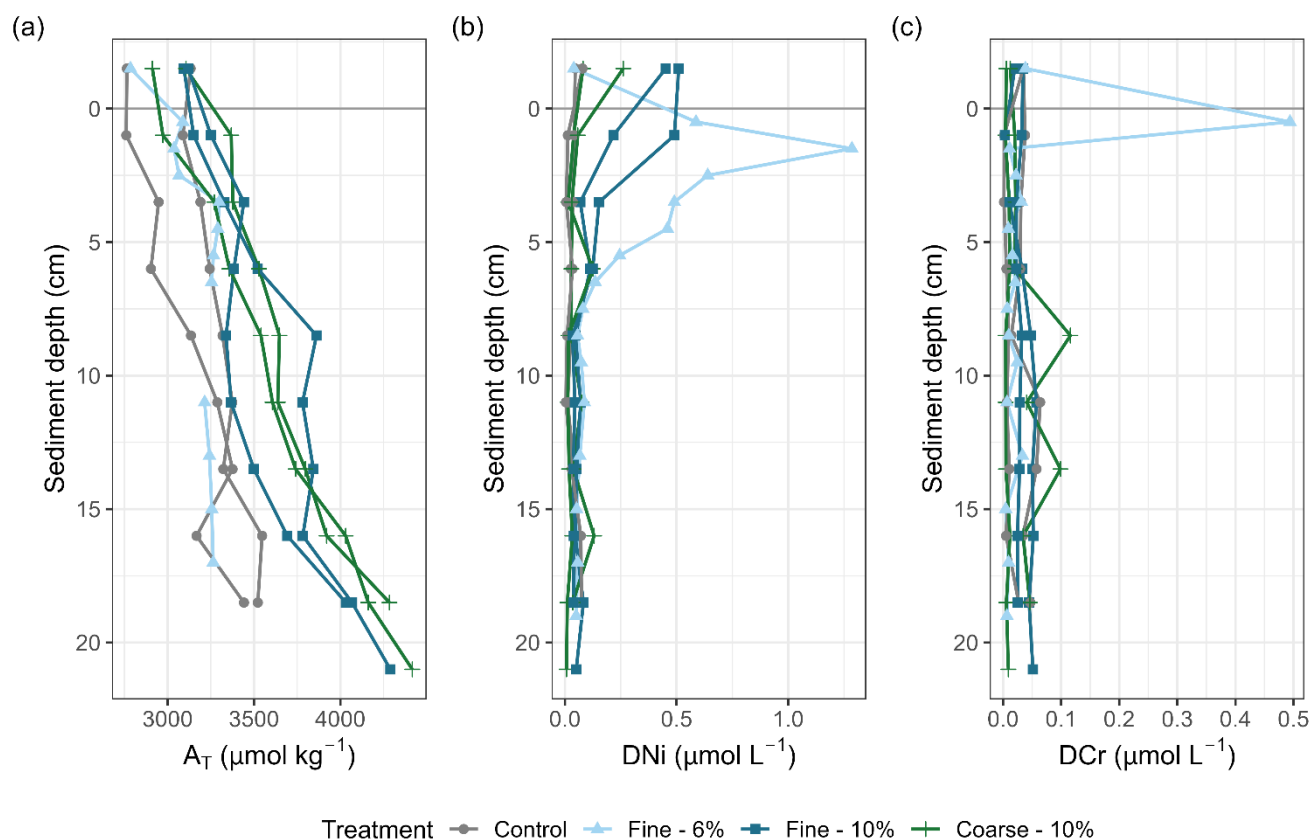


Figure 5. Sediment porewater concentrations of **(a)** total alkalinity (A_T ; $\mu\text{mol kg}^{-1}$), **(b)** dissolved nickel (DNi; $\mu\text{mol L}^{-1}$), and **(c)** dissolved chromium (DCr; $\mu\text{mol L}^{-1}$) measured at the end of the mesocosm experiment. Colours and symbols indicate treatments. Points represent measurements at successive depths within individual mesocosms (one or two mesocosms per treatment). The horizontal grey line at 0 cm indicates the sediment–water interface, with values above this line representing analyte concentrations in the overlying water.

3.3 Mesocosms: sediment–water DNi and DCr fluxes and porewater concentrations

Averaged across the three olivine-amended treatments, DNi fluxes were significantly higher than in the control during both sessions ($p < 0.0001$; Fig. 4b; Table C7). The magnitude of the treatment response also differed significantly between sessions ($p < 0.001$; Table C4). During session 3, the estimated DNi flux was $3.28 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the Fine–6% treatment (95% CI: 2.11–4.43) and $4.31 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the Fine–10% treatment (95% CI: 3.31–5.31), compared with $0.04 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the control (95% CI: -0.98 – 1.05) and $0.40 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the Coarse–10% treatment (95% CI: -0.77 – 1.57). The Fine–10% flux was significantly higher than the Coarse–10% flux ($p < 0.0001$), but did not differ significantly from the Fine–6% flux ($p = 0.19$). During session 6, the estimated DNi flux increased to $5.25 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the Fine–6%



treatment (95% CI: 4.07–6.45) and $8.74 \mu\text{mol m}^{-2} \text{ day}^{-1}$ in the Fine–10% treatment (95% CI: 7.71–9.79), whereas fluxes again remained low in the control ($0.10 \mu\text{mol m}^{-2} \text{ day}^{-1}$; 95% CI: -0.92 – 1.15) and Coarse–10% treatment ($0.65 \mu\text{mol m}^{-2} \text{ day}^{-1}$; 95% CI: -0.57 – 1.87). In session 6, the Fine–10% flux was significantly higher than both the Fine–6% and Coarse–
405 10% fluxes ($p < 0.0001$ for both comparisons). Notably, the Coarse–10% DNi flux estimates were approximately 11 and 6 times higher than the corresponding control estimates in sessions 3 and 6, respectively, although neither difference was statistically significant ($p = 0.64$ and $p = 0.50$).

The ratio of DNi fluxes in the Fine–10% and Fine–6% treatments was 1.31 during session 3 and 1.66 during session 6, compared with a ratio of 1.67 between their olivine loading levels. DNi fluxes therefore scaled approximately with olivine
410 loading during both sessions, albeit a bit less in session 3. At 10% loading, the estimated DNi flux in the fine-grained treatment was 10.8 and 13.4 times that in the coarse-grained treatment during sessions 3 and 6, respectively. These ratios were comparable to or somewhat greater than the 9.12-fold difference in BET surface area between the fine and coarse olivine (7.329 versus $0.804 \text{ m}^2 \text{ g}^{-1}$, respectively; Table 1), indicating that the grain-size effect on DNi flux was broadly consistent with the difference in BET surface area.

415 In both fine-grained treatments, porewater DNi concentrations were highest within the upper 5 cm of sediment and generally decreased to near-zero values with increasing depth (Fig. 5b). Concentrations above $\sim 0.1 \mu\text{mol L}^{-1}$ persisted through the upper 7.5 cm of the sediment. In the Coarse–10% treatment, elevated concentrations were observed in the overlying water, but rapidly declined to near-zero levels in the sediment. DNi concentrations remained near-zero throughout the included control mesocosms. In the overlying water (depth -1.5 cm; Fig. 5b), concentrations reached $0.5 \mu\text{mol L}^{-1}$ in the two fine-
420 grained treatments and $0.25 \mu\text{mol L}^{-1}$ in the coarse-grained, while they remained near-zero in the control.

No evidence of olivine-induced DCr release was detected, as none of the olivine treatments differed significantly from the control ($p > 0.13$; Fig. 4c; Tables C5, C7). Estimated DCr fluxes were close to zero during session 3, ranging from -0.08 to $0.06 \mu\text{mol m}^{-2} \text{ day}^{-1}$. Flux estimates were generally more negative during session 6, ranging from -0.26 to $-0.12 \mu\text{mol m}^{-2} \text{ day}^{-1}$ but this pattern occurred in both the control and olivine-amended treatments. Neither olivine loading level nor grain
425 size significantly affected DCr fluxes ($p = 0.95$ and $p = 0.96$, respectively). Porewater DCr concentrations were broadly similar across treatments and showed no consistent pattern, except for a pronounced deviation in the upper centimetres of the Fine–6% profile (Fig. 5c).

The relationship between the A_T and DNi fluxes showed distinct treatment- and session-specific patterns (Fig. 4d). During session 3, the model-derived estimates for both fine-grained treatments fell above the theoretical relationship expected from
430 stoichiometric dissolution. During session 6, both treatments were closer to the theoretical relationship, with the Fine–10% estimate lying almost directly on the theoretical line and the Fine–6% estimate remaining slightly above it. In contrast, the Coarse–10% treatment remained substantially above the theoretical relationship for coarse olivine during both sessions, as a result of relatively high A_T fluxes paired with low DNi fluxes. Individual mesocosm estimates were variable but broadly reflected these treatment- and session-specific patterns.



3.4 Mesocosms: tissue trace metal content and pseudofeces counts of lugworms

At the time of sample collection, lugworm length and dry weight medians were 31.7 mm and 19.8 mg (Fig. A1), consistent with juvenile sizes reported for *A. marina* (De Wilde and Berghuis, 1979), and were variable but not significantly different among treatments ($p = 0.87$ and $p = 0.52$, respectively).

Ni concentrations in lugworm tissues differed significantly between treatments ($\chi^2(3) = 79.37$, $p < 0.0001$; Fig. 6a). The highest concentrations were observed in the two fine-grained treatments at a median of $1.45 \mu\text{mol g}^{-1}$ d.w., which is more than ~10 times higher than the control ($0.15 \mu\text{mol g}^{-1}$ d.w.). The Coarse-10% treatment showed an intermediate median value of $0.84 \mu\text{mol g}^{-1}$ d.w. Post-hoc comparisons confirmed that all olivine treatments showed significantly higher tissue Ni concentrations than the control ($p < 0.001$). Additionally, Ni concentrations in the Fine-10% treatment were significantly higher compared to the Coarse-10% treatment ($p < 0.01$). Cr concentrations in lugworm tissues were two to three orders of magnitude lower than Ni but nevertheless differed significantly among treatments ($\chi^2(3) = 29.75$, $p < 0.0001$; Fig. 6b). Median Cr concentrations were highest in the Fine-10% ($0.011 \mu\text{mol g}^{-1}$ d.w.) and Fine-6% ($0.0094 \mu\text{mol g}^{-1}$ d.w.) treatments, compared to lower levels in the Coarse-10% ($0.00558 \mu\text{mol g}^{-1}$ d.w.) and Control ($0.00019 \mu\text{mol g}^{-1}$ d.w.) groups. Post-hoc comparisons confirmed that both fine-grained treatments had significantly higher Cr concentrations compared to the control ($p < 0.01$). The Coarse-10% treatment did not differ significantly from the control ($p = 0.46$).

Lugworm tissue content of Zn, included as a reference element expected to remain stable across treatments and to facilitate comparison with literature values, did not differ significantly among treatments ($\chi^2(3) = 1.10$, $p = 0.78$). Median values ranged from 0.84 to $0.88 \mu\text{mol g}^{-1}$ (Fig. A2), indicating consistent Zn concentrations irrespective of olivine addition.

Counts of adult lugworm pseudofeces in the mesocosms showed an overall declining trend across all treatments over the course of the experiment (Fig. 6c). An initial decline occurred in the two fine-grained treatments after olivine addition, whereas counts initially remained stable in the Coarse-10% and control treatments. After olivine addition, some lugworms in the fine-grained treatments were observed on the sediment surface covered in fine olivine particles, and several individuals showed visible bleeding (Fig. A3). During the second half of the experiment, counts were below 10 in most mesocosms, despite efforts to supplement lugworm populations with field-collected individuals.

By the end of the experiment, adult pseudofeces counts decreased to zero in most mesocosms. These counts reflect adult lugworm presence and activity only, rather than the abundance of the entire lugworm population. Dense mats of small pseudofeces from juvenile lugworms appeared in nearly all mesocosms, but the timing varied: they were first observed before olivine addition in some mesocosms and afterwards in others. Because juvenile pseudofeces counts were capped at 100, their absolute numbers are unknown (Fig. A4). Small pseudofeces remained present across all mesocosms, even as adult numbers declined.

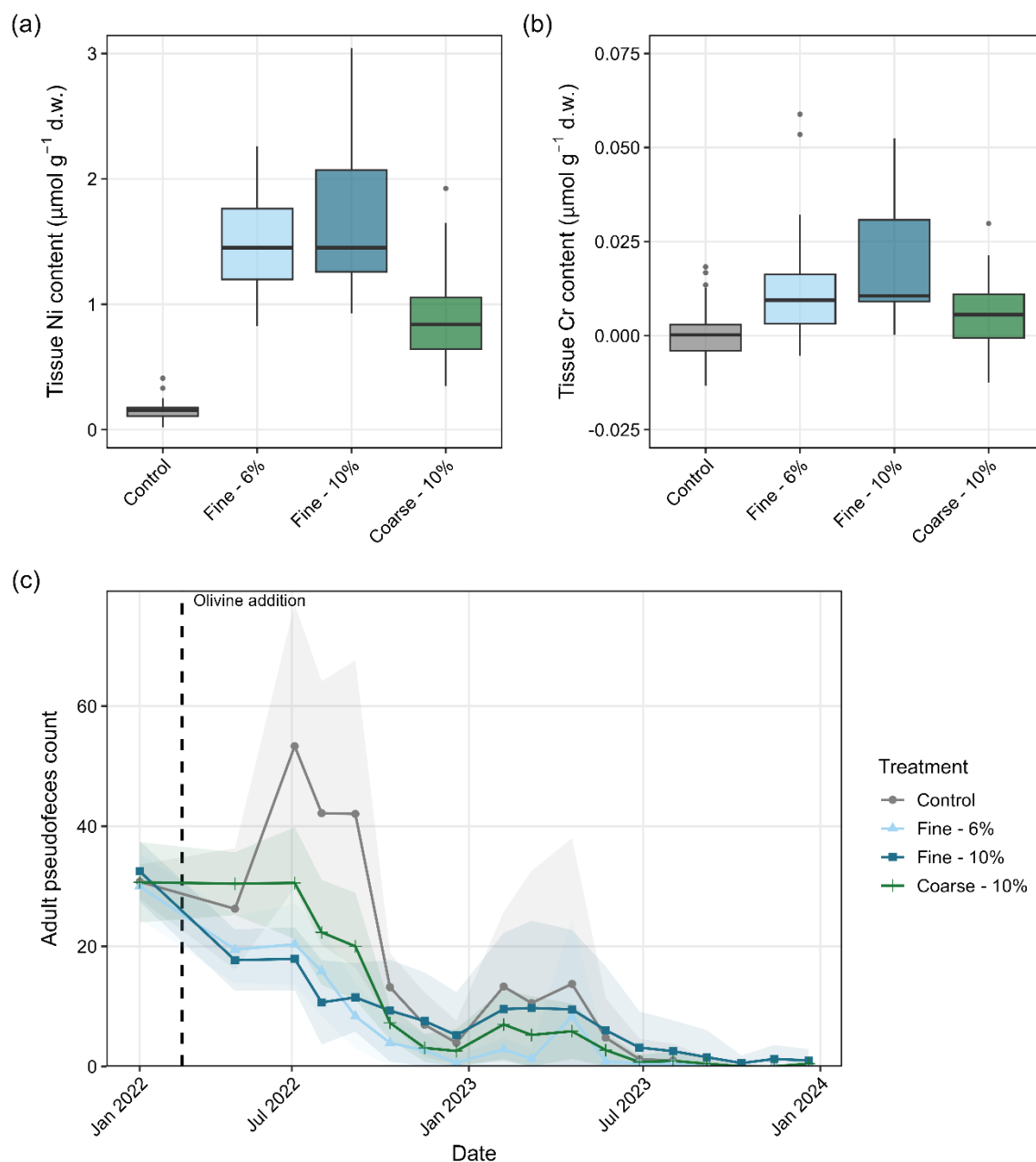


Figure 6. Boxplots showing (a) nickel (Ni) and (b) chromium (Cr) content ($\mu\text{mol g}^{-1} \text{ d.w.}$) in tissues of lugworms collected at the end of the mesocosm experiment. (c) Counts of adult lugworm pseudofeces over the course of the experiment. Points indicate treatment means per session, and shaded areas represent $\pm$ SD among mesocosms. The dashed line marks the time of olivine addition. Colours and symbols indicate treatments.



470 4 Discussion

4.1 Bioturbation enhances A_T and DNi release from pure olivine sand

The “benthic weathering engine” hypothesis proposes that bioturbation by benthic macrofauna may enhance olivine dissolution through two mechanisms: sediment ingestion and bioirrigation (Meysman and Montserrat, 2017). During sediment ingestion, olivine grains are exposed to a chemically reactive gut environment. In the gut, a combination of low
475 pH, microbial and enzymatic activity, and mechanical abrasion may enhance silicate mineral dissolution (Mayer et al., 1997; Needham et al., 2004). Bioirrigation, i.e. the flushing of animal burrows, promotes export of mineral dissolution products from the sediment, which stimulates sustained dissolution by preventing the porewater from reaching saturation (Meysman et al., 2006; Meysman and Montserrat, 2017; Geerts et al., 2025a). Furthermore, bioirrigation deepens oxygen penetration and stimulates aerobic organic matter mineralisation (Aller and Cochran, 2019). The resulting CO_2 production generates
480 acidity that can promote “metabolic dissolution”, a mechanism known to enhance $CaCO_3$ dissolution in sediments (Jahnke et al., 1997; Rao et al., 2014).

The microcosm experiment conducted here provides proof of concept for this benthic weathering engine hypothesis. Both A_T and DNi accumulation were higher in the bioturbated olivine sediment than in the treatment without lugworms (Figs. 2a, b), indicating that bioturbation enhanced the dissolution of olivine and subsequent export of weathering products. This aligns
485 with previous work highlighting bioturbation as a key process regulating A_T release from natural coastal sediments (Braeckman et al., 2014; Rao et al., 2014; Michaud et al., 2021).

The observed flux ratios of $A_T : DNi$ provide additional support for efficient olivine dissolution and solute export under bioturbated conditions. Ratios from bioturbated microcosms clustered around the theoretical value expected from stoichiometric olivine dissolution (Fig. 2c), suggesting that most of the generated A_T was efficiently exported to the
490 overlying water, without substantial net loss. In contrast, the $A_T : DNi$ ratio without bioturbation was lower than the theoretical value, indicating lower A_T release relative to DNi (Fig. 2c). Without bioirrigation, porewater accumulation of weathering products likely occurred in this diffusion-driven system, potentially slowing down the olivine dissolution rate through increased saturation (Geerts et al., 2025a). The associated changes in porewater carbonate chemistry may also have increased $CaCO_3$ saturation and promoted secondary precipitation, thereby consuming part of the generated A_T (Morse et al.,
495 2007). The same mechanism could also explain the decline in overlying water A_T during the second half of the experiment (Fig. 2a), while DNi concentrations continued to increase, because elevated saturation states can initiate $CaCO_3$ precipitation and subsequent A_T loss (Moras et al., 2022). However, because carbonate saturation states and solid-phase $CaCO_3$ formation were not assessed, this explanation remains speculative.

The microcosm experiment was conducted with pure olivine sand. Although informative as an end-member, this deliberately
500 simplified, high-exposure scenario lacked natural sediment and therefore many of the biogeochemical interactions that may influence olivine dissolution or A_T export. The mesocosm experiment therefore examined olivine amendment under more environmentally realistic conditions, using natural intertidal sediments inhabited by bioturbating lugworms.



4.2 Olivine amendment increases A_T fluxes, but the treatment effect weakens over time

In the mesocosm experiment, olivine amendment produced a statistically significant increase in sediment–water A_T fluxes. However, we observed substantial variation in A_T fluxes within treatments and between sessions (Fig. 3b). Similar variability has been reported in shorter-term sediment incubation experiments of olivine-based mERW lasting ~3 months (Fuhr et al., 2023). In that study, A_T fluxes of olivine-amended sediments were not different from unamended controls, highlighting the difficulty of resolving the effects of mineral addition against a variable natural background. Evidence from longer-term mesocosm experiments (~1 year) nevertheless indicates that olivine amendment can enhance sedimentary A_T release (Fuhr et al., 2025). In this long-term experiment, an initial 167 % increase in A_T fluxes was observed within two weeks of olivine addition, from $6.21 \text{ mmol m}^{-2} \text{ day}^{-1}$ in the controls to $16.6 \text{ mmol m}^{-2} \text{ day}^{-1}$ in the amended treatment. That study used very fine olivine ($d_{50} = 5.85 \text{ }\mu\text{m}$), whereas the material in our mesocosm experiment was considerably coarser (d_{50} values of 34 and 158 μm for the fine and coarse fractions, respectively; Table 1). Despite this difference, our flux estimates represented comparable relative increases of 174 % in Fine–6%, 152 % in Fine–10%, and 109 % in Coarse–10%.

In general, finer olivine particles would be expected to dissolve more rapidly because they provide a larger reactive surface area per unit of mass applied (Oelkers et al., 2018; Geerts et al., 2025a). However, despite the large difference in grain size and A_{BET} between the two olivine fractions (Table 1), neither grain size nor loading had a statistically significant effect on sediment–water A_T fluxes. One possible explanation for this discrepancy is the recently described “additionality problem”: enhanced A_T generation from anthropogenic mineral additions may increase CaCO_3 saturation and thereby suppress natural A_T generation from CaCO_3 dissolution, reducing the net increase in A_T (Bach, 2024). It is possible that the finer olivine in our experiment dissolved more rapidly within the sediment, but that the resulting increase in olivine-derived A_T was partly offset by a greater reduction in carbonate-derived A_T . However, as we did not partition the individual sources of A_T , we cannot determine to what extent such buffering may have occurred.

Furthermore, the magnitude of the treatment effect declined over time (Figs. 3a, b). A similar temporal trend was observed in a study by Flipkens et al. (2023b), where rotating-bottle experiments were used to assess the effects of bedload transport on olivine dissolution. In these experiments, initially elevated A_T release from olivine also decreased over time. Scanning electron microscopy (SEM) analysis on fresh olivine revealed that grains were covered by very small adhering particles ($\leq 10 \text{ }\mu\text{m}$), likely generated during mechanical crushing. Because these very fine particles dissolve more rapidly than larger grains, they were proposed to have caused the initially elevated A_T fluxes. The olivine used in our mesocosms came from the same source (Sibelco mine, Åheim, Norway), and therefore a similar effect of these fine adhering particles may have contributed to the stronger initial treatment effect.

Another possible explanation for the declining A_T fluxes is that bioturbation by the resident lugworm population progressively mixed the initially surface-deposited olivine into deeper sediment layers (Kristensen et al., 2012; Aller and Cochran, 2019). In the mesocosms, porewater A_T concentrations gradually increased with sediment depth and were generally higher in the olivine-amended treatments (Fig. 5a). The increased concentrations of A_T and other mineral weathering



products locally raise saturation states in the porewater, thereby gradually slowing down the olivine dissolution rate within the sediment (Geerts et al., 2025a). Therefore, vertical redistribution of olivine provides a plausible mechanism for the decreased treatment effect over time. However, sedimentary olivine content was not measured, and so we can only provide indirect evidence for this mechanism.

540 A final possible explanation for the declining A_T treatment effect is the decrease in adult lugworm activity over the course of the experiment. Adult pseudofeces counts declined broadly over the same period as mean A_T fluxes (Figs. 3b, 6c). Reduced adult activity may have decreased bioirrigation and sediment reworking, thereby contributing to this pattern. Larger polychaetes have been shown to exert a stronger influence on organic matter mineralisation and associated metabolic dissolution compared to smaller individuals (Michaud et al., 2021). Although juveniles remained present in all mesocosms
545 (Fig. A4), their activity may not have fully compensated for the declining activity of adult lugworms. However, pseudofeces counts provide only an indirect proxy for lugworm activity and do not quantify bioirrigation. In order to accurately constrain the effects of lugworm activity, future studies should aim to combine pseudofeces counting with direct measurements of bioirrigation, for example by using fluorescent tracers (De Borger et al., 2020). The potential contribution of declining lugworm activity to the weakening A_T treatment effect could thus not be quantified here.

550 **4.3 Sedimentary DNi export depends strongly on olivine grain size**

Unlike A_T , sediment–water fluxes of DNi showed a clear response to olivine grain size and a weaker, session-dependent response to loading (Fig. 4b). Estimated DNi fluxes from the fine-grained treatments were approximately 50–110 times those of the corresponding controls. At equal loading, the DNi flux in the Fine–10% treatment was 10.8 and 13.4 times that in the Coarse–10% treatment during sessions 3 and 6, respectively. These ratios are comparable or somewhat greater than the 9.1-
555 fold difference in BET surface area between these two fractions (Table 1), indicating that the grain size effect on DNi export scaled broadly with the difference in reactive surface area (Oelkers et al., 2018; Geerts et al., 2025a). The somewhat greater ratios could indicate either lower DNi release per unit surface area of coarse olivine or retention of a larger proportion of the released Ni within the sediment. The flux measurements alone cannot distinguish between these processes.

Within the fine-grained treatments, the ratio between the 10% and 6% treatments was 1.31 during session 3 and 1.66 during
560 session 6, approximately following their 1.67-fold difference in olivine loading. Fine–10% did not differ significantly from Fine–6% during session 3 but did during session 6, indicating that the loading effect was weaker than the grain-size effect and variable between sessions. Although the flux estimates in the Coarse–10% treatment were approximately 11 times the control during session 3 and 6 times during session 6, neither difference was statistically significant. While these results do not demonstrate an absence of DNi release from coarse olivine, its flux estimates were approximately one order of
565 magnitude lower than those in the fine-grained treatments, demonstrating that DNi export was substantially smaller from the coarse olivine, an effect that was not present for the A_T fluxes.

DNi release during olivine dissolution in seawater has previously been documented in laboratory experiments (Montserrat et al., 2017; Fuhr et al., 2022; Flipkens et al., 2023a, b). In sediment-based studies, Fuhr et al. (2023, 2024) measured DNi in



porewater and bottom water following olivine amendment, but concentrations remained below their detection limit of ~ 0.2 $\mu\text{mol L}^{-1}$, preventing flux calculations. Jankowska et al. (2026) also measured porewater DNi concentrations after a field trial, but did not quantify its sediment–water flux. To our knowledge, our results therefore provide the first direct quantification of sediment–water DNi fluxes from olivine-amended natural coastal sediments and demonstrate that enhanced DNi export can remain detectable several months after mineral addition.

The observed DNi release was accompanied by elevated concentrations in the overlying water of the olivine-amended mesocosms, reaching $\sim 0.5 \mu\text{mol L}^{-1}$ in the fine-grained and $\sim 0.25 \mu\text{mol L}^{-1}$ in the coarse-grained treatments (Fig. 5b). These concentrations exceeded the European environmental quality standard (EQS) of $0.147 \mu\text{mol L}^{-1}$ for Ni in surface waters (European Commission, 2008; Flipkens et al., 2021), while chronic guideline values as low as $0.102 \mu\text{mol L}^{-1}$ have been recommended to ensure protection of marine biota (Gissi et al., 2020). However, these protective guidelines are not direct toxicity thresholds, and their exceedance does not imply that adverse effects occurred.

Moreover, the mesocosm setup used here contained a confined water reservoir of ~ 600 L, allowing released DNi to accumulate. In a recent field trial of mERW, olivine amendment temporarily increased porewater DNi concentrations up to $\sim 0.7 \mu\text{mol L}^{-1}$, but produced no detectable increase in the overlying water (Jankowska et al., 2026). After 3 months, porewater concentrations no longer differed significantly from those at control sites. These findings illustrate that water column exposure depends strongly on local circulation and residence time, and that rapid dilution can occur under dynamic conditions, whereas poorly flushed systems may be more vulnerable to DNi accumulation (Flipkens et al., 2021; Geerts et al., 2025b). Nevertheless, rapid dilution alone does not determine suitability of an mERW field site, because sufficient surface water retention is also required for atmospheric CO_2 equilibration and effective monitoring (He and Tyka, 2023; Guo et al., 2025).

Olivine amendment enhanced DNi fluxes but produced no detectable DCr flux in our experiment (Fig. 4c). This contrast reflects the distinct mineralogical associations of Ni and Cr in olivine. Ni is incorporated directly in the crystal lattice of olivine, where Ni^{2+} can substitute for the associated divalent cations (Mg^{2+} , Fe^{2+}). Consequently, when olivine dissolves, Ni is released to the surroundings (Santos et al., 2015; Montserrat et al., 2017; Flipkens et al., 2023b). Cr on the other hand, is incorporated in olivine-rich rocks in the form of chromite (FeCr_2O_4) inclusions, which are insoluble in water (Santos et al., 2015; Flipkens et al., 2021). Our results are consistent with the recent field trial by Jankowska et al. (2026), where olivine amendment increased porewater concentrations of DNi, but not DCr.

A noteworthy increase in DCr concentrations occurred in the upper centimetres of the Fine–6% treatment, indicating that localised Cr mobilisation cannot be excluded (Fig. 5c). However, its absence from the other porewater profiles and from the sediment–water fluxes provides no evidence of a consistent treatment response. One caveat is that locally released Cr(III) could potentially be oxidised to the more mobile and toxic Cr(VI) through reactions with manganese (Mn) oxides in Mn-rich sediments, warranting site-specific risk assessments (Zhuang et al., 2025). Nevertheless, while Cr toxicity should not be disregarded completely, the collective results support previous assessments identifying Ni release as the principal trace metal



of concern associated with olivine-based mERW (Montserrat et al., 2017; Bach et al., 2019; Flipkens et al., 2021; Zhuang et al., 2025).

The contrasting treatment responses of A_T and DNi fluxes suggest a decoupling between the export of these solutes. During session 3, A_T fluxes differed markedly among treatments ranging from -1.16 to $8.93 \text{ mmol m}^{-2} \text{ day}^{-1}$, whereas by session 6, they had converged between 4.21 and $4.64 \text{ mmol m}^{-2} \text{ day}^{-1}$ (Fig. 4a). Despite this convergence, DNi fluxes during session 6 remained strongly elevated in Fine-6% ($5.25 \text{ } \mu\text{mol m}^{-2} \text{ day}^{-1}$) and Fine-10% ($8.74 \text{ } \mu\text{mol m}^{-2} \text{ day}^{-1}$), consistent with sustained olivine dissolution in these treatments. Consequently, their A_T : DNi relationships approached the theoretical ratio expected from stoichiometric dissolution. The similarity in A_T fluxes among the fine-grained treatments and the control, despite pronounced differences in DNi export, provides indirect support for the additionality problem described in Sect. 4.2. Specifically, continued olivine dissolution did not produce a corresponding increase in net A_T export, consistent with olivine-derived A_T being offset by suppression of natural A_T generation through carbonate dissolution (Bach, 2024; Geerts et al., 2025a). This pattern was less apparent during session 3 and in Coarse-10% during both sessions, for which the A_T : DNi relationships remained above the corresponding theoretical line (Fig. 4d). This excess of A_T relative to DNi may reflect contributions from other A_T sources, retention of released Ni within the sediment, or both. Potential mechanisms for sedimentary Ni retention are considered in the following section.

4.4 Sedimentary retention may limit DNi export

Although the two experiments differed in design, comparison of the A_T : DNi flux ratio in the bioturbated microcosms with the relationship between A_T and DNi fluxes in the mesocosms suggests that addition of a natural sediment matrix altered the export of DNi. In the bioturbated microcosms, bioirrigation led to sustained porewater exchange and the ratio approached the theoretical value (Fig. 2c). In contrast, the relationships in the olivine-amended mesocosms exceeded their corresponding theoretical values in most cases, except for the fine-grained treatments in session 6 (Fig. 4d). This pattern suggests that less DNi was exported per unit of A_T when olivine was mixed into natural sediment. Furthermore, porewater profiles of DNi in the mesocosms showed only slightly elevated concentrations in the upper 7.5 cm of the sediment (Fig. 5b). These findings suggest that under more natural conditions, Ni may be retained in sedimentary solid phases rather than remaining dissolved in the porewater.

Several mechanisms could plausibly retain Ni in natural sediments. Following its release as Ni^{2+} , Ni can bind to organic ligands such as carboxyl and amino groups in particulate organic matter (Sheng et al., 2004). Ni can also adsorb to Fe or Mn (oxyhydr)oxides and, because of its strong affinity for Mn oxides, be retained through surface complexation and co-precipitation during Mn^{2+} oxidation (Kay et al., 2001; Bruggmann et al., 2024). Upon burial into deeper anoxic zones, these redox-active phases can dissolve again and Ni^{2+} may be remobilised, but can then subsequently be retained again through co-precipitation or adsorption onto authigenic iron sulphides or pyrite (Morse and Luther, 1999; Schippers and Jørgensen, 2002; Bruggmann et al., 2024). These coupled processes could transfer Ni from dissolved to solid phases and thereby limit sediment–water DNi export.



635 However, because neither solid phase Ni nor the individual processes contributing to net A_T generation were quantified, their
respective contributions to the observed A_T : DNi relationships could not be determined. Future studies should therefore aim
to combine porewater and particulate trace metal analyses with stable isotope measurements that could help partition the
contributions of olivine weathering, carbonate dissolution and other sedimentary processes to net A_T generation (Fuhr et al.,
2023; Kreuzburg et al., 2025). Nevertheless, Ni retention in sediments does not eliminate biological exposure, as both
640 porewater and solid phases provide potential exposure pathways for benthic organisms (Flipkens et al., 2021).

4.5 Deposit feeding lugworms accumulate Ni following olivine exposure

Tissue Ni content of lugworms increased following olivine exposure in both experiments, demonstrating biological uptake
under both the high-exposure microcosm and semi-natural mesocosm conditions. In the mesocosms, higher tissue Ni
accumulation broadly followed the grain size response in DNi export (Fig. 4b): concentrations were highest in the two fine-
645 grained treatments and intermediate for the coarse-grained olivine (Fig. 6a). However, the difference between the two grain
size fractions was considerably smaller compared to the difference in DNi fluxes. Furthermore, tissue Ni content also did not
have a clear response to loading level, as concentrations were similar in Fine-6% and Fine-10%, suggesting that
bioaccumulation did not scale proportionally with olivine loading, although this corresponds to the DNi flux pattern during
session 3 (Fig. 4b).

650 Bioaccumulation of Ni in benthic invertebrates exposed to olivine has been previously examined in laboratory experiments.
After 35 days of exposure to natural sediment containing 1–100% fine olivine ($d_{50} = 24 \mu\text{m}$), Ni concentrations in the
amphipod *Gammarus locusta* reached a maximum of $3.7 \mu\text{mol g}^{-1}$ d.w. when pure olivine sand was used (Flipkens et al.,
2023a). At the same loading level as our Fine-10% mesocosm treatment, concentrations in the amphipods reached
 $\sim 0.8 \mu\text{mol g}^{-1}$ d.w., compared to $1.45 \mu\text{mol g}^{-1}$ d.w. in our lugworms (Fig. 6a). These concentrations are of the same order of
655 magnitude, although the lugworms in our mesocosms were exposed for much longer than 35 days. Moreover, the amphipods
were not depurated prior to analysis, which may have increased their measured metal concentrations (Flipkens et al., 2023a).
An experiment with the polychaete *Alitta virens*, where animals were left to depurate prior to analysis, showed more limited
accumulation of Ni ($\sim 0.31 \mu\text{mol g}^{-1}$ d.w.) after exposure to pure olivine sand for 28 days (Gogina et al., 2022; Jankowska et
al., 2024). In comparison, lugworms in our pure olivine microcosms accumulated Ni up to $2.7 \mu\text{mol g}^{-1}$ d.w. after 28 days
660 (Fig. 2d). Therefore, our results suggest a link between Ni bioaccumulation and feeding ecology. While *A. virens* is an
omnivorous predator, scavenger and surface deposit feeder, *A. marina* is a depth deposit feeder that ingests large amounts of
sediment (Cadée, 1976; Nielsen et al., 1995; Retraubun et al., 1996). Upon ingestion, particles are exposed to a highly
reactive chemical environment in the worm gut that can enhance metal solubilisation at levels that are several orders of
magnitude higher than those occurring in the surrounding seawater or sediment (Mayer et al., 1997; Chen and Mayer, 1999;
665 Chen et al., 2000). Ni mobilised from ingested particles can form metal–ligand complexes, potentially facilitating uptake
across the gut epithelium (Chen et al., 2000). As such, gut-mediated metal mobilisation provides a plausible mechanism for
enhanced metal uptake by bulk sediment deposit feeders such as *A. marina*. Direct exposure to ingested particles and



subsequent metal mobilisation may also help explain why the difference between grain size fractions was considerably smaller for tissue Ni content than for DNi export.

670 The accumulation of Ni in lugworm tissues demonstrates exposure and uptake, but does not allow conclusions about adverse toxicological effects. In the amphipod *G. locusta*, chronic exposure to sediment containing 10% or more fine olivine led to reduced growth and reproduction (Flipkens et al., 2023a). In contrast, no effects on growth or survival were observed in the chronic, pure olivine exposure study with the polychaete worm *A. virens* and the bivalve *Macoma nasuta*, although the latter exhibited reduced burrowing activity (Jankowska et al., 2024). Similarly, a one-year field trial found no increases in Ni
675 accumulation or adverse effects on biomass of oysters at an olivine-amended intertidal beach (Jankowska et al., 2026). Importantly, oysters are suspension feeders rather than deposit feeders and therefore do not experience the same exposure pathway as the lugworms in our study. The absence of Ni accumulation or adverse effects on oyster biomass can therefore not be generalised to the benthic community as a whole. Because *A. marina* is an important prey for fish, crabs and seabirds, its accumulation of Ni also presents a potential exposure pathway to higher trophic levels (Wells, 1966; Bergman et al.,
680 1988). However, evidence of Ni biomagnification through marine food webs is limited and trophic transfer to predators seems unlikely to occur (Bryan and Langston, 1992; Gray, 2002).

Olivine amendment also affected Cr concentrations in lugworms, with significantly higher concentrations in the fine-grained treatments than in the control (Fig. 6b), despite the absence of detectable olivine-induced DCr export (Fig. 4c). Nevertheless, absolute Cr concentrations were two to three orders of magnitude lower than those of Ni (Fig. 6a), despite being present in
685 olivine at similar levels (Table 1). Furthermore, Cr occurs in olivine as Cr(III), which has low potential for toxicity, and the more bioavailable and toxic Cr(VI) is unlikely to form under normal seawater conditions, although localised oxidation may occur in Mn-rich sediments (DesMarias and Costa, 2019; Flipkens et al., 2021; Zhuang et al., 2025). Overall, although the statistical treatment effect on tissue Cr concentrations should be acknowledged, the biological relevance of this response remains uncertain and appears minor relative to Ni.

690 One limitation in the mesocosm experiment is that we observed a thin layer of sediment residue in 73% of lugworm samples after acid digest. Therefore, we cannot exclude that some olivine particles were present in this sediment layer and may have contributed to an upward shift in Ni or Cr tissue concentrations during digestion. Median Ni, Cr and Zn concentrations in control lugworms from the mesocosm experiment nevertheless fell within ranges reported for *A. marina* from natural intertidal environments, thus supporting the plausibility of our baseline measurements (Bird et al., 2011; Casado-Martinez et al., 2013). Moreover, the broadly corresponding responses of tissue Ni accumulation (Fig. 6a) and sediment–water DNi
695 fluxes (Fig. 4b) support a genuine treatment effect on the release of Ni and its bioaccumulation after olivine amendment, even if residual particles may have influenced the final tissue concentrations.

4.6 Adult lugworm activity declines across treatments as juveniles recruit

Despite the increased exposure and uptake, lugworm activity showed no clear long-term response to olivine amendment,
700 leaving the ecological relevance of Ni bioaccumulation uncertain. Adult pseudofeces counts declined over time in all



treatments, including the control (Fig. 6c), and the cause of this treatment-wide decline could not be determined. In contrast, small juvenile pseudofeces were observed across all mesocosms, either before or after olivine amendment (Fig. A4), indicating that juvenile lugworms were present and active independent of treatment. This demonstrates that conditions in all mesocosms were suitable for continued recruitment, although sublethal effects from chronic Ni exposure in the olivine-amended treatments cannot be excluded.

Although olivine amendment had no clear long-term effect on lugworm activity, an acute response was observed in the fine-grained treatments. Immediately following addition of fine olivine, adult pseudofeces counts declined and some lugworms emerged at the sediment surface, covered in olivine particles and showing visible bleeding (Figs. 6c, A3). No comparable decline in pseudofeces occurred in the control or Coarse-10% treatments. Freshly ground olivine typically consists of angular grains with very sharp edges (Montserrat et al., 2017; Flipkens et al., 2023b). Particle sharpness has been proposed to cause avoidance behaviour in marine gastropods and reduced burrowing activity in bivalves exposed to olivine (Flipkens et al., 2024; Jankowska et al., 2024).

The deposition of very fine particles itself provides another possible explanation for the initial decline in adult pseudofeces counts. Previous work has shown that deposition of mud layers as thin as 2 cm can impair burrow maintenance and faecal casting in lugworms, thereby substantially reducing their activity (Montserrat et al., 2011; Mestdagh et al., 2018). Because the observed effects occurred immediately after olivine addition, physical disturbance of the sediment and abrasion by sharp particles provide more plausible explanations than effects resulting from gradual Ni accumulation. Overall, the pseudofeces data provided no evidence of a sustained treatment-specific ecological response in adult activity or juvenile presence, although the acute effect following fine olivine addition warrants further investigation.



720 5 Conclusions

Our microcosm experiment provides proof of concept for the benthic weathering engine hypothesis. Bioturbation clearly enhanced the release of both A_T and DNi , albeit under simplified conditions using pure olivine sand. In natural sediment, olivine amendment increased A_T fluxes overall, although neither grain size nor loading had a significant effect and differences between treatments weakened over time. In contrast, fine-grained olivine substantially increased DNi release
725 from the sediment and Ni accumulation in lugworm tissues. In comparison, there was no evidence for olivine-induced DCr release, and tissue Cr accumulation remained minor relative to Ni. Adult lugworm activity declined similarly across treatments, while juvenile recruitment occurred in all mesocosms, providing no evidence of an olivine-induced effect on the lugworm population.

The primary ecological concern associated with olivine-based mERW therefore remains the release of Ni. Dilution may
730 reduce water-column exposure at well-flushed field sites, but it does not eliminate benthic exposure through enriched porewater or the ingestion of Ni-bearing particles (Flipkens et al., 2021; Jankowska et al., 2026). The elevated tissue Ni concentrations measured here demonstrate that such exposure can result in biological uptake, although its ecological consequences remain unresolved.

Across the full 15-session experiment, coarse olivine produced net A_T fluxes comparable to those of fine olivine. However,
735 its DNi flux estimates were approximately one order of magnitude lower than those of fine olivine during both trace metal sessions, and Ni accumulation in lugworm tissues was also lower. Moreover, grinding olivine to fine particle sizes substantially increases the energy demand and lifecycle emissions associated with mineral processing (Hangx and Spiers, 2009; Strefler et al., 2018; Foteinis et al., 2023). Under the conditions examined here, coarser olivine may therefore provide a more favourable balance between A_T generation, associated Ni exposure, and the economic costs and CO_2 emissions
740 associated with olivine production. The progressive weakening of the A_T treatment effect shows that short-term experiments may not adequately capture mERW performance over extended periods, highlighting the need for long-term mesocosm and field studies. Together, our findings demonstrate that coarse olivine generated net A_T fluxes comparable to fine olivine but was associated with substantially lower ecological risks from Ni release and exposure.



Appendix A – Additional figures

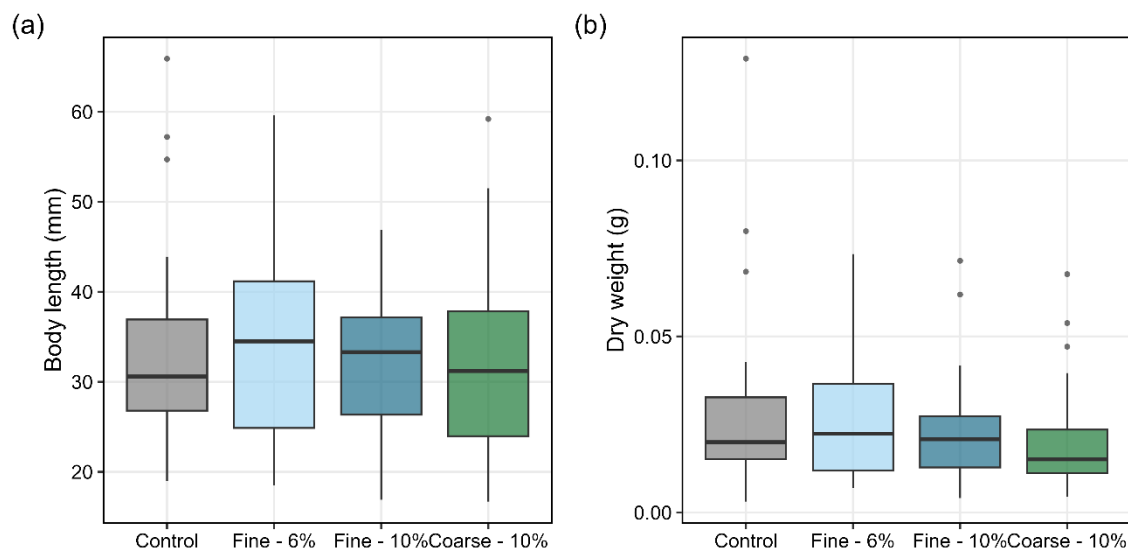


Figure A1. Boxplots showing distribution of (a) lugworm body length (mm) and (b) dry weight (g) across the four mesocosm treatments, indicated by colour.

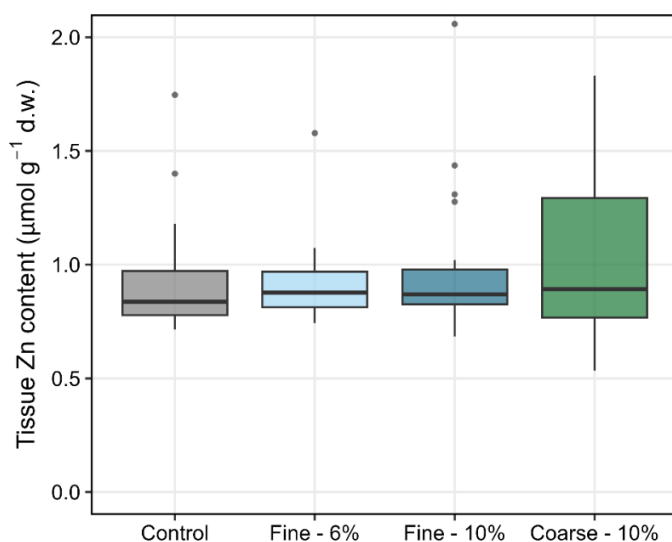


Figure A2. Boxplot showing tissue concentrations of Zn (µmol g⁻¹ d.w.) in lugworms across the four mesocosm treatments, indicated by colour.

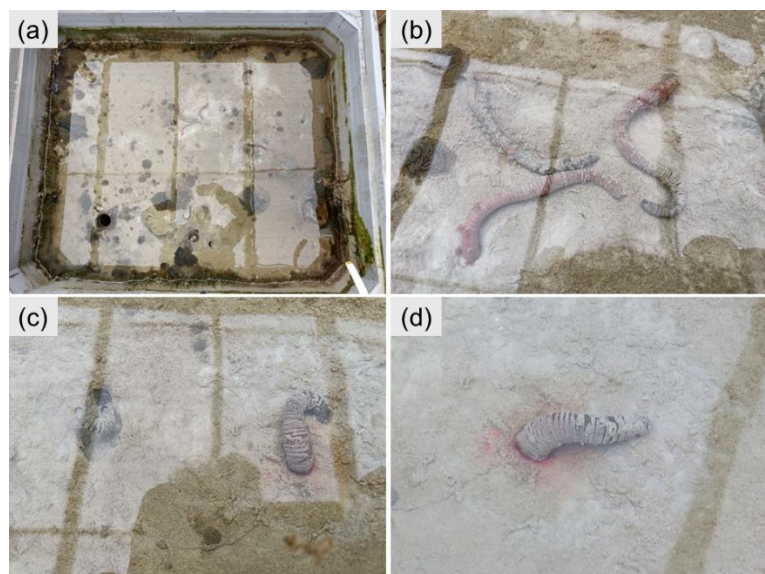


Figure A3. (a) Overview of a representative mesocosm after olivine addition of the fine grain size ($d_{10}-d_{90}$: 6–112 μm). (b) Close-up of worms that emerged from the sediment after olivine addition, partially covered in fine sediment particles. (c) and (d) close-ups of worms partly emerging from the sediment, bleeding through their skin surface. Photographs were taken on 22/02/2022.

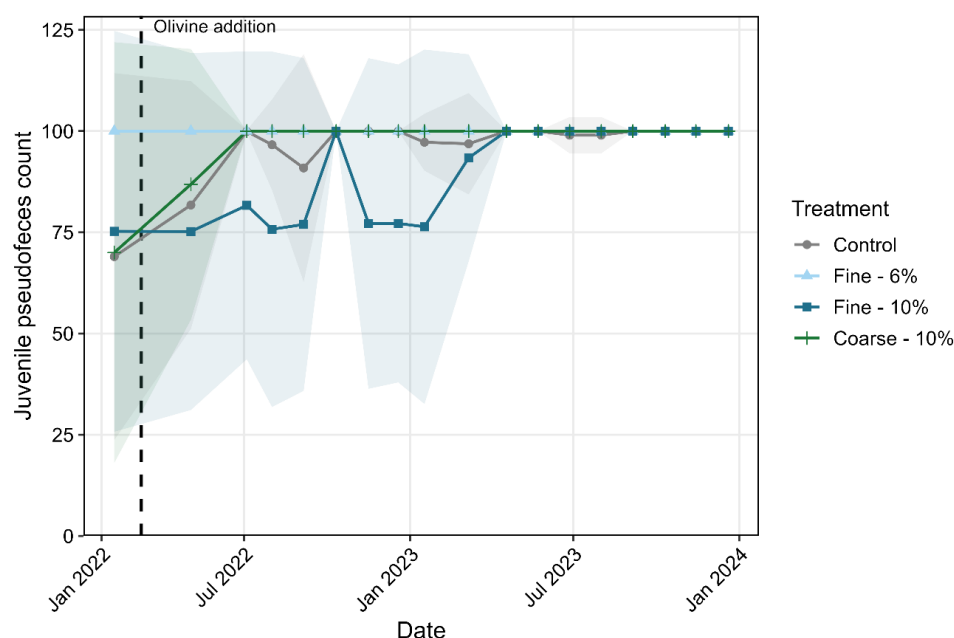


Figure A4. Counts of juvenile lugworm pseudofeces over the course of the mesocosm experiment. Points indicate treatment means per session, and shaded areas represent $\pm$ SD among mesocosms. The dashed line marks the time of olivine addition. Colours and symbols indicate treatments. Juvenile pseudofeces were counted to a maximum of 100.



760 **Appendix B – Olivine physicochemical characterisation**

The three olivine types used in the microcosm and mesocosm experiments were previously characterised by Flipkens et al. (2023a, b). The fine and coarse materials used in the mesocosm experiment correspond to the 3–99 μm and 93–332 μm fractions, respectively, characterised by Flipkens et al. (2023a), while the microcosm material was the same olivine characterised by Flipkens et al. (2023b). The following methods are derived from the supporting information associated with those two publications.

Grain size analysis

Volumetric grain-size distributions were determined by laser diffraction using a Mastersizer 2000 particle-size analyser (Malvern Panalytical, UK). Measurements followed the instrument's standard operating procedure and were performed without chemical pretreatment of the material. The particle diameters at 10%, 50% and 90% of the cumulative volume distribution were reported as d_{10} , d_{50} and d_{90} , respectively. These values are presented in Table 1 of the main manuscript.

Elemental composition

Elemental composition was determined after a modified chromite-ore microwave-assisted acid digestion (CEM Microwave Sample Preparation Note 50S-47). Dried material (0.100 g; 48 h at 60 °C) was weighed into an 80 mL quartz pressure vessel. Ultrapure orthophosphoric acid (2.6 mL; approximately 85%) and sulphuric acid (1.4 mL; $\geq 96\%$) were added, and the vessel was heated at 240 °C for 30 min in a Discover SP-D 80 microwave system (CEM Corporation, USA). After cooling, 2.0 mL of TraceMetal Grade nitric acid (67–69%) was added and the sample was heated at 240 °C for a further 15 min.

The digest was transferred to a 50 mL polypropylene tube and diluted with ultrapure water to 50 mL (an 8.3-fold dilution of the acid digest). Samples were centrifuged for 5 min; the source protocols report 3000 rpm for the microcosm material and $1600 \times g$ for the fine and coarse materials. The clear supernatant was transferred to a clean tube and analysed by inductively coupled plasma–optical emission spectrometry (ICP–OES; iCAP 6300 Duo, Thermo Scientific, USA). NIM-D dunite reference material (SARM-6, MINTEK) and procedural blanks were included for quality control. Recoveries for certified elements ranged from 72% to 93% and the maximum accepted relative standard deviation was 5%. Elemental composition of the olivine materials is reported in Table B1.



Table B1. Elemental composition of the three experimental olivine materials. Concentrations are expressed as $\mu\text{mol g}^{-1}$ dry weight and presented as mean $\pm$ SD.

Element	Microcosm olivine	Fine olivine	Coarse olivine
Mg	12,362 $\pm$ 276	9,043 $\pm$ 488	9,901 $\pm$ 469
Fe	898 $\pm$ 14	652 $\pm$ 16	721 $\pm$ 33
Al	29.7 $\pm$ 1.4	120 $\pm$ 3	65 $\pm$ 3
Mn	12.43 $\pm$ 0.28	11 $\pm$ 0.7	12 $\pm$ 0.3
Cr	58 $\pm$ 3	30 $\pm$ 2	23 $\pm$ 0.9
Ni	43 $\pm$ 0.8	36 $\pm$ 2	38 $\pm$ 0.9
Co	3.11 $\pm$ 0.07	3.3 $\pm$ 0.22	3.6 $\pm$ 0.08
Zn	0.967 $\pm$ 0.014	0.70 $\pm$ 0.045	0.69 $\pm$ 0.011

Note: Values are means $\pm$ SD ($n = 5$). Fine- and coarse-olivine values are direct measurements of the olivine materials in Flipkens et al. (2023a); Microcosm Mg, Fe, Al, Mn, Co and Zn were converted from rounded molar coefficients in Flipkens et al. (2023b) using 144.8 g mol^{-1} and are therefore approximate.

X-ray diffraction analysis for mineralogical composition

Mineralogical composition was determined by powder X-ray diffraction using a D8 ECO Advance diffractometer (Bruker, Germany) equipped with a Cu anode operated at 40 kV and 25 mA and an energy-dispersive position-sensitive LynxEye XE detector. The incident beam was collimated to a fixed length of 17 mm. Samples were first pulverised until all grains passed a 500 μm sieve. A 2 g subsample was then mixed with 5% zincite as an internal standard and micronised to a grain diameter of $\leq 10 \mu\text{m}$ by wet grinding with ethanol in a McCrone Micronizing Mill. The resulting slurry was dried to obtain a powder for analysis.

Mineral phases were identified using the DIFFRAC.EVA software. Diffractograms were interpreted semi-quantitatively by Rietveld refinement using BGMN with Profex version 5.0 as the user interface (Bergmann et al., 1998; Doebelin and Kleeberg, 2015). Mineralogical composition of the olivine materials is reported in Table B2.



Table B2. Semi-quantitative mineralogical composition of the three experimental olivine materials determined by X-ray diffraction. Given values represent approximate wt.%.

Mineral phase	Microcosm olivine	Fine olivine	Coarse olivine
Forsterite	~86	~69	~83
Enstatite	~7	~5	~8
Chlorite	~1	~9	~2
Antigorite	~2	~6	~2
Talc	<1†	~7	~1
Hornblende	~1†	~2	~2
Quartz	~1	~1	~1
Gibbsite	<1†	<<1†	<<1†
Magnetite	~1†	<<1†	<1†
Annite	—	<<1†	<<1†

Note: The dagger identifies phases that are tentative. <<1 denotes a trace contribution far below 1 wt.%, and — denotes a phase that was not reported. Values may not total exactly 100% because of rounding and the uncertain quantification of trace phases.

BET specific surface area analysis

Specific surface area was determined from argon adsorption measurements using the Brunauer–Emmett–Teller method with an Autosorb-1 gas-sorption analyser (Quantachrome, USA). Prior to analysis, a dried 7.5 g aliquot of the materials was outgassed for 16 h at 200 °C. The resulting BET specific-surface-area values are reported in Table 1 of the main manuscript.



Appendix C – Statistical tables

815 Table C1 summarises the fluxes from the microcosm experiment calculated with FLUXER. Tables C2-C5 summarise the
820 final linear mixed-effects models. Tables C6-C7 report model-derived sediment-water fluxes and treatment contrasts with
95% confidence intervals from 10,000 parametric bootstrap simulations. Table C8 documents bootstrap diagnostics.

Table C1. Replicate-specific initial sediment–water fluxes of total alkalinity (A_T) and dissolved nickel (DNi) in the
820 microcosm experiment. Fluxes were derived from the initial slopes of quadratic regressions fitted to measurements from
days 0, 1, 7, 14, 21 and 28 using FLUXER. CI 2.5 and CI 97.5 indicate the lower and upper limits of the 95% confidence
interval. The table also reports the regression F-statistic, p-value, small-sample corrected Akaike information criterion
(cAIC) and adjusted R^2 .

Treatment	Replicate	Parameter	Flux (mmol m ⁻² day ⁻¹)	CI 2.5	CI 97.5	StdErrFlux	Fvalue	pF	FitcAIC	Adj R ²
Olivine - no BT	1	A_T	1.891	0.816	2.966	0.338	39.248	0.007	102.923	0.939
Olivine - no BT	2	A_T	1.829	0.182	3.476	0.383	13.089	0.071	Inf.	0.858
Olivine - no BT	3	A_T	1.421	0.279	2.564	0.359	31.076	0.010	103.656	0.923
Olivine - no BT	4	A_T	1.913	0.866	2.959	0.329	28.916	0.011	102.604	0.918
Olivine - BT	1	A_T	8.125	2.264	13.986	1.842	14.733	0.028	123.277	0.846
Olivine - BT	2	A_T	8.569	6.742	10.396	0.574	135.565	0.001	109.288	0.982
Olivine - BT	3	A_T	7.048	1.833	12.263	1.639	11.606	0.039	121.876	0.809
Olivine - BT	4	A_T	11.710	5.663	17.756	1.900	41.121	0.007	123.651	0.941
Olivine - no BT	1	DNi	0.007	0.004	0.009	0.001	120.357	0.001	30.420	0.979
Olivine - no BT	2	DNi	0.007	0.004	0.011	0.001	68.167	0.003	33.636	0.964
Olivine - no BT	3	DNi	0.007	0.004	0.009	0.001	107.082	0.002	30.791	0.977
Olivine - no BT	4	DNi	0.006	0.004	0.008	0.001	134.315	0.001	28.215	0.982
Olivine - BT	1	DNi	0.011	-0.008	0.030	0.006	4.677	0.120	54.544	0.595
Olivine - BT	2	DNi	0.017	0.009	0.024	0.002	91.056	0.002	43.327	0.973
Olivine - BT	3	DNi	0.015	-0.001	0.031	0.005	15.058	0.027	52.517	0.849
Olivine - BT	4	DNi	0.018	-0.004	0.040	0.007	7.578	0.067	56.266	0.725



Table C2. Linear mixed-effects model for total alkalinity (A_T) fluxes across all 15 flux sessions. Formula: $A_T \sim \text{elapsed time} \times \text{olivine}/(\text{grain size} \times \text{loading}) + (\text{elapsed time} \mid \text{session}/\text{mesocosm})$. The model was fitted by restricted maximum likelihood (REML) to 979 observations from 210 mesocosm-within-session groups and 15 sessions.

Fixed effects					
Term	Estimate	SE	df	t	p
Intercept	1634.38	13.87	26.3	117.82	<0.001
Elapsed time	1.891	0.5526	38.0	3.42	0.0015
Olivine	70.80	10.13	194.2	6.99	<0.001
Elapsed time $\times$ olivine	3.292	0.6313	188.9	5.22	<0.001
Elapsed time $\times$ olivine $\times$ coarse grain size	-0.8023	0.6261	186.5	-1.28	0.202
Elapsed time $\times$ olivine $\times$ high loading	-0.4248	0.6261	186.5	-0.68	0.498
Random effects					
Group	Effect	Variance	SD	Correlation	
Mesocosm	within	Intercept	3903.22	62.48	
session					
Mesocosm	within	Elapsed time	8.328	2.886	0.334
session					
Session		Intercept	1785.82	42.26	
Session		Elapsed time	1.987	1.410	-0.169
Residual			807.10	28.41	

Note: A_T was modelled as mmol m^{-2} ; coefficients involving elapsed time are therefore in $\text{mmol m}^{-2} \text{ day}^{-1}$. The reference treatment was the control, with Fine-6% as the reference combination within olivine-amended treatments. Because grain size and loading were undefined for controls and no Coarse-6% treatment existed, 14 non-estimable columns were dropped from the fixed-effect model matrix. Analytical A_T replicates from each mesocosm and sampling occasion were averaged before calculating areal amounts. The fitted model was non-singular, but a maximum scaled-gradient convergence warning was reported (0.0101; tolerance 0.002).



Table C3. Linear mixed-effects model for A_T fluxes during trace-metal flux sessions 3 and 6.

835 Formula: $AT \sim \text{session} \times \text{treatment} \times \text{elapsed time} + (\text{elapsed time} \parallel \text{mesocosm within session})$. The model was fitted by REML to 139 observations from 28 mesocosm-within-session groups.

Fixed effects					
Term	Estimate	SE	df	t	p
Intercept	1650.83	26.28	20.1	62.82	<0.001
Session 6	-71.69	37.22	20.2	-1.93	0.068
Fine-6%	143.60	40.11	20.0	3.58	0.002
Fine-10%	109.80	37.14	20.0	2.96	0.008
Coarse-10%	102.14	40.11	20.0	2.55	0.019
Elapsed time	-1.158	1.856	20.0	-0.62	0.540
Session 6 × Fine-6%	-134.97	56.83	20.2	-2.38	0.028
Session 6 × Fine-10%	-35.67	52.62	20.2	-0.68	0.506
Session 6 × Coarse-10%	-56.68	56.83	20.2	-1.00	0.330
Session 6 × elapsed time	5.367	2.629	20.1	2.04	0.0545
Fine-6% × elapsed time	9.958	2.834	20.0	3.51	0.002
Fine-10% × elapsed time	10.088	2.624	20.0	3.84	0.001
Coarse-10% × elapsed time	5.453	2.834	20.0	1.92	0.069
Session 6 × Fine-6% × elapsed time	-9.529	4.015	20.1	-2.37	0.028
Session 6 × Fine-10% × elapsed time	-9.777	3.718	20.1	-2.63	0.016
Session 6 × Coarse-10% × elapsed time	-5.380	4.015	20.1	-1.34	0.195
Random effects					
Group	Effect	Variance	SD	Correlation	
Mesocosm session	within Intercept	2454.99	49.55	0 (specified)	
Mesocosm session	within Elapsed time	12.725	3.567		
Residual		528.98	23.00		

Note: A_T was modelled as mmol m^{-2} ; coefficients involving elapsed time are therefore in $\text{mmol m}^{-2} \text{day}^{-1}$. Session 3 and the control treatment were the reference levels. The double-bar random-effect notation specifies an uncorrelated random intercept and elapsed-time slope. The same replicate-averaged A_T observations were used. The model converged, was full rank, and was non-singular.

840



Table C4. Linear mixed-effects model for dissolved nickel (DNi) fluxes during flux sessions 3 and 6. Formula: $\text{DNi} \sim \text{session} \times \text{treatment} \times \text{elapsed time} + (1 \mid \text{mesocosm within session})$. The model was fitted by REML to 140 observations from 28 mesocosm-within-session groups.

Fixed effects						
Term	Estimate	SE	df	t	p	
Intercept	8.477	21.70	24.8	0.39	0.699	
Session 6	-0.4067	30.79	25.1	-0.01	0.990	
Fine-6%	91.39	33.15	24.8	2.76	0.011	
Fine-10%	133.50	30.70	24.8	4.35	<0.001	
Coarse-10%	15.39	33.15	24.8	0.46	0.647	
Elapsed time	0.0351	0.5107	104.0	0.07	0.945	
Session 6 × Fine-6%	85.25	47.04	25.1	1.81	0.082	
Session 6 × Fine-10%	38.02	43.55	25.1	0.87	0.391	
Session 6 × Coarse-10%	3.024	47.04	25.1	0.06	0.949	
Session 6 × elapsed time	0.0665	0.7386	104.0	0.09	0.928	
Fine-6% × elapsed time	3.248	0.7801	104.0	4.16	<0.001	
Fine-10% × elapsed time	4.276	0.7222	104.0	5.92	<0.001	
Coarse-10% × elapsed time	0.3631	0.7801	104.0	0.47	0.643	
Session 6 × Fine-6% × elapsed time	1.902	1.128	104.0	1.69	0.095	
Session 6 × Fine-10% × elapsed time	4.367	1.045	104.0	4.18	<0.001	
Session 6 × Coarse-10% × elapsed time	0.1861	1.128	104.0	0.17	0.869	
Random effects						
Group	Effect	Variance	SD	Correlation		
Mesocosm	within	Intercept	1586.00	39.83		
session						
Residual		527.05	22.96			

Note: Estimates and standard errors were converted from mmol to μmol ; coefficients involving elapsed time are therefore in $\mu\text{mol m}^{-2} \text{ day}^{-1}$. Session 3 and the control treatment were the reference levels. A likelihood-ratio comparison fitted by maximum likelihood supported retention of the session × treatment × elapsed-time interaction ($\chi^2 = 21.085$, $df = 3$, $p < 0.001$). The final REML model converged, was full rank, and was non-singular.



Table C5. Linear mixed-effects model for dissolved chromium (DCr) fluxes during flux sessions 3 and 6. Formula: $DCr \sim$ session $\times$ elapsed time + olivine + elapsed time $\times$ olivine + elapsed time $\times$ coarse grain size + elapsed time $\times$ high loading + (1 | mesocosm within session). The model was fitted by REML to 140 observations from 28 mesocosm-within-session groups.

Fixed effects					
Term	Estimate	SE	df	t	p
Intercept	-0.5722	2.311	33.8	-0.25	0.806
Session 6	6.798	2.181	34.0	3.12	0.004
Elapsed time	0.0616	0.0730	105.7	0.84	0.401
Olivine	7.668	2.406	33.5	3.19	0.003
Session 6 $\times$ elapsed time	-0.1851	0.0694	105.7	-2.67	0.009
Elapsed time $\times$ olivine	-0.1384	0.0951	119.0	-1.46	0.148
Elapsed time $\times$ coarse grain size	-0.00443	0.0899	132.0	-0.05	0.961
Elapsed time $\times$ high loading	0.0053	0.0898	132.0	0.06	0.953
Random effects					
Group	Effect	Variance	SD	Correlation	
Mesocosm	within session	24.02	4.901		
Residual		16.64	4.079		

Note: Estimates and standard errors were converted from mmol to μmol ; coefficients involving elapsed time are therefore in $\mu\text{mol m}^{-2} \text{ day}^{-1}$. Session 3 and the control treatment were the reference levels. The model allowed the background temporal slope to differ between sessions but constrained treatment-related slope differences to be equal across sessions. The model converged, was full rank, and was non-singular.



Table C6. Model-derived sediment-water flux estimates and parametric bootstrap confidence intervals. The fitted-model estimate, bootstrap median, and percentile 95% confidence interval are shown for each treatment. Confidence intervals were calculated from 10,000 parametric bootstrap simulations.

Analyte	Session	Treatment	Model estimate	Bootstrap median	95% CI	Unit
A _T	All	Control	1.89	1.88	0.79 to 2.95	mmol m ⁻² day ⁻¹
A _T	All	Fine-6%	5.18	5.19	4.02 to 6.35	mmol m ⁻² day ⁻¹
A _T	All	Fine-10%	4.76	4.74	3.69 to 5.84	mmol m ⁻² day ⁻¹
A _T	All	Coarse-10%	3.96	3.95	2.77 to 5.10	mmol m ⁻² day ⁻¹
A _T	3	Control	-1.16	-1.14	-4.76 to 2.41	mmol m ⁻² day ⁻¹
A _T	3	Fine-6%	8.80	8.81	4.63 to 13.00	mmol m ⁻² day ⁻¹
A _T	3	Fine-10%	8.93	8.90	5.29 to 12.60	mmol m ⁻² day ⁻¹
A _T	3	Coarse-10%	4.29	4.31	0.09 to 8.60	mmol m ⁻² day ⁻¹
A _T	6	Control	4.21	4.19	0.56 to 7.86	mmol m ⁻² day ⁻¹
A _T	6	Fine-6%	4.64	4.58	0.50 to 8.90	mmol m ⁻² day ⁻¹
A _T	6	Fine-10%	4.52	4.57	0.87 to 8.24	mmol m ⁻² day ⁻¹
A _T	6	Coarse-10%	4.28	4.29	0.17 to 8.51	mmol m ⁻² day ⁻¹
DNi	3	Control	0.04	0.03	-0.98 to 1.05	μmol m ⁻² day ⁻¹
DNi	3	Fine-6%	3.28	3.29	2.11 to 4.43	μmol m ⁻² day ⁻¹
DNi	3	Fine-10%	4.31	4.31	3.31 to 5.31	μmol m ⁻² day ⁻¹
DNi	3	Coarse-10%	0.40	0.39	-0.77 to 1.57	μmol m ⁻² day ⁻¹
DNi	6	Control	0.10	0.10	-0.92 to 1.15	μmol m ⁻² day ⁻¹
DNi	6	Fine-6%	5.25	5.25	4.07 to 6.45	μmol m ⁻² day ⁻¹
DNi	6	Fine-10%	8.74	8.74	7.71 to 9.79	μmol m ⁻² day ⁻¹
DNi	6	Coarse-10%	0.65	0.64	-0.57 to 1.87	μmol m ⁻² day ⁻¹
DCr	3	Control	0.061	0.061	-0.078 to 0.205	μmol m ⁻² day ⁻¹
DCr	3	Fine-6%	-0.077	-0.078	-0.225 to 0.075	μmol m ⁻² day ⁻¹
DCr	3	Fine-10%	-0.071	-0.071	-0.209 to 0.068	μmol m ⁻² day ⁻¹
DCr	3	Coarse-10%	-0.076	-0.077	-0.230 to 0.075	μmol m ⁻² day ⁻¹
DCr	6	Control	-0.124	-0.125	-0.265 to 0.019	μmol m ⁻² day ⁻¹
DCr	6	Fine-6%	-0.262	-0.262	-0.416 to -0.105	μmol m ⁻² day ⁻¹
DCr	6	Fine-10%	-0.257	-0.255	-0.399 to -0.115	μmol m ⁻² day ⁻¹
DCr	6	Coarse-10%	-0.261	-0.262	-0.419 to -0.104	μmol m ⁻² day ⁻¹

Note: Only session-specific estimates are shown for the two-session models. The model estimate, rather than the bootstrap median, was used as the point estimate in the main text and figures. Negative values indicate net removal from the overlying water.



Table C7. Treatment contrasts for sediment-water fluxes. Differences are fitted-model estimates. Percentile 95% confidence intervals were calculated by evaluating each contrast within every one of the 10,000 parametric bootstrap simulations. Model-based *p*-values were obtained using Satterthwaite degrees of freedom.

Analyte	Session	Contrast	Difference	Bootstrap median	95% CI	p	Unit
A _T	All	Mean olivine vs. Control	2.74	2.74	1.79 to 3.71	<0.001	mmol m ⁻² day ⁻¹
A _T	All	Fine-10% vs. Fine-6%	-0.42	-0.44	-1.64 to 0.80	0.498	mmol m ⁻² day ⁻¹
A _T	All	Fine-10% vs. Coarse-10%	0.80	0.81	-0.43 to 2.05	0.202	mmol m ⁻² day ⁻¹
DNi	3	Mean olivine vs. Control	2.63	2.63	1.44 to 3.85	<0.001	μmol m ⁻² day ⁻¹
DNi	3	Fine-10% vs. Fine-6%	1.03	1.02	-0.49 to 2.54	0.190	μmol m ⁻² day ⁻¹
DNi	3	Fine-10% vs. Coarse-10%	3.91	3.91	2.38 to 5.44	<0.001	μmol m ⁻² day ⁻¹
DNi	3	Coarse-10% vs. Control	0.36	0.35	-1.17 to 1.89	0.643	μmol m ⁻² day ⁻¹
DNi	6	Mean olivine vs. Control	4.78	4.77	3.54 to 5.99	<0.001	μmol m ⁻² day ⁻¹
DNi	6	Fine-10% vs. Fine-6%	3.49	3.49	1.91 to 5.10	<0.001	μmol m ⁻² day ⁻¹
DNi	6	Fine-10% vs. Coarse- 10%	8.09	8.11	6.50 to 9.68	<0.001	μmol m ⁻² day ⁻¹
DNi	6	Coarse-10% vs. Control	0.55	0.55	-1.05 to 2.12	0.502	μmol m ⁻² day ⁻¹
DCr	Both	Fine-6% vs. Control	-0.14	-0.14	-0.32 to 0.05	0.148	μmol m ⁻² day ⁻¹
DCr	Both	Fine-10% vs. Control	-0.13	-0.13	-0.31 to 0.05	0.138	μmol m ⁻² day ⁻¹
DCr	Both	Coarse-10% vs. Control	-0.14	-0.14	-0.32 to 0.05	0.151	μmol m ⁻² day ⁻¹

865 **Note:** The mean olivine contrast assigns equal weight to the Fine-6%, Fine-10%, and Coarse-10% treatments. Because the final DCr model constrained treatment-related slope differences to be equal across sessions, its contrasts apply jointly to sessions 3 and 6. No multiple-comparison adjustment was applied.



Table C8. Diagnostics for the parametric bootstrap analyses. All analyses used bootMer() with type = "parametric", use.u = FALSE, and 10,000 simulations.

Model	Seed	Simulations	Failed fits	Convergence warnings	Singular-fit messages
AT, 15 sessions	123	10,000	0	1,190	152
AT, sessions 3 and 6	124	10,000	0	2	0
DNi, sessions 3 and 6	125	10,000	0	1	0
DCr, sessions 3 and 6	126	10,000	0	0	0

Note: No bootstrap refit failed, so all 10,000 simulations contributed to each confidence interval. Warning and singular-fit counts are recorded fitting messages rather than necessarily distinct simulations; the categories may overlap.



Code and data availability

875 The code used for analysis in this study is available upon request. Interested parties may contact the corresponding author. The data supporting the findings of this study have been deposited in Zenodo (Van Heurck et al., 2026; DOI: 10.5281/zenodo.22957871).

Author contributions

880 BVH was responsible for investigation, formal analysis and writing – original draft, review and editing. FM contributed to conceptualisation, methodology, investigation and writing – review and editing. AH contributed to methodology, investigation and writing – review and editing. DVC contributed to supervision and writing – review and editing. SDW, CG, GL and DAF contributed to investigation. MK contributed to conceptualisation, investigation and writing, review and editing. FJRM was responsible for supervision, conceptualisation, funding acquisition and writing – review and editing.

Competing interests

885 The contact author has declared that none of the authors has any competing interests.

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